

Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence

James D. Bever

Department of Ecology and Evolution, University of California Irvine, 321 Steinhaus Hall, Irvine, CA 92697–2525, U.S.A.

Abstract

Numerical models have suggested that the dynamics within mutualisms are not important for the maintenance of diversity. In this study it is demonstrated that the dynamics within mutualism can contribute to the maintenance of diversity within its participants, using a general model of frequency dependence between two mutualistically interacting guilds. Specifically, it is demonstrated that while mutualisms may exhibit positive feedback in density, there may be a negative feedback within a mutualism as a result of the change in composition within the interacting guild. Such a negative feedback results from an asymmetry in the delivery of benefit between participants of the mutualism that generates a negative interguild frequency dependence. This dynamic contributes to the maintenance of diversity within the interacting guilds. Conditions are identified for the maintenance of diversity and the maximization of benefit from mutualism within the context of the model. The utility of these conditions for testing hypotheses using data from the mutualistic interaction between plants and mycorrhizal fungi is then demonstrated.

Keywords

Arbuscular mycorrhizal fungi, coevolution, community dynamics, diversity, feedback, frequency dependence, guild dynamics, mutualism.

Ecology Letters (1999) 2: 52–61

INTRODUCTION

Over the last 20 years, a succession of general ecological models have successfully described general features of the numerical dynamics of mutualisms (e.g. Vandermeer & Boucher 1978; Dean 1983; Addicott & Freedman 1984; Wolin & Lawlor 1984). While these analyses focused on factors contributing to the maintenance of the mutualistic interactants, they did not address the conditions in which dynamics among mutualists would contribute to the maintenance of diversity within any one guild (e.g. within plants in their interaction with root symbionts). Similarly, explicit models of coevolution of mutualists predict the dynamics in frequency to result in a loss of genetic diversity within single populations (Law 1985; Law & Koptur 1986), while generating divergence among populations (Kiestler *et al.* 1984). The absence of linkage between the dynamics of mutualism and the maintenance of diversity, or other broader issues within ecology and evolution, has been identified as a contributing factor to the lack of experimental work on this interaction relative to that on antagonistic interactions (May 1975; Boucher *et al.* 1982; Bronstein 1994).

The loss of diversity during coevolution of mutualistically interacting populations results from assumptions of positive interguild frequency dependence within coevolutionary models (Kiestler *et al.* 1984; Templeton & Gilbert 1985; Law & Koptur 1986). That is, if host A derives more benefit from association with the mutualistic symbiont X than from association with the mutualistic symbiont Y, then symbiont X is assumed also to derive more benefit than Y from association with host A. While symmetric fitness relations, which generate positive interguild frequency dependence, are certainly possible within a mutualism, the nature of the coevolutionary dynamics are not necessarily constrained by the nature of the ecological interaction (Levin & Udovic 1977). Counterintuitive coevolutionary dynamics have been found in models of competitive (e.g. Roughgarden 1976; Slatkin 1980) and exploitative (e.g. Abrams 1991; Frank 1996) interactions.

In this paper, the range of ecological and coevolutionary dynamics is illustrated using a simple model of interguild frequency dependence. Using this model, the conditions in which the dynamics within a mutualism promote the maintenance of diversity within populations

and communities is identified. The implications of these dynamics for the evolution of the strength of mutualism are also investigated. Finally, published data in the context of this model to gain inference into the dynamics of the plant-mycorrhizal fungal mutualism are analysed.

ASSUMPTIONS OF THE MODEL

This model was developed with specific reference to the common and ecologically critical mutualisms between plants and their root symbionts. Most plant species, for example, take up the essential nutrient phosphorus from the soil with the aid of a particular group of symbiotic fungi, called arbuscular or vesicular arbuscular mycorrhizal (VAM) fungi. These fungi, in turn, are obligately dependent upon the plants for their carbohydrates. While much progress has been made on the physiology of this association (Brundrett 1991), little is known about the population and community dynamics that result from this interaction. Plant species and genotypes, however, are known to respond differentially to fungal isolates (Nemec 1978; Wilson 1988; Dhillon 1992; Adjoud *et al.* 1996; Van der Heijden *et al.* 1998a) and fungal isolates are known to respond differentially to different plant species (Johnson *et al.* 1992; Sanders & Fitter 1992; Bever *et al.* 1996). In fact, the rank order of the plant and fungal growth rates can be reversed depending on the mutualists with which they are associated. This mutual interdependence of the relative performance of populations and communities is likely to be a common feature of intimate mutualistic interactions, and it suggests that an active dynamic of the composition of mutualistic populations and communities is possible. This model develops the simple consequences of this feature of mutualisms.

The model takes its simplest form with two interacting populations each composed of two asexual genotypes; however, the model would be unchanged by consideration of the ecological situation of two interacting guilds each composed of two species. This model is therefore used to draw inferences about both coevolutionary and ecological dynamics among mutualists. Within coevolutionary contexts, the model investigates interspecific frequency dependence, while within an ecological context the model investigates interguild frequency dependence. For convenience, the model is described in terms of asexually reproducing "types" and refers to the interacting species/guilds using the more general term of guilds.

The dynamics resulting from this mutual interdependence of relative fitnesses are analysed by first assuming that the interguild frequency dependence generated by this interdependence is not altered by density or intraguild frequency. The data are not available to evaluate these assumptions for mutualistic systems, though these

assumptions are common starting places in population genetic models. For two types of plants, A and B, and two types of the fungi, X and Y, the fitness (or growth rate) relations are assigned as described in Fig. 1. Plant fitness is initially assumed to be a linear function of fungal frequency, and fungal fitness is similarly assumed to be a linear function of plant frequency.

This plant-fungal relationship can be constrained to be any particular type of ecological interaction. For example, the interaction can be constrained to be mutualistic by setting the fitness of both plant types, A and B, to be higher in the presence of either fungal types X or Y than in the absence of both these types, and setting the rate of increase of both fungal types, X and Y, to be greater in the presence of either plant, A or B, than in their absence. Note that the constraint of mutualism does not affect the possible frequency-dependent fitness relations amongst the mutualists.

Dynamics resulting from these assumptions are most easily analysed using the assumption of continuous change over time. The rates of change of the numbers of plant types A and B are described as $dN_A/dt = W_A N_A$, and $dN_B/dt = W_B N_B$. This is a standard exponential growth model, where W_A , the average fitness of plant type A, $= ap_X + bp_Y$ and $W_B = cp_X + dp_Y$. The variables p_X and p_Y are the frequencies of fungal types X and Y among all fungal types (i.e. $p_X = N_X/(N_X + N_Y)$, etc.). The parameters a , b , c , and d represent the fitnesses of plant types A and B with fungal types X and Y as described in Fig. 1. The equation for instantaneous change in the frequency of plant type A, p_A , is

$$\frac{dp_A}{dt} = \frac{d\left(\frac{N_A}{N_A + N_B}\right)}{dt} = \left(\frac{1}{N_A + N_B}\right) \frac{dN_A}{dt} - \left(\frac{N_A}{(N_A + N_B)^2}\right) \left(\frac{dN_A}{dt} + \frac{dN_B}{dt}\right). \quad (1)$$

After substituting the equations for dN_A/dt and dN_B/dt , this expression reduces to

$$\begin{aligned} \frac{dp_A}{dt} &= p_A p_B (W_A - W_B) \\ &= p_A (1 - p_A) [(a - c)p_X + (b - d)p_Y]. \end{aligned} \quad (2)$$

Using a similar approach, the expression for the rate of change of the frequency of fungal type X is derived as

$$\begin{aligned} \frac{dp_X}{dt} &= p_X p_Y (W_X - W_Y) \\ &= p_X (1 - p_X) [(k - m)p_A + (l - n)p_B] \end{aligned} \quad (3)$$

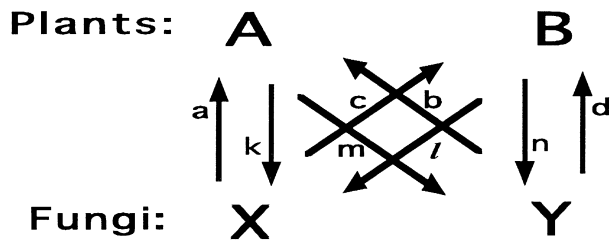


Figure 1 Depiction of the coevolutionary fitness sets. The arrows represent the direction of fitness effects and the letters adjacent to the arrows indicate the relative magnitudes of these fitness values. Plant fitness is assumed to be a linear function of the frequency of fungal types, with the pairwise fitness values being represented by the letters a–d. Similarly, letters k–n represent the fitness values of the fungi when associated with the plant types individually.

where k , l , m , and n represent the fitnesses of fungal types X and Y when in association with plants A and B as depicted in Fig. 1.

The dynamics described by these equations will be coevolutionary so long as the relative fitness of the plant types (W_A/W_B) depends upon fungal frequency, and the relative fitness of the fungal types (W_X/W_Y) depends upon plant frequency. The relative fitness of the plant types depends upon fungal frequency in all situations except when $a = b$ and $c = d$ or when $a = c$ and $b = d$. Similarly, the relative fitness of fungus X depends upon plant frequency in all situations except when $k = l$ and $n = m$, or when $k = m$ and $l = n$.

ANALYSIS OF DYNAMICS

The universe of coevolutionary dynamics possible under this model are presented in the phase plane diagrams in Fig. 2, and the four categories of dynamics are summarized in Fig. 3. Both interactants may proceed directly to fixation (Situation I, Fig. 3a). This occurs when the fitness of one plant type is always higher than that of the second and the fitness of one fungal type is always higher than that of the second. Alternatively, the frequency within one species, the plant for example, may proceed directly to fixation while the direction of change in the fungus depends upon the frequency of plant types (Situation II, Fig. 3b). This occurs when the fitness of one plant type is always higher than that of the second, while the rank of fitnesses of the fungi depends upon the frequency of the plant types. A single stable corner equilibrium exists for both Situation I and Situation II (Appendix).

If neither a single plant type nor a single fungal type has higher fitness in all associations, an internal equilibrium will exist. The stability of this internal equilibrium depends upon the sign of the product of the plant and

fungal “interaction coefficients” (I_P and I_F , respectively), where

$$I_P = a - b - c + d$$

$$I_F = k - l - m + n \quad (4)$$

These interaction coefficients correspond to the statistical test of a plant type–fungal type interaction on plant fitness and fungal fitness, respectively (see Bever *et al.* 1997 for an explicit development of an analogous test). When the product of these interaction coefficients is positive, the equilibrium is unstable (Fig. 2 and Appendix). Under this condition, the frequencies of plant types and fungal types will proceed to fixation at one of two stable corner equilibria, with the particular equilibrium depending upon the initial plant and fungal frequencies. This situation results when the fungal type, say fungus X, that most benefits plant A is also the fungal type that receives the most benefit from plant A (Situation III, Fig. 3c). As a result of this symmetry in fitness relations, an increase in the frequency of plant A causes an increase in the frequency of fungus X, which then further increases the frequency of plant A. In this positive feedback or positive interguild frequency-dependent dynamic, intermediate frequencies are unstable. Genetic variation within a population for specific responses among the interactants will be lost as a result of the interaction. This result is similar to that obtained for symmetric fitness sets within a mutualism by Law & Koptur (1986). While positive interguild frequency dependence is not expected to maintain variation within populations, it is likely to maintain variation between populations and, in fact, may drive population differentiation (Keister *et al.* 1984). Depending on initial frequencies, different stable states (e.g. all A and X or all B and Y) may be reached and maintained in different populations.

The dynamic is very different around an internal equilibrium when the product of the interaction coefficients is negative (Situation IV, Fig. 3d). In this situation, the internal equilibrium is neutrally stable. Perturbations will result in oscillations of constant amplitude around the equilibrium (Appendix). Variation is therefore maintained, though vulnerable to stochastic processes. This dynamic results from asymmetric fitness relations between plants and fungi, in which the fungal type that receives the most benefit from plant A provides the greatest benefit to plant B. The resulting negative feedback or negative interguild frequency-dependent dynamic maintains variation within the mutualistically interacting guilds. Note that a negative sign of the product of the interaction coefficients provides a necessary, though not wholly sufficient, condition for the maintenance of diversity within a mutualism.

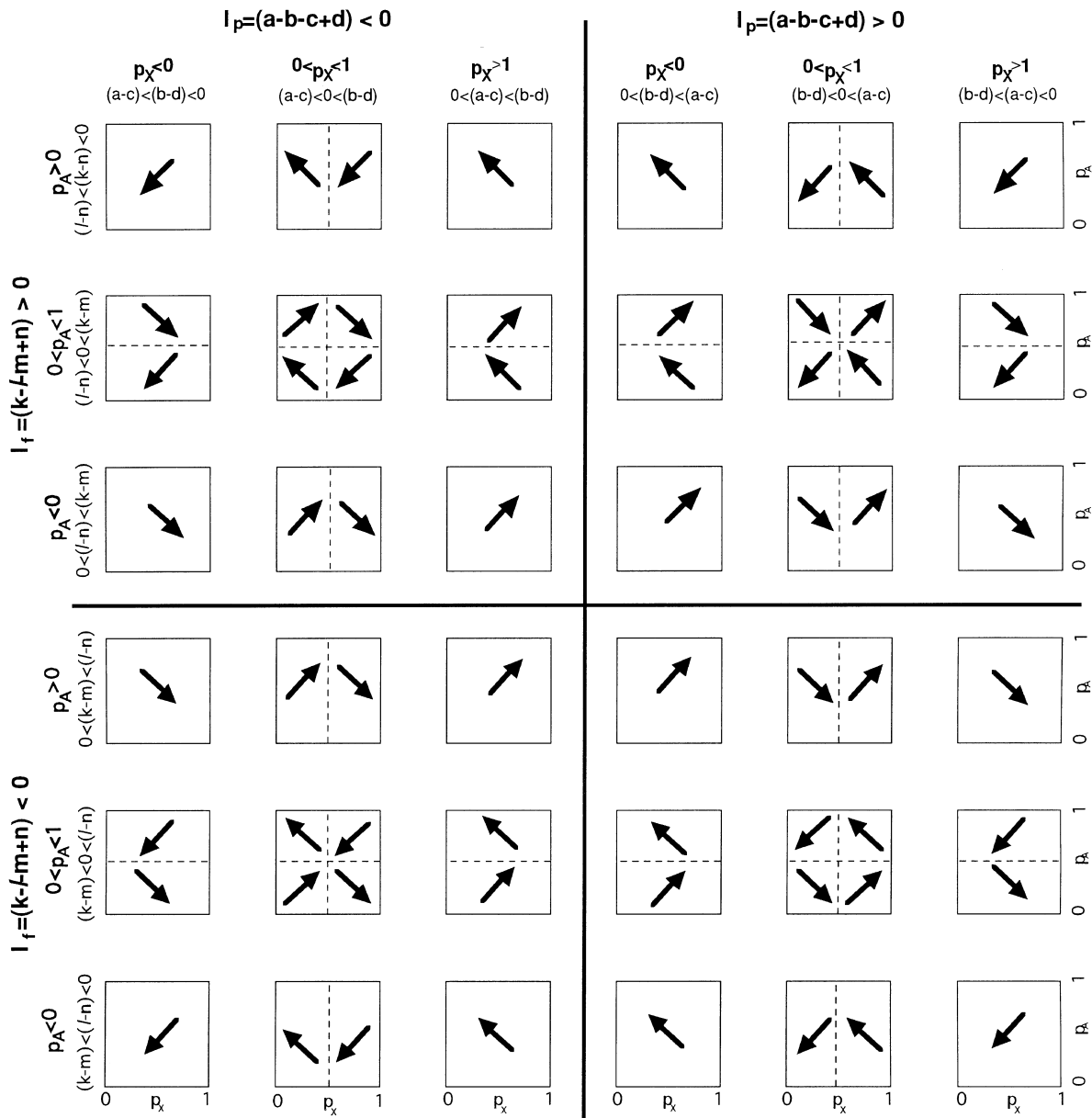
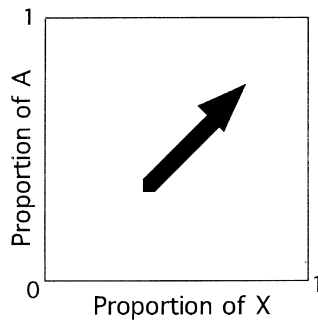


Figure 2 Phase plane representations of the possible dynamics of interguild frequency-dependent coevolution. In each of the 36 squares, the vertical axis is the frequency of the plant type A and the horizontal axis is the frequency of fungal type X. The arrows represent the direction of change and the vertical and horizontal dotted lines represent the $dp_A/dt = 0$ and the $dp_X/dt = 0$ isoclines, respectively [$p_X = (d-b)/I_F$; $p_A = (n-l)/I_F$]. Each of these 36 squares are phase plane representations of the dynamics resulting from the conditions described in the margins. They are arranged such that the plant fitness sets stay the same as we move up or down the columns but change as we move along the rows. Conversely, the fungal fitness sets stay the same as we move along the rows but change as we move up and down the columns.

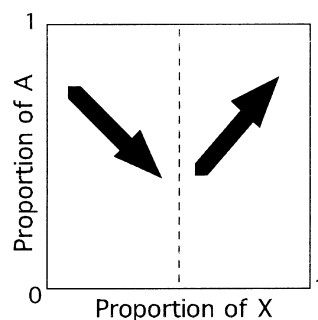
The negative feedback dynamics observed in Situation IV are similar to those observed in coevolutionary models of host-pathogen or predator prey systems (e.g. Mode 1958; Stewart 1971; Barrett 1988; Seger 1992). From these systems, it is known that the neutral stability of the internal equilibrium depends upon simplifying assumptions

made in this model. In models of discrete time, for example, the equilibrium is unstable, though it can be stabilized by many factors, including diploidy (Stewart 1971), mutation, recombination, or intraguild frequency dependence (Seger 1988, 1992). Regardless of the particulars, variation will be much more likely to be

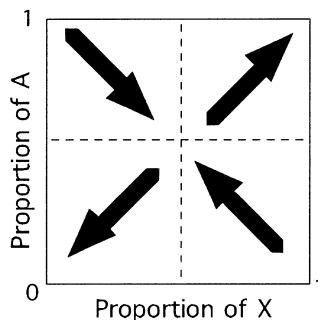
(a)
Situation I: $a > c, b > d; k > m, l > n.$



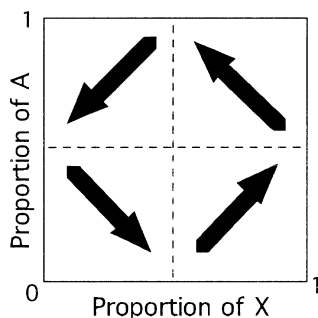
(b)
Situation II: $a > c, d > b; k > m, l > n.$



(c)
Situation III: $a > c, d > b; k > m, n > l.$



(d)
Situation IV: $a > c, d > b; m > k, l > n.$



maintained as a result of negative feedback than positive feedback, and therefore the essential contrast between the two dynamic behaviours is robust to these assumptions.

MAGNITUDE OF MUTUALISM

Coevolution of mutualists can result in an increase in the strength or magnitude of mutualism. In fact, one possible result of coevolution is the maximization of mutualism between the two guilds. Such a process, for example, was imagined by Darwin when he used the coadaptation of plants and pollinators to illustrate the process of adaptation (Darwin 1859, p. 95). While negative frequency dependence has been demonstrated to prevent the maximization of population fitness (e.g. Li 1955), the potential for negative frequency dependence within a mutualism had not been widely appreciated. The current model is therefore used to investigate the evolution of magnitude of mutualism between the two guilds. Specifically, the question of how likely the coevolutionary process will result in the maximization of benefit which the plants, for example, receive from the fungi is asked.

Figure 3 Examples of the four possible dynamical situations resulting from interguild frequency dependence. (a) An example of Situation I in which plant and fungal frequencies each increase directly to 1. This corner equilibrium is stable. In this example, plant fitness sets are constrained such that $a > c$ and $b > d$ and fungal fitness sets are constrained such that $k > m$ and $l > n$. That is, plant A has higher fitness than plant B with both fungi X and Y. Similarly, fungus X has higher fitness than fungus Y with both plants A and B. (b) An example of Situation II in which the fungal frequency increases directly to 100% X, but the plant frequency may increase or decrease depending upon the fungal frequency. Again, the corner equilibrium (1, 1) is stable. In this example, plant fitness sets are constrained such that $a > c$ and $d > b$ and fungal fitness is constrained such that $k > m$ and $l > n$. That is, plant A has greater fitness than plant B with fungus X but less with fungus Y. As in (a), fungus X has higher fitness than fungus Y with both plants A and B. (c) An example of Situation III, positive frequency dependence, where either 100% A and 100% X or 100% B and 100% Y are stable equilibrium. As in the example in situation II, $a > c$, $d > b$, and $k > m$, but in this situation $n > l$. That is, plant A has greater fitness than plant B with fungus X and fungus X has greater fitness than fungus Y with plant A. Similarly, plant B has greater fitness than plant A with fungus Y and fungus Y has greater fitness than fungus X with plant B. (d) An example of Situation IV, negative frequency dependence, in which the plant and fungal frequencies cycle in a counter clockwise direction. In this example, again the plant fitness is constrained such that $a > c$ and $d > b$. But in this situation, $m > k$ and $l > n$. That is, plant A has greater fitness than plant B with fungus X, but fungus X has greater fitness than fungus Y with plant B. Similarly, plant B has greater fitness than plant A with fungus Y, but fungus Y has greater fitness than fungus X with plant A.

The magnitude of mutualism is defined as the weighted benefit to each population from the association, i.e. the difference between the average fitness of the population with mutualists and the average fitness of the population without mutualists. Assuming that the fitnesses of the two plant types are equal in the absence of the fungus (n_P), the magnitude of fitness benefit from the mutualism for plants can then be written:

$$M_P = [p_A(ap_X + bp_Y) + p_B(cp_X + dp_Y)] - n_P$$

$$= ap_X p_A + bp_Y p_A + cp_X p_B + dp_Y p_B - n_P. \quad (5)$$

The probabilities that this value will be maximized by coevolution given the null assumption that the fitness parameters are arranged by chance are then determined. In Situation I, as illustrated in Fig. 3(a), for example, M_P will be maximized when $a > b, c, d$. Given the constraint on plant fitness in this example ($a > c$ and $b > d$), the magnitude of benefit to the plant population may be, but is not necessarily, maximized at equilibrium. In fact, there are six permutations of the rank order of plant fitnesses that satisfy these constraints ($a > b > c > d, a > b > d > c, a > c > b > d, b > a > c > d, b > a > d > c$, and $b > d > a > c$), each equally likely under our null assumptions. Therefore, at fixation, M_P will be maximized with a probability of 1/2, will reach an intermediate level with a probability of 1/3, and will reach a lowest level with a probability of 1/6. A similar analysis can be used to demonstrate a symmetric result for the magnitude of benefit to the fungal population, M_F . Under the null assumption of random and unconstrained arrangement of fitness sets, the probability of maximizing benefit to the plant population is independent of the probability of maximizing benefit to the fungal population, and can therefore be calculated as the product of the individual probabilities as presented in Table 1. Identical probabilities can also be derived for Situations II and III (Fig. 3b, c).

In Situation IV (Fig. 3d), negative interguild frequency dependence maintains intermediate plant and fungal frequencies. M_P and M_F will not be maximized or minimized, but will be remain at intermediate values. In

fact, because M_P will increase with higher frequencies of the A–X association or the B–Y association, and each of these associations will reach a relatively high frequency during each cycle (Fig. 3d), M_P (and similarly M_F) will oscillate with twice the periodicity of the oscillations in plant and fungal frequencies. Thus, our expectations for whether coevolution will maximize global fitness depends upon the coevolutionary dynamic. In Situations I, II, and III there is a 25% chance that benefit delivered to both mutualist populations will be maximized. In Situation IV, however, coevolution will not maximize benefit.

TESTING HYPOTHESES ON THE INTERACTION OF PLANTS AND VESICULAR ARBUSCULAR MYCORRHIZAL FUNGI

This general model of interguild frequency dependence poses two hypotheses. Specifically, (i) do the dynamics within mutualism contribute to the maintenance of diversity within individual guilds, and (ii) do the dynamics among mutualists result in the maximization of benefit to its participants (i.e. in coadaptation)? Here these hypotheses are tested by analysing published data on the interaction of plants and arbuscular mycorrhizal fungi.

The largest data set that allows estimation of the relative growth rates, and by implication the fitness of both plants and fungi, is that of Hetrick & Bloom (1986). They grew five domesticated plant species in association with three VAM fungal species in pots within a greenhouse and measured both plant biomass and number of VAM fungal spores. While analysis at this community level is an appropriate use of the model, the dynamics may not be representative of that in nature because the plants and fungi were not derived from a naturally co-occurring community. Furthermore, while plant mass frequently correlates with plant fitness, fungal spore production is not an ideal estimate of fungal fitness because much of new root infection is likely through hyphal extension (Brundrett 1991). Nevertheless, these data allow an initial analysis of the dynamics of this mutualism and, moreover, illustrate one methodology for empirically evaluating the dynamics of mutualism in general.

Table 1 Probabilities of maximizing benefit from mutualism as a result of coevolutionary fixation

Benefit to fungus from plant:	Benefit to plant from fungus		
	Maximized	Second from maximum	Third from maximum
Maximized	0.25	0.167	0.083
Second from maximum	0.167	0.111	0.055
Third from maximum	0.083	0.055	0.028

Interguild frequency-dependent coevolution in Situations I, II, and III will result in the fixation of plant and fungal types. This table presents the null probabilities (assuming the fitness sets are arranged by chance) that the benefit the plant and fungal population derives from their association is maximized as a result of coevolution in these situations.

Of the 30 comparisons of pairs of plants and pairs of fungi in Hetrick & Bloom (1986), 18 were Situation I and 12 were Situation II. Plants and fungi were significantly more likely to simultaneously maximize their fitness than our null expectations (Table 2, $G = 18.2$, 3 d.f., $P < 0.01$ using G test). Therefore, for these plant-VAM fungal combinations, the expectation of coadaptation of mutualists was apparently supported.

The above analysis accepts spore number as a direct estimate of VAM fungal fitness. Because VAM fungal species differ dramatically in spore size, as well as in reproductive allocation and phenology (Schenck & Perez 1990), comparisons of spore number across species may not be informative about their relative growth rates. These data are reanalysed assuming that all fungal species have equivalent fitness when averaged over the host plants. This has the effect of constraining the dynamics to be either positive or negative interguild frequency dependence (Situation III or Situation IV). This frequency dependence was tested with use of the interaction coefficients for plants and fungi (eqn 4). Specifically, a positive or negative product of the interaction coefficients indicates positive or negative interguild frequency dependence, respectively (Appendix). Furthermore, the magnitude of this product gives an estimate of the strength of the interguild interaction. Therefore, a predominance of positive or negative feedback can be tested using a Wilcoxon's signed-rank test (Sokal & Rohlf 1981) on the products of the interaction coefficients. A test using all 30 sets of plant and fungal pairs suggests that positive feedback is predominant ($T_s = 140$, $n = 30$, $P < 0.06$). Hence, these data appear to support the common assumption of positive interguild frequency-dependent dynamics within mutualisms, as well as the expectation of coadaptation. While extrapolation from these results to naturally co-occurring systems must be qualified, this

Table 2 Expected and observed numbers of cases where the mean population fitness will be maximized as a result of coevolution of plants and VAM fungi

Mean fungal fitness:	Mean plant fitness	
	Maximized	Not maximized
Maximized	18 (7.5)	6 (7.5)
Not maximized	4 (7.5)	2 (7.5)

The observed values are derived from the data of Hetrick & Bloom (1986). The expected values (derived from Table 1) are presented in parentheses. Since the expected number of cases where the plant or fungal types are third from maximal fitness at fixation is too low for a valid test, the categories where fitness is not maximized have been pooled. These data suggest that plants and fungi are significantly more likely to simultaneously maximize their fitness than expected by chance ($P < 0.01$ using G test).

analysis nevertheless points to ways in which expectations about the interguild frequency dynamics within a mutualism can be empirically tested.

DISCUSSION

Most models of coevolution are developed in reference to specific ecological interactions. The few general models have focused on density-dependent coevolution (e.g. Levins 1975; Leon & Charlesworth 1978). The expectations of density-dependent coevolution, however, may not hold if coevolution is also frequency dependent (Roughgarden 1976; Levin & Udovic 1977). The general model of interspecific frequency-dependent coevolution presented here allows the identification of similarities of coevolutionary dynamics in a diversity of ecological interactions. For example, both the coevolution of avirulence and the coevolution of greater mutualism are likely to occur in systems characterized by positive interspecific frequency-dependent coevolution. The similarity of these processes has previously been noted in the context of other models (e.g. Roughgarden 1975; Wilson 1983). Perhaps the greatest value of this general model of coevolution is as an heuristic aid in understanding dynamics in poorly explored interactions, such as that between mutualists. In this paper, this generic framework was used to illustrate that the commonly held expectation of loss of diversity among mutualists is not justified on theoretical grounds. Rather the dynamics within a mutualism can directly contribute to the maintenance of diversity within a population or community. This possibility has not been widely appreciated. For example, a recent review of the mechanisms through which mycorrhizal fungi can influence plant species coexistence, neglects to mention the possible importance of the compositional change within the mycorrhizal fungal community (Zobel & Moora 1997). Interestingly, mycorrhizal fungal diversity has recently been found to contribute to an increase in plant species diversity (van der Heijden *et al.* 1998).

The assumption of positive interspecific frequency dependence of mutualists is likely reasonable for some biological situations, but is unlikely to be a necessary consequence of the coevolution of mutualists. For example, Templeton & Gilbert (1985) modelled the coevolution of *Heliconius* butterflies as a positive feedback process resulting from Mullerian mimicry. Predators learn not to eat the colourful, but distasteful *Heliconius*. Different species of *Heliconius* butterflies have, consequently, evolved similar wing colour patterns that facilitate the learning of the predator (see review in Sheppard *et al.* 1985). Hence for this system, the assumption of positive interspecific frequency dependence

captures an important component of the dynamics. Yet even in this system, the high cost of chemical defenses coupled with unequal investment in defense between the species could result in negative interspecific frequency-dependent dynamics. These dynamics within mutualistic Mullerian mimetic populations would be similar to that of a nonmutualistic Batesian mimicry, and this could potentially lead to the dissolution of the mutualism, as explicitly modelled by Hadler *et al.* (1982).

Similarly, either dynamic may be consistent with the biology of nutritional mutualisms such as the plant–mycorrhizal fungus association. Fungal inoculum production may be expected to increase with the mass of plant roots and hence the fitness of the plant, suggesting a positive feedback dynamic. Alternatively, the fungus that gives the least phosphorus in return for a unit of carbohydrate may have the greatest fungal fitness. For nutritional mutualisms such as mycorrhizae, the nature of the feedback relations is not immediately apparent and needs to be investigated empirically. The analysis of published data on this mutualism presented here suggests that, while not conforming exclusively to a single dynamic, the expectations of co-adaptation and positive frequency dependence are preliminarily supported; however, other work illustrates that negative feedback can also result (J.D. Bever, unpublished data).

The assumption of positive interspecific frequency dependence in the coevolution of mutualists has served as a causal basis for an association of mutualism with low speciation rates and asexual reproduction (Law & Lewis 1983) and the low specificity of association (Law 1985; Law & Koptur 1986). The present model contributes to this discussion by removing the *a priori* basis for such associations. One might argue in converse, that the existence of these associations serves as support for the generality of positive interspecific frequency dependence within mutualism. However, the generality of these patterns themselves has been questioned (e.g. Borowicz & Juliano 1991; Bever 1992), with the current data base being limited by the poorly understood diversity and biology of many mutualistic participants (e.g. mycorrhizal fungi: Morton 1990; Bever *et al.* 1996). Evaluation of the correlation of mutualistic habit and evolutionary patterns necessarily awaits a better understanding of the biology of mutualistic symbionts. Interestingly, recent molecular data have demonstrated that the rate of evolutionary divergence is accelerated in lichenizing fungi compared with related nonmutualists (Lutzoni & Pagel 1997).

This model of interguild frequency dependence is very simplistic, being built upon assumptions of the absence of density dependence, linear interguild frequency dependence, and continuous change over time. Any alteration of these assumptions could result in different dynamics,

some of which were discussed within. Nevertheless, this model does illustrate potentially important consequences of one aspect of mutualism, and of the interaction between plants and mycorrhizal fungi in particular, i.e. the specificity of mutualistic responses. As other aspects of mutualisms, such as the spatial structure and environmental dependence of the plant–mycorrhizal fungal interaction, may also be critical to the dynamics of the interaction, as well as the evolution of mutualism itself (Wilson 1983; Bronstein 1994), they suggest fruitful avenues for further conceptual work on mutualism.

Bronstein (1994) recently identified the need for general hypotheses to motivate and unify the study of mutualism. This work directly contributes to this goal by identifying two general and testable hypotheses. First, by identifying negative feedback as a possible result of the dynamics amongst mutualists, this work opens the question of whether the dynamics within mutualisms can directly contribute to the maintenance of diversity in its interactants. Secondly, this work identifies that the coadaptation of mutualists may not be the end product of coevolutionary dynamics, even in the presence of positive interguild frequency dependence. The empirical question remains of how likely the dynamics of mutually interacting populations result in the best possible matching of mutualists. Finally, one manner in which these hypotheses can be tested is presented.

ACKNOWLEDGEMENTS

I gratefully acknowledge the encouragement and advice of J. Antonovics, R. Holt, M. Rausher, W. Morris, J. Morton, S. Bentivenga, S. Frank, J. Vandermeer, and three anonymous reviewers. M. Rausher, D. Hall, L. Altenberg, and M. Rose provided advice on the mathematics. I am grateful for the support of USDA grants 92-37101-7461 and 94-37101-0354 and NSF grant DEB-9615941 during this study.

APPENDIX: ANALYSES OF DYNAMICS DUE TO INTERSPECIFIC FREQUENCY-DEPENDENT COEVOLUTION

As derived in the text, the expressions for instantaneous change of the frequency of plant type A among all plant types (A and B), p_A , and of the frequency of fungal type X among all fungal types (X and Y), p_X , are written as follows:

$$\begin{aligned} F_1 &= dp_A/dt = p_A p_B^*[(a-c)p_X + (b-d)p_Y] \\ F_2 &= dp_X/dt = p_X p_Y^*[(k-m)p_A + (l-n)p_B]. \end{aligned} \quad (A1)$$

Corner equilibria X, Y	Criteria		
	Stable node	Saddle point	Unstable node
1, 1	$a > c, k > m$	$c > a, k > m$ or $a > c, m > k$	$c > a, m > k$
1, 0	$c > a, l > m$	$a > c, l > n$ or $c > a, n > l$	$a > c, n > l$
0, 1	$b > d, m > k$	$b > d, k > m$ or $d > b, m > k$	$d > b, k > m$
0, 0	$d > b, n > l$	$d > b, l > n$ or $b > d, n > l$	$b > d, l > n$

Table A1 Conditions for local stability of the corner equilibria

There are potentially five equilibria, including the four corner equilibria and one possible internal equilibrium given by

$$p_X = (d - b)/I_P$$

and

$$p_A = (n - l)/I_F, \quad (\text{A2})$$

where $I_P = (a - b - c + d)$ and $I_F = (k - l - m + n)$. I_P and I_F can be thought of as interaction coefficients of the plant and fungal fitnesses, respectively.

The stability of the corner and internal equilibria can be assessed by evaluating the Jacobian matrix of partial derivatives, \mathbf{J} , at the equilibria (Edelstein-Keshet 1988). The Jacobian matrix,

$$\mathbf{J}(p_A, p_X) = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \quad (\text{A3})$$

where

$$a_{11} = \partial F_1 / \partial p_A = [(a - c)p_X + (b - d)p_Y](1 - 2p_A),$$

$$a_{12} = \partial F_1 / \partial p_X = p_A p_B I_P,$$

$$a_{21} = \partial F_2 / \partial p_A = p_X p_Y I_F,$$

and

$$a_{22} = \partial F_2 / \partial p_X = [(k - m)p_A + (l - n)p_B](1 - 2p_X).$$

Evaluating the Jacobian matrix at the corner equilibria (1, 1), $a_{11} = c - a$, $a_{12} = 0$, $a_{21} = 0$, and $a_{22} = m - k$. The equilibrium is stable when the eigenvalues of this matrix are real and negative. This is true when $a > c$ and $k > m$. The corner will be a saddle point when $a < c$ and $k > m$ or $a > c$ and $k < m$. Finally, the corner will be an unstable node if $a < c$ and $k < m$. This same analysis can be repeated for the other three corners to give the stability conditions summarized in Table 1. At the internal equilibrium (p_X, p_A), a_{11} and a_{22} are equal to zero and $a_{12} = p_A p_B I_P$ and $a_{21} = p_X p_Y I_F$. The stability of the internal equilibrium depends upon the sign of the interaction coefficients, I_P and I_F . When the product of the interaction coefficients is positive ($I_P I_F > 0$), the internal equilibrium is a saddle point and the dynamics are that of positive feedback (Situation III). When the product of the interaction coefficients is negative ($I_P I_F < 0$), the internal equilibrium is a neutral centre and the dynamics are that of

negative feedback (Situation IV). Overall, the local stability analysis confirms the graphical analysis (Fig. 2).

Whether the internal equilibrium Situation IV is truly neutrally stable depends upon analyses of higher order terms of the Taylor approximation around this equilibrium. Analysis of these terms can be difficult. However, for this model, neutral stability can be confirmed (as has been done for simple predator-prey models, e.g. Renshaw 1991), by combining eqn A1 into a single equation by division. This can be rearranged to give the following

$$\begin{aligned} & \frac{[(k - m)p_A + (1 - n)p_B]dp_A}{p_A p_B} \\ &= \frac{[(a - c)p_X + (b - d)p_Y]dp_X}{p_X p_Y} \end{aligned} \quad (\text{A4})$$

Integrating both sides and rearranging gives

$$\begin{aligned} (l - n)\text{Ln}[p_A] + (m - k)\text{Ln}[p_B] + (d - b)\text{Ln}[p_X] \\ + (a - c)\text{Ln}[p_Y] = C, \end{aligned} \quad (\text{A5})$$

where C is a constant. This equation traces the change of frequency of plant and fungal frequencies within phase plane diagrams (as depicted in Figs 2 and 3). Under the conditions for Situation IV as identified in Fig. 2, this equation gives a family of closed ellipses, confirming the neutral stability of the cycles.

REFERENCES

- Abrams, P.A. (1991). The effects of interacting species on predator-prey coevolution. *Theoret. Population Biol.*, 39, 241–262.
- Addicott, J.F. & Freedman, H.I. (1984). On the structure and stability of mutualistic systems: analysis of predator-prey and competition models as modified by the action of a slow-growing mutualist. *Theoret. Population Biol.*, 26, 320–339.
- Adjoud, D., Plenchette, C., Halli-Hargas, R. & Lapeyrie, F. (1996). Response of 11 eucalyptus species to inoculation with three arbuscular mycorrhizal fungi. *Mycorrhiza*, 6, 129–135.
- Barrett, J.A. (1988). Frequency-dependent selection on plant-fungal interactions. *Phil. Trans. R. Soc. London, B*, 319, 473–483.
- Bever, J.D. (1992). *Ecological and evolutionary dynamics between plants and their soil communities*. PhD Thesis, Duke University.
- Bever, J.D., Morton, J.B., Antonovics, J. & Schultz, P.A. (1996). Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. *J. Ecol.*, 84, 71–82.

- Bever, J.D., Westover, K. & Antonovics, J. (1997). Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *J. Ecol.*, 85, 561–573.
- Borowicz, V.A. & Juliano, S.A. (1991). Specificity in host–fungus associations: do mutualists differ from antagonists? *Evol. Ecol.*, 5, 385–392.
- Boucher, D.H., James, S. & Keeler, K.H. (1982). The ecology of mutualisms. *Annu. Rev. Ecol. Syst.*, 13, 315–347.
- Bronstein, J.L. (1994). Our current understanding of mutualism. *Q. Rev. Biol.*, 69, 31–51.
- Brundrett, M. (1991). Mycorrhizas in natural ecosystems. *Adv. Ecol. Res.*, 21, 171–313.
- Darwin, C. (1859). *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
- Dean, A. (1983). A simple model of mutualism. *Am. Naturalist*, 121, 409–417.
- Dhillon, S.S. (1992). Host-endophyte specificity of vesicular-arbuscular mycorrhizal colorization of *Oryza sativa* L. at the pre-transplant stage in low and high phosphorus. *Soil Biol. Biochem.*, 24, 405–411.
- Edelstein-Keshet, L. (1988). *Mathematical Models in Biology*. New York: Random House.
- Frank, S.A. (1996). Models of parasite virulence. *Q. Rev. Biol.*, 71, 37–78.
- Hadler, K.P., de Mottoni, P. & Tessei, A. (1982). Mimetic gain in Batesian and Mullerian mimicry. *Oecologia*, 53, 84–92.
- Hetrick, B.A.D. & Bloom, J. (1986). The influence of host plant on production and colonization ability of vesicular-arbuscular mycorrhizal spores. *Mycologia*, 78, 32–36.
- Johnson, N.C., Tilman, D. & Wedin, D. (1992). Plant and soil controls on mycorrhizal fungal communities. *Ecol.*, 73, 2034–2042.
- Kiester, A.R., Lande, R. & Schemske, D.W. (1984). Models of coevolution and speciation in plants and their pollinators. *Am. Naturalist*, 124, 220–243.
- Law, R. (1985). Evolution in a mutualistic environment. In *The Biology of Mutualism*, ed. Boucher, D.H. London: Croom Helm, pp. 145–170.
- Law, R. & Koptur, S. (1986). On the evolution of non-specific mutualism. *Biol. J. Linnean Soc.*, 27, 251–267.
- Law, R. & Lewis, D.H. (1983). Biotic environments and the maintenance of sex – some evidence from mutualistic symbioses. *Biol. J. Linnean Soc.*, 20, 249–276.
- Leon, J.A. & Charlesworth, B. (1978). Ecological versions of Fisher's fundamental theorem of natural selection. *Ecol.*, 59, 457–464.
- Levin, S.A. & Udovic, J.D. (1977). A mathematical model of coevolving populations. *Am. Naturalist*, 111, 657–675.
- Levins, R. (1975). Evolution in communities near equilibrium. In *Ecology and Evolution of Communities*, ed. Cody, M.L. & Diamond, J.M. Cambridge, MA: Belknap Press, pp. 16–50.
- Li, C.C. (1955). The stability of an equilibrium and the average fitness of a population. *Am. Naturalist*, 89, 281–295.
- Lutzoni, F. & Pagel, M. (1997). Accelerated evolution as a consequence of transitions to mutualism. *Proc. Natl. Acad. Sci.*, 94, 11422–11427.
- May, R.M. (1975). Models of two interacting populations. In *Theoretical Ecology*, ed. May, R.M. Philadelphia: W.B. Saunders, pp. 49–70.
- Mode, C.J. (1958). A mathematical model for the co-evolution of obligate parasites and their hosts. *Evol.*, 12, 158–165.
- Morton, J.B. (1990). Species and clones of arbuscular mycorrhizal fungi (Glomales, Zygomycetes): Their role in macro- and microevolutionary processes. *Mycotaxon*, 37, 493–515.
- Nemec, S. (1978). Response of six citrus rootstocks to three species of *Glomus*, a mycorrhizal fungus. *Proc. Florida State Hort. Soc.*, 91, 10–14.
- Renshaw, E. (1991). *Modelling Biological Populations in Space and Time*. Cambridge: Cambridge University Press.
- Roughgarden, J. (1975). Evolution of marine symbiosis – A simple cost-benefit model. *Ecol.*, 56, 1201–1208.
- Roughgarden, J. (1976). Resource partitioning among competing species – A coevolutionary approach. *Theoret. Population Biol.*, 9, 388–424.
- Sanders, I.R. & Fitter, A.H. (1992). Evidence for differential responses between host–fungus combinations of vesicular-arbuscular mycorrhizas from a grassland. *Mycol. Res.*, 96, 415–419.
- Schenck, N.C. & Perez, Y. (1990). *Manual for the Identification of VA Mycorrhizal Fungi*. Gainesville: Synergistic Publications.
- Seger, J. (1988). Dynamics of some simple host–parasite models with more than two genotypes in each species. *Phil. Trans. R. Soc. London B.*, 319, 541–555.
- Seger, J. (1992). Evolution of exploiter–victim relationships. In *Natural Enemies*, ed. Crawley, M.J. London: Blackwell Scientific, pp. 3–25.
- Sheppard, P.M.F.R.S., Turner, J.R.G., Brown, K.S., Benson, W.W. & Singer, M.C. (1985). Genetics and the evolution of Mullerian mimicry in *Heliconius* butterflies. *Phil. Trans. R. Soc. London B.*, 308, 433–613.
- Slatkin, M. (1980). Ecological character displacement. *Ecol.*, 61, 163–177.
- Sokal, R.R. & Rohlf, F.J. (1981). *Biometry*. New York: Freeman.
- Stewart, F.M. (1971). Evolution of dimorphism in a predator–prey model. *Theoret. Population Biol.*, 2, 493–506.
- Templeton, A.R. & Gilbert, L.E. (1985). Population genetics and the coevolution of mutualism. In *The Biology of Mutualism*, ed. Boucher, D.H. London: Croom Helm, pp. 128–144.
- Van der Heijden, M.G.A., Boller, T., Wiemken, A. & Sanders, I.R. (1998a). Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecol.*, 79, 2082–2091.
- Van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglou, P., Streitwolf-Engel, R., Boller, T., Wiemken, A. & Sanders, I.R. (1998b). Mycorrhizal fungal diversity determines plant diversity, ecosystem variability and productivity. *Nature*, 395, 69–72.
- Vandermeer, J.H. & Boucher, D.H. (1978). Varieties of mutualistic interaction in population models. *J. Theoret. Biol.*, 74, 549–558.
- Wilson, D.S. (1983). The effect of population structure on the evolution of mutualism: a field test involving burying beetles and their phoretic mites. *Am. Naturalist*, 121, 851–870.
- Wilson, D.O. (1988). Differential plant response to inoculation with two VA mycorrhizal fungi isolated from a low-pH soil. *Plant Soil*, 110, 69–75.
- Wolin, C.L. & Lawlor, L.R. (1984). Models of facultative mutualism: density effects. *Am. Naturalist*, 124, 843–862.
- Zobel, M. & Moora, M. (1997). Plant coexistence in the interactive environment: arbuscular mycorrhiza should not be out of mind. *Oikos*, 78, 202–208.

BIOSKETCH

James D. Bever uses theoretical and empirical approaches to investigate the impact of soil organisms, particularly mutualistic mycorrhizal fungi, on the dynamics of plant populations and communities.

Editor, R. Holt

Manuscript received 18 September, 1998

First decision made 29 September, 1998

Manuscript accepted 18 November 1998