Population Dynamics and Mutualism: Functional Responses of Benefits and Costs

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ABSTRACT: We develop an approach for studying population dynamics resulting from mutualism by employing functional responses based on density-dependent benefits and costs. These functional responses express how the population growth rate of a mutualist is modified by the density of its partner. We present several possible dependencies of gross benefits and costs, and hence net effects, to a mutualist as functions of the density of its partner. Net effects to mutualists are likely a monotonically saturating or unimodal function of the density of their partner. We show that fundamental differences in the growth, limitation, and dynamics of a population can occur when net effects to that population change linearly, unimodally, or in a saturating fashion. We use the mutualism between senita cactus and its pollinating seed-eating moth as an example to show the influence of different benefit and cost functional responses on population dynamics and stability of mutualisms. We investigated two mechanisms that may alter this mutualism's functional responses: distribution of eggs among flowers and fruit abortion. Differences in how benefits and costs vary with density can alter the stability of this mutualism. In particular, fruit abortion may allow for a stable equilibrium where none could otherwise exist.

Keywords: benefits and costs, density dependence, functional response, mutualism, population dynamics, stability.

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It has long been recognized that interspecific interactions play major roles in determining the abundance of populations (Gause and Witt 1935). While there is still much to learn about how competition and predation influence a population's abundance and dynamics, the effects of these interactions are still far better known than are the effects of mutualism. For example, theory on competition and predation has progressed beyond phenomenological models to incorporate the biological mechanisms responsible for population dynamics by explicitly modeling mechanisms such as exploitation in competition and predator satiation and prey refugia in predator-prey interactions (Rosenzweig and MacArthur 1963; Tilman 1982). Equivalent theoretical approaches for mutualism that provide a general mechanism for its influence on population dynamics have lagged. This is despite the fundamental role of mutualism in ecological and evolutionary processes (Herre et al. 1999; Bronstein 2001*b*).

Our current knowledge of the dynamics of mutualism centers around a few key generalizations. First, nearly all mutualisms inherently involve both benefits and costs for interacting species (Roughgarden 1975; Keeler 1981, 1985; Boucher et al. 1982; Janzen 1985; Addicott 1986*b*; Pierce et al. 1987; Cushman and Beattie 1991; Bronstein 2001*b*; cf. Connor 1995). Benefits are goods and services that organisms cannot obtain affordably, or at all, in the absence of their partner(s). These benefits include the acquisition of nutrients, transportation of oneself or one's gametes, and protection from the biotic or abiotic environment. Costs include investments in structures to attract mutualists, substances to reward them, and the energy and time spent obtaining those rewards. Both costs and benefits directly or indirectly affect the reproduction and survival of mutualists. Second, benefits and costs are rarely fixed traits of species interactions but instead usually vary with the abundance or density of partners (Addicott 1979; Cushman and Whitham 1989; Herre 1989; Breton and Addicott 1992; Bronstein 1994; Nefdt and Compton 1996; Herre and West 1997; Morales 2000). Third, there is positive feedback between mutualist populations. However, at least when populations are large, this must be countered

by negative effects in order for mutualistic populations to have bounded growth and to maintain some stability (Gause and Witt 1935; Vandermeer and Boucher 1978; Goh 1979; Travis and Post 1979; Heithaus et al. 1980; Addicott 1981; May 1981; Soberon and Martinez del Rio 1981; Dean 1983; Rai et al. 1983; Addicott and Freedman 1984; Wolin and Lawlor 1984; Pierce and Young 1986; Wright 1989; Ingvarsson and Lundberg 1995; Lundberg and Ingvarsson 1998). This negative feedback on mutualistic populations could include resource limitation or negative effects imposed by a third species such as a competitor or predator. It could also include, as is the focus of this article, a change in the net effect of the mutualism itself as populations grow.

Despite these generalizations and the impressive body of empirical work on mutualism, there has been little inclusion of benefits, costs, and the density-dependent nature of positive feedback into mutualism theory. Many investigators have suggested that benefits and costs should somehow be incorporated into studies of how mutualism affects the growth and dynamics of populations (Addicott 1979, 1984, 1986*a*; Inouye and Taylor 1979; Soberon and Martinez del Rio 1981; May 1982; Rai et al. 1983; Addicott and Freedman 1984; Wolin and Lawlor 1984; Cook 1985; Wolin 1985; Pierce and Young 1986; Cushman and Whitham 1989; Breton and Addicott 1992; Bronstein 1994; Morales 2000). In this article, we attempt to do this by developing a theoretical approach that incorporates the generalizations above. This approach is based on deriving functional responses in terms of benefits and costs to one mutualist as a function of the population size of its mutualistic partner. Prior studies have presented benefits and costs to the recipient as varying with the density of the recipient itself. Here, we employ functional responses in which variation in benefits and costs to a recipient population are instead a function of the density of the recipient's mutualistic partner. In this study, we used both a general model for mutualism and a model for one particular mutualism to show how different benefit and cost functional responses can alter population growth, limitation, and dynamics resulting from mutualism.

Conceptual and Theoretical Development: Functional Responses of Gross Benefits, Costs, and Net Effects

In its most general application, a functional response represents how the rate of change of one population varies with the density or abundance of individuals of another population. In contrast to predator-prey interactions, little effort has been made to investigate the appropriate types of functional responses for mutualism. Most models of mutualism have simply used a Lotka-Volterra or type 2 functional response (Roughgarden 1983; Wolin 1985;

DeAngelis et al. 1986). We suggest that functional responses for mutualists should be derived in a mechanistic way that reflects both the benefits and costs experienced from the interaction. Because benefits and costs alter the rates of reproduction and/or survival, functional responses can incorporate how the abundance of a mutualist modifies the intrinsic growth rate of its partner. The difference between gross benefits and costs equals the net effect of mutualism on the rate of change in the size of a mutualist's population. We interpret this net effect of one mutualist on another as the functional response relating mutualistic species. Although not necessarily formulated as such, functional responses in terms of benefits and costs are beginning to be proposed for a variety of mutualisms (Herre 1989; Fonseca 1993; Gange and Ayers 1999; Bronstein 2001*a*; Holland and DeAngelis 2001).

For insight into the forms that functional responses may take, we consider how gross benefits and costs to a mutualist, say mutualist 2, depend on the abundance of its partner, mutualist 1. We first develop a general conceptual framework and later apply this to one particular mutualism, that between senita cacti and their obligate moth pollinators. In the conceptual framework and models presented in this section, we intend for mutualist 1 and mutualist 2 to represent an obligate species-specific mutualism. However, they could also represent multiple mutualistic species, lumped together as mutualist 1, interacting with a single or aggregate group of mutualistic species, indicated by mutualist 2. Our models do not consider multispecies facultative mutualisms. For such mutualisms, effects of one mutualist on the benefits and costs of its partner may vary depending on the relative abundance of the mutualists interacting with that partner. Nevertheless, logic similar to that developed here can be applied to multispecies, facultative mutualisms, although more complex models would be needed.

Many scenarios are plausible for benefit and cost functional responses. A few basic forms are shown in figure 1. Gross benefits to mutualist 2 must be 0 in the absence of mutualist 1, such that gross benefits increase from the origin. In contrast, the cost to mutualist 2 is not necessarily 0 if mutualist 1's abundance is 0; costs could diminish, increase from the origin, or be constant as the abundance of mutualist 1 rises from 0 (fig. 1). The shape of the cost curve depends on whether costs are fixed or variable investments (Addicott 1984) and whether they are construction costs of mutualist 2 or exerted on mutualist 2 by mutualist 1. For example, the cost of nectar production to a plant could be fixed if nectar is not replenished once consumed, or variable if it is. In this example, nectar production represents a construction cost for a plant, while seed eating by larvae of yucca moths represents a cost exerted on yucca plants.
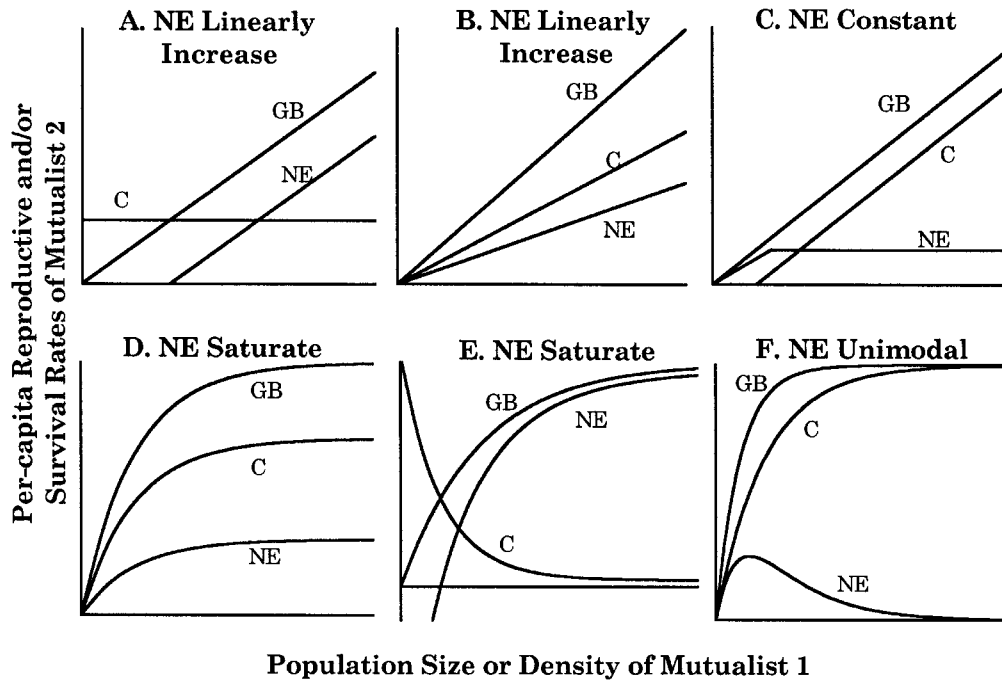
Figure 1: Models of some potential functional response curves in terms of gross benefits (*GB*), costs (*C*), and net effects (*NE*) on the per capita rate of reproduction and/or survival of a mutualist population, mutualist 2, as a function of its partner's population size, mutualist 1. Gross benefits positively affect the rate of reproduction and/or survival, while costs negatively affect the rate of reproduction and/or survival: NE = GB − *C*.

In figure 1*A*, as the abundance of mutualist 1 increases, costs to mutualist 2 remain constant while the gross benefits to mutualist 2 increase linearly. Thus, the net effect to mutualist 2 increases linearly, but it does not become positive until the abundance of mutualist 1 passes a threshold. In figure 1*B*, both costs and gross benefits to mutualist 2 increase as the abundance of mutualist 1 increases, but the rate of increase is greater for gross benefits than for costs. These two scenarios give rise to ever-increasing net effects for mutualist 2 as the abundance of mutualist 1 increases. This net-effects relationship is often assumed in theoretical studies (in which net effects are commonly referred to as the "benefit" of mutualism).

In nature, however, various limitations prohibit net effects of mutualism from ever increasing as in figure 1*A* and 1*B*. Instead, gross benefits and/or costs saturate or diminish with increases in population size, such that net effects saturate or diminish as well. One possible scenario is for gross benefits and costs to rise in parallel, with costs being negligible until a threshold abundance of mutualist 1 is reached (fig. 1*C*). Consequently, the net effect increases rapidly and then saturates. Saturating net effects also result when both gross benefits and costs increase asymptotically and saturate, with costs saturating lower than gross benefits (fig. 1*D*). In many pollination mutualisms, net effects

to plants are likely to increase asymptotically and saturate as pollinator abundance increases, but the exact shape of the net effect curve will vary depending on the functional responses of gross benefits and costs (fig. 1*C*–1*E*). For example, the number of flowers pollinated may increase with pollinator abundance, but as the fraction of flowers pollinated approaches unity, the marginal value of additional pollinators decreases. In this example, the net effect for plants saturates, but the exact shape of this curve depends on whether costs of nectar production are fixed, increase linearly, or saturate with pollinator abundance. This depends on whether the plant species in question replenishes nectar once consumed.

Net effects that asymptotically increase and saturate may be in a negative range (i.e., costs exceeding gross benefits) until a threshold abundance of mutualists is reached. This scenario may result from numerous combinations of gross benefits and costs, such as those in figure 1*A* and 1*E*. An example of this functional response may occur in aphid-ant interactions. Many aphids provide ants with nutrient-rich excretions (honeydew) in exchange for protection from their predators. When ants are rare, costs of honeydew to aphid growth and reproduction may exceed gross benefits of predator protection (Stadler and Dixon 1998; Yao et al. 2000).

Other shapes of functional responses are possible. For example, both gross benefits and costs could asymptotically increase and saturate at the same level, with costs accumulating more slowly than gross benefits, such that net effects are a unimodal function of abundance (fig. 1*F*). Unimodal net effects have been proposed for pollinating seed-eater mutualisms (see "Case Study" below; Bronstein 2001*a*; Holland and DeAngelis 2001) and for plants interacting with myrmecophytic ants (Fonseca 1993, 1999). For ant-defense mutualisms, gross benefits of reduced herbivory to plants should asymptotically increase and saturate as ant colony size on the plant increases. Gross benefits saturate because, at some ant colony size per plant, the addition of more ants to the plant does not increase ant inhibition of herbivory. The cost to plants of providing food resources for ants increases linearly with ant abundance, such that maximum net benefit to plants occurs at an intermediate ant colony size (Fonseca 1993, 1999). Net effects for plants interacting with mycorrhizal fungi may also be unimodal (Gange and Ayers 1999).

In summary, numerous different combinations of gross benefits and costs may occur depending on the mutualism in question, but they result in only a few general forms for net effect functional responses. We suspect that asymptotically saturating net effects (as in fig. 1*D* and 1*E*) are the most widespread in nature, but other shapes may also occur, including unimodal net effects, linearly increasing net effects, and possibly an exponential decay in net effects. Furthermore, while we have presented gross benefits, costs, and net effects as smooth functions of abundance, some could be step functions (fig. 1*C*).

Functional Responses and the Dynamics of Mutualists

Above, we expressed the functional response in terms of gross benefits and costs to each mutualist. Below, we investigate how these functional responses affect the equilibrium sizes and dynamics of mutualistic populations. We use the equilibrium solution of the dynamic equation for the population of mutualist 2 to determine how its size and dynamics vary with the population size of its partner. For simplicity, we assume that both gross benefits and costs affect the reproduction of mutualist 2, such that the net effect functional response can be incorporated into the reproduction term of the dynamic equation. We use the following model for the population dynamics of mutualist 2:

$$\frac{dN_2}{dt} = B_n N_2 - dN_2 - gN_2^2, \tag{1}$$

where N_2 is the population size of mutualist 2, B_n is the net effect to mutualist 2, d is the mortality rate, and g is

the rate of self-limitation. In general, B_n could be a function $f(N_1, N_2)$ (i.e., the functional response) of both N_1 (the population size of mutualist 1) and N_2. The first term represents the population growth rate of mutualist 2 as determined by the net effect of the mutualism, the second term reduces population size due to mortality, and the third term is self-limitation.

Using equation (1), we analyzed the effects of functional responses on population sizes and dynamics by deriving zero isoclines for three different functional responses, each dependent only on N_1: where the net effect of the mutualism to mutualist 2 increases linearly with population size of mutualist 1 (fig. 1*B*), where the net effect increases and saturates (fig. 1*D*), and where the net effect is a unimodal function of mutualist 1's abundance (fig. 1*F*). For a linearly increasing functional response, we use

$$B_n = mN_1 + a, \tag{2}$$

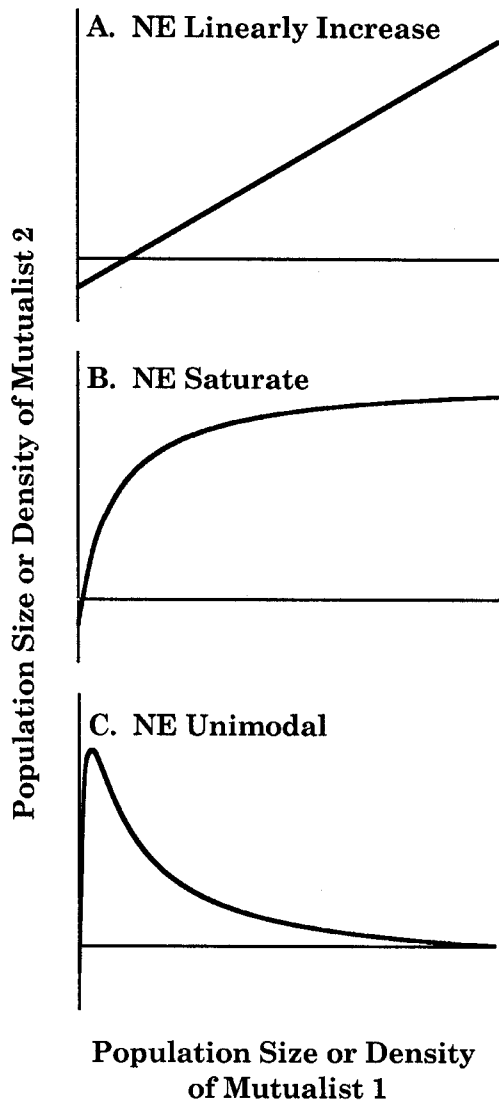where $m > 0$ and $a \leq 0$. For saturating and unimodal net effects, we use

$$B_n = \frac{\gamma_1 N_1}{1 + \gamma_1 N_1}, \tag{3}$$

$$B_n = \frac{\gamma_1 N_1}{1 + \gamma_1 N_1} - \frac{\gamma_2 N_1}{1 + \gamma_2 N_1}, \tag{4}$$

respectively. In equation (3), γ_1 represents the rate at which net effects are accrued by mutualist 2 as a function of mutualist 1's population size. In equation (4), γ_1 and γ_2 ($\gamma_1 > \gamma_2$) represent the rate at which gross benefits and costs are accrued.

The different functional responses incorporated into equation (1) result in different zero isoclines in the N_1-N_2 state plane (fig. 2). For the state-plane diagrams in figure 2, N_2 has a negative growth rate when above the isocline, whereas the growth rate is positive for N_2 below the isocline. Some minimum abundance of mutualist 1 is required before its positive effects on the population growth of mutualist 2 can overcome the negative effects of the mortality rate, d, of mutualist 2. When net effects to N_2 increase linearly with N_1, then the zero isocline of N_2 increases linearly as N_1 rises (fig. 2*A*). The boundary on population size with a linear functional response is set by self-limitation. However, when net effects to N_2 saturate or are unimodal as a function of N_1, then the zero isocline of N_2 increases asymptotically or is unimodal with increases in N_1 (fig. 2*B*, 2*C*), such that these functional responses can limit population size below that imposed by self-limitation.

It is evident from the isoclines in figure 2 that the effect of mutualism on population size can be drastically dif-

A. NE Linearly Increase

B. NE Saturate

C. NE Unimodal

Population Size or Density of Mutualist 1

(y-axis label: Population Size or Density of Mutualist 2)

Figure 2: Zero isoclines ($dN_2/dt = 0$) of the population of mutualist 2 for three different functional responses of net effects (NE) to mutualist 2 as a function of the population size of mutualist 1. The different functional responses correspond to the net effect curves in equations (2)–(4) that were incorporated into equation (1). For any particular value of N_1, if N_2 is above the isocline, then N_2 will decrease, whereas if N_2 is below the isocline, then N_2 will increase. Note that in all three figures, the y-intercept is a negative value.

functional response. For the saturating functional response, larger densities of mutualist 1 lead to only very small additional increases in mutualist 2. For a unimodal functional response, however, larger densities of mutualist 1 lead to densities of mutualist 2 smaller than the maximum abundance. This occurrence for a unimodal functional response should not be interpreted as an antagonistic outcome of the interaction, however, because mutualist 1 still has a positive effect on mutualist 2; it is just a smaller positive effect than occurs at the maximum.

Case Study: Pollination Mutualism between Senita Cacti and Senita Moths

We now use the pollination mutualism between senita cacti and senita moths (Fleming and Holland 1998; Holland and Fleming 1999*a*, 1999*b*) to demonstrate how functional responses can shed light on the dynamics of mutualists. We review its natural history and then derive dynamic equations for cactus and moth populations that explicitly incorporate functional responses in terms of benefits and costs. Using these equations, we investigate the population dynamics and stability of this mutualism in relation to how costs to the plant population are altered by the moth's oviposition and pollination behavior and how the cost of fruit abortion alters recruitment of moths.

The Senita Pollination Mutualism

Flowers of senita cacti (*Lophocereus schottii*) are dependent on pollination by female senita moths (*Upiga virescens*), which also lay their eggs within flowers. The entire life cycle of moths is obligately associated with cacti. Fruit production depends on moth pollination, but some immature fruit never reach maturity because moth larvae consume them. Not all flowers produced during a reproductive season set fruit, despite sufficient pollination by moths. Many pollinated flowers abort because resources (e.g., water) limit fruit maturation and also because fruit abortion could possibly prevent moths from becoming so abundant that nearly all fruit contain larval seed eaters (Holland and Fleming 1999*a*, 1999*b*; Holland 2001; Holland and DeAngelis 2001; DeAngelis and Holland 2002). Eggs and larvae in aborting fruit invariably die. Larvae in flowers that did not abort enter into fruit and consume developing ovules. As they exit fruit, larvae bore into cactus stems, where they later pupate and emerge as adults. None of the ovules in a fruit containing a larva, including those not eaten, contributes to seed production because the fruit is induced to abscise as the larva bores out of it. However, not all fruit abscise due to larval attack because some flowers do not have eggs laid within them and, of those that do, some eggs and larvae die before larval seed eating.

ferent depending on the net effect functional response. For example, there is a range of densities of mutualist 1 for both asymptotically saturating and unimodal net effect functional responses that, as the density of mutualist 1 increases, lead to sharp increases in the density of mutualist 2. However, further increases in mutualist 1 beyond this range of densities has differing effects depending on the

Both gross benefits and costs affect reproduction in cacti. Seed production is increased through fruit set attributable to moth pollination and decreased through the abscission of larva-infested fruit, allowing the net effect to cacti to be expressed in terms of mature fruit production. For moths, both gross benefits and costs of the mutualism affect recruitment into the adult population, rather than reproduction per se. Cacti benefit moths by providing them with flowers as oviposition sites because without flowers moths do not lay eggs. Immature fruit provide larvae with food needed for growth and survival. However, recruitment of new moths into the adult population is reduced by fruit abortion because eggs and larvae in aborting fruit die. Recruitment is also reduced by cacti because fruit resources appear to permit no more than one larva from successfully developing per fruit.

Functional Responses and Population Dynamics of Senita Cacti and Senita Moths

Knowledge of the natural history of these species suggests the probable shapes of functional responses for the mutualism. We take a population view and assume that gross benefits and costs to the cactus population are related, respectively, to rates at which moths pollinate flowers and larvae cause fruit loss. Thus, gross benefits and costs are functions of the abundance of moths (M) relative to the rate of flower production by the plant population. Flower production equals the product of the number of plants (P) and the average number of flowers per plant per night (F). We derive a functional response for gross benefits of pollination by modeling the plant population as a static set of flowers over each night's production and by modeling the pollinator population as randomly searching for and visiting these flowers. The visitation rate per flower should be proportional to the ratio of pollinators to flowers, or M/FP. Thus, a ratio-dependent functional response is appropriate, as has been formulated earlier for this type of search (Thompson 1939).

The functional response for gross benefits to cacti is expressed as the fraction of flowers pollinated. It is assumed to increase asymptotically as the number of pollinators increases relative to flowers and to saturate at 1.0. As pollinators increase, more flowers can be pollinated. However, this effect diminishes as the fraction of pollinated flowers approaches 1.0 because most to all flowers have been pollinated. Assuming that the search and visitation of flowers by pollinators is spatially a Poisson process, $1 - \exp(-\gamma_1 M/FP)$ is the fraction of flowers pollinated, and thus $FP[1 - \exp(-\gamma_1 M/FP)]$ is the number of flowers pollinated over the entire population. Similarly, oviposition and larval-induced abscission of fruit can be described by the same model as flower pollination, but the rates of

these two processes may differ. We assume that the fraction of flowers abscising as immature fruit due to larvae has the form $1 - \exp(-\gamma_2 M/FP)$, where γ_2 represents the rate of larval infestation of fruit. This cost functional response increases asymptotically and saturates at 1.0 because it is possible for a larva to occupy every fruit if pollinators are sufficiently abundant for enough eggs to be laid. Because not all eggs and early instar larvae survive, the number of pollinated flowers increases more rapidly than does the number of fruit destroyed by larvae (i.e., $\gamma_1 > \gamma_2$). Assuming that the processes of pollination and oviposition occur independently (an assumption that will be relaxed later), the number of flowers that are pollinated and not destroyed is $FP[1 - \exp(-\gamma_1 M/FP)]\{1 - [1 - \exp(-\gamma_2 M/FP)]\}$.

The dynamics of the cactus population can be described by inserting these functional responses into the general equation (1), to obtain

$$\frac{dP}{dt} = (1 - a)\alpha FP\left[1 - \exp\left(\frac{-\gamma_1 M}{FP}\right)\right]$$
$$\times \left\{1 - \left[1 - \exp\left(\frac{-\gamma_2 M}{FP}\right)\right]\right\} - d_1 P - gP^2, \quad (5)$$

with the addition of two parameters, $(1 - a)$ and α. Some fraction of flowers, even if pollinated, do not set fruit. This fraction of unpollinated flowers that abscise plus pollinated flowers that abort is represented by a, such that the total fraction of flowers that can potentially set fruit is $(1 - a)$. The parameter α is the fraction of mature fruit produced that ultimately lead to new cacti. The rates at which gross benefits and costs are accrued are represented by γ_1 and γ_2, respectively. The gross benefit, cost, and net effect functional responses in this model (eq. [5]) correspond to those depicted graphically in figure 1F. This model represents the long-term dynamics of the system. The model ignores short-term seasonal effects of flowering phenology and pollinator diapause, which have been considered elsewhere (Holland and DeAngelis 2001).

A dynamic equation for the senita moth population that incorporates gross benefit and cost functional responses is

$$\frac{dM}{dt} = (1 - a)\alpha FP\left[1 - \exp\left(\frac{-\gamma_1 M}{FP}\right)\right]$$
$$\times \left[1 - \exp\left(\frac{-\gamma_2 M}{FP}\right)\right] - d_2 M. \quad (6)$$

Gross benefits and costs to the moth population are ex-

pressed in terms of recruitment. The first term represents net effects to moth recruitment and the second term, d_2M, is mortality. Given the dynamic equation for cacti, recruitment into the moth population cannot be greater than that allowed by the cactus functional response, $(1 - a)FP[1 - \exp(-\gamma_1 M/FP)][1 - \exp(-\gamma_2 M/FP)]$. Thus, we use the functional response of the cactus population as a starting point because the number of new moths recruited from eggs is ultimately determined by the number of flowers setting fruit. Gross benefit of the mutualism to moth recruitment is the number of flowers that are effectively oviposited, which is given by $FP[1 - \exp(-\gamma_1 M/FP)][1 - \exp(-\gamma_2 M/FP)]$, "effectively" meaning that oviposition results in survival of eggs to pupae. This is a unimodal function of FP, as in figure 1F. The cost is fruit abortion $(-a)$, which lowers recruitment by reducing effective ovipositions.

The state variables of this model are P and M. We analyzed the behavior of this system by setting $dP/dt = 0$ and $dM/dt = 0$ in equations (5) and (6) and examining their zero isoclines in the P, M state plane. The cactus zero isocline forms a closed curve, with both ends emanating from the origin (fig. 3A). Within this curve, $dP/dt > 0$, while outside of it, $dP/dt < 0$ (the signs are shown in fig. 3B, a variation of fig. 3A described below). The shape of the cactus isocline reflects the assumptions built into the functional response. In particular, the cactus population decreases either if the moth population is too low (due to insufficient pollination) or if it is too high (due to high levels of larval fruit consumption). The cactus population also shows a decreasing growth rate if it is too large due to the self-limitation term, $-gP^2$, in equation (5), explaining why the cactus isocline is a closed curve.

The moth zero isoclines are two straight lines emanating from the origin. There are two isoclines for the moth population because of the unimodal functional response assumed in equation (6). Because there is no self-limitation, such as $-gP^2$, of the cactus population, these lines do not form a closed curve. The moth population has a positive growth rate only between the lines and is negative to the right of the lower line. In the positive part of the plane, cactus and moth isoclines can intersect at most twice to form two equilibrium points, a stable node and an unstable saddle point. Also, a singular point occurs at the origin $(0, 0)$. We did not undertake a full exploration here of the behavior of variables in the vicinity of the singular point $(0, 0)$. A similar singular point has been analyzed in detail by Jost et al. (1999) for a predator-prey system with a ratio-dependent functional response.

Some typical trajectories for the isoclines in figure 3A are shown in figure 4. Nearly all trajectories in this state plane converge on the stable equilibrium point (e.g., trajectories b and c in fig. 4). However, some trajectories,
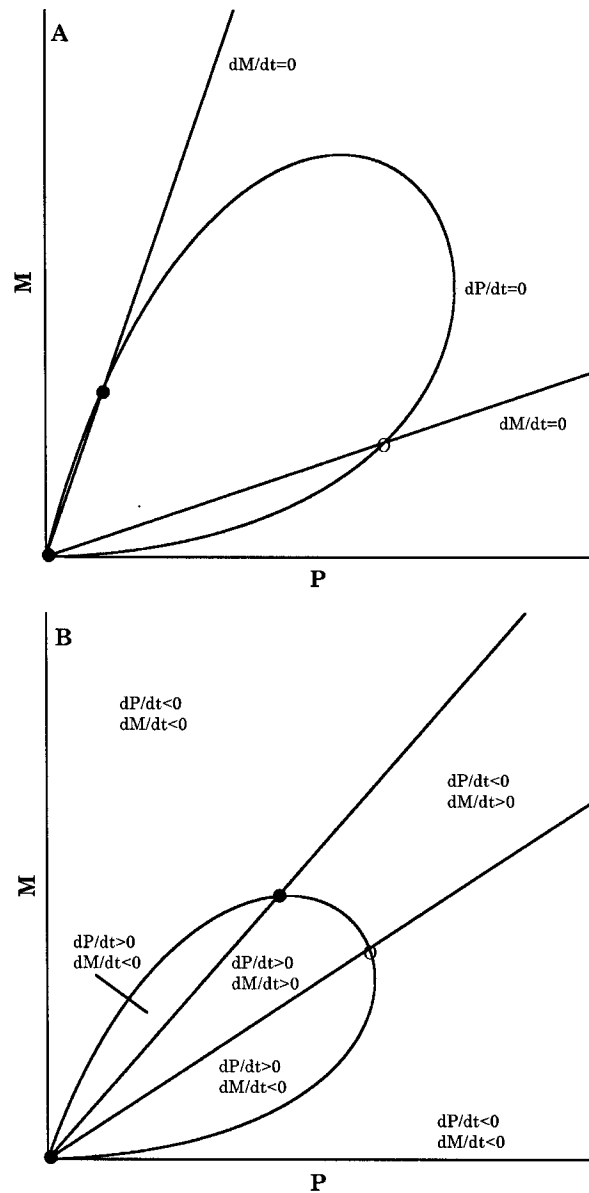
Figure 3: Diagram of the P, M state plane for equations (5) and (6), showing zero isoclines of plants and moths formed by plotting M versus P for $dP/dt = 0$ and $dM/dt = 0$, respectively. There are two equilibrium points, a locally stable one (*solid circle*) and a locally unstable one (*open circle*). Note that the origin $(0, 0)$ is a singular point that repels some trajectories, but attracts others. A, There are no fruit abortions, or $a = 0.0$. B, There are fruit abortions, with $a = 0.3$. The other parameter values are $F = 20$, $\alpha = 0.13$, $\gamma_1 = 4.0$, $\gamma_2 = 2.0$, $d_1 = 0.1$, $d_2 = 0.75$, and $g = 0.001$.

starting with either very high or very low ratios of M/FP, can result in extinction of both mutualists (e.g., trajectories a and d in fig. 4). Extinction of moth and cactus populations in trajectory a results from the increasingly negative
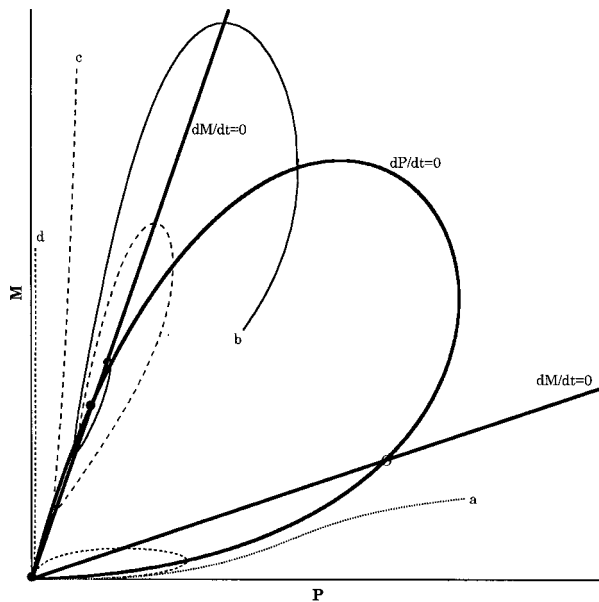
Figure 4: Diagram of the *P*, *M* state plane showing four (*a–d*) example trajectories that result from equations (5) and (6). Each trajectory proceeds away from the letter designating its trajectory. Parameter values are the same as in figure 3*A*. In addition to the singular point at the origin (0, 0), there are two equilibrium points, a locally stable one (*solid circle*) and an unstable one (*open circle*).

fects of fruit abortion in this study are consistent with prior studies. This can be seen by comparing the state-plane diagram where $a = 0.0$ (fig. 3*A*) with that in which $a = 0.3$ (fig. 3*B*). When *a* increases from 0.0 to 0.3, the slopes of the zero isoclines of the moth tend to converge so that the stable equilibrium point moves to the right to a larger value of *P*. This is because fruit abortion limits the exploitation of the cactus population by the moth population, such that fruit production is actually greater with fruit abortion than without it. Even though the area of the state plane where $dP/dt > 0$ becomes smaller as *a* increases, this change in the cactus zero isocline is not enough to counter the shift to the right in the stable equilibrium point. The reduction in state space where $dP/dt > 0$ results because fruit abortion and reduced fruit set decrease the maximum possible production of fruit.

Other Possible Functional Responses of Senita Cacti and Senita Moths

growth rate of the moth population, as the number of cacti increases, to the right of the lower moth isocline. This negative growth rate seems paradoxical, because a moth population at a low abundance relative to cacti is expected to grow. The reason for the negative growth rate is that the model assumes pollination and oviposition events are independent. This assumption means that the chance that a flower is both pollinated and oviposited decreases with an increasing number of flowers, leading to fewer "effective" ovipositions. We believe that this model assumption underlying the functional response is not biologically reasonable, and we make an adjustment in the functional response below (see "Variation 1") to correct for this.

Using a model for pollinating seed-eater mutualisms, Holland and DeAngelis (2001) and DeAngelis and Holland (2002) showed that fruit production could be greater when plants reduced fruit set and experienced fruit abortion (i.e., $a > 0$ and $1 - a < 1.0$ in eq. [5]) compared to when no fruit abortion occurred. However, they did not analyze the general stability of both plant and pollinator dynamics. Because fruit abortion imposes a cost on pollinator recruitment, it could alter the stability and equilibrium size of the cactus population. In this study, we used a more general model of plant and pollinator dynamics. The ef-

The model represented by equations (5) and (6) serves as a simple starting point for the derivation of functional responses for cacti and moths. However, any such formulation is a gross approximation at best. To determine the robustness of the general form of the model, we examined the zero isoclines using a type 2 functional response to replace the $(1 - \text{exponential})$ terms in the original model. The type 2 functional response showed the same general response to changes in *M/FP*, but the exact curvature of the functional response differed from the $(1 - \text{exponential})$ terms. We do not show the zero isoclines of this model, but they do show the same general shape of the original model. Thus, the general results of the original model are not very sensitive to the exact shapes of the functional response curves. Below, we evaluate two variations on the original model that result from changing the biological assumptions of the functional responses.

Variation 1. The functional response $(1 - a)\alpha FP[1 - \exp(-\gamma_1 M/FP)]\{1 - [1 - \exp(-\gamma_2 M/FP)]\}$ that we used in the original model contains the implicit assumption that pollination and oviposition are independent random events. Thus, there is a likelihood that some pollinated flowers are not oviposited into and that some flowers that are oviposited into are not pollinated. In nature, however, pollination and oviposition are behaviorally correlated because female moths pollinate flowers as a way of provisioning their offspring with food. When this phenomenon is incorporated into the functional response, the first term of the cactus equation becomes

$$(1-a)\alpha FP\left[1-\exp\left(\frac{-\gamma_1 M}{FP}\right)\right]\frac{\{1-[1-\exp(-\gamma_2 M/FP)]\}}{[1-\exp(-\gamma_1 M/FP)]},$$

(7)

equaling $(1-a)\alpha FP[\exp(-\gamma_2 M/FP)-\exp(-\gamma_1 M/FP)]$. The functional response in the first term of the moth equation now becomes

$$(1-a)\alpha FP\left[1-\exp\left(\frac{-\gamma_1 M}{FP}\right)\right]\frac{[1-\exp(-\gamma_2 M/FP)]}{[1-\exp(-\gamma_1 M/FP)]},\quad(8)$$

equaling $(1-a)\alpha FP[1-\exp(-\gamma_2 M/FP)]$.

In equation (8), gross benefit to recruitment of new moths is the number of flowers on which "effective" oviposition (i.e., survival of eggs to pupae) occurs; this is given by $FP[1-\exp(-\gamma_2 M/FP)]$. This functional response increases asymptotically and saturates as M/FP increases, representing two facts: first, a point is reached at which further increases in flower abundance result in no more ovipositions because the reproductive biology inherent to the moths limits the maximum number of eggs moths can lay, and, second, the number of ovipositions that can result in a pupa is limited, because each fruit has enough resources for the development of only one larva. In equation (8), the cost of fruit abortion reduces recruitment of new moths by lowering the number of flowers on which effective oviposition occurs, which is given by $aFP[1-\exp(-\gamma_2 M/FP)]$. The cost of fruit abortion increases asymptotically and saturates as M/FP increases, but it saturates at a level lower than gross benefits.

The main difference between the state plane for the functional responses of variation 1 and the original model is that there is now only one line representing the moth's zero isocline, and there is at most only one nonzero equilibrium point (fig. 5). This result produces important differences between the dynamics of this model and the original one. The lower moth zero isocline of figure 3 has converged with the *P*-axis. Because pollination and oviposition are behaviorally associated in variation 1, it is no longer possible for moths to go extinct from high egg and larval mortality associated with the abscission of unpollinated flowers, as in the original model. We view variation 1 as more biologically reasonable model than the original model because pollination behavior has likely evolved in association with oviposition to increase the likelihood of egg and larval survival.

The state space where $dP/dt > 0$ is slightly reduced in this model (cf. figs. 3*B*, 5*B*) because ovipositions are now limited to pollinated flowers that may set fruit. This results in each oviposition having a greater chance of leading to larval seed consumption. The reduced area where
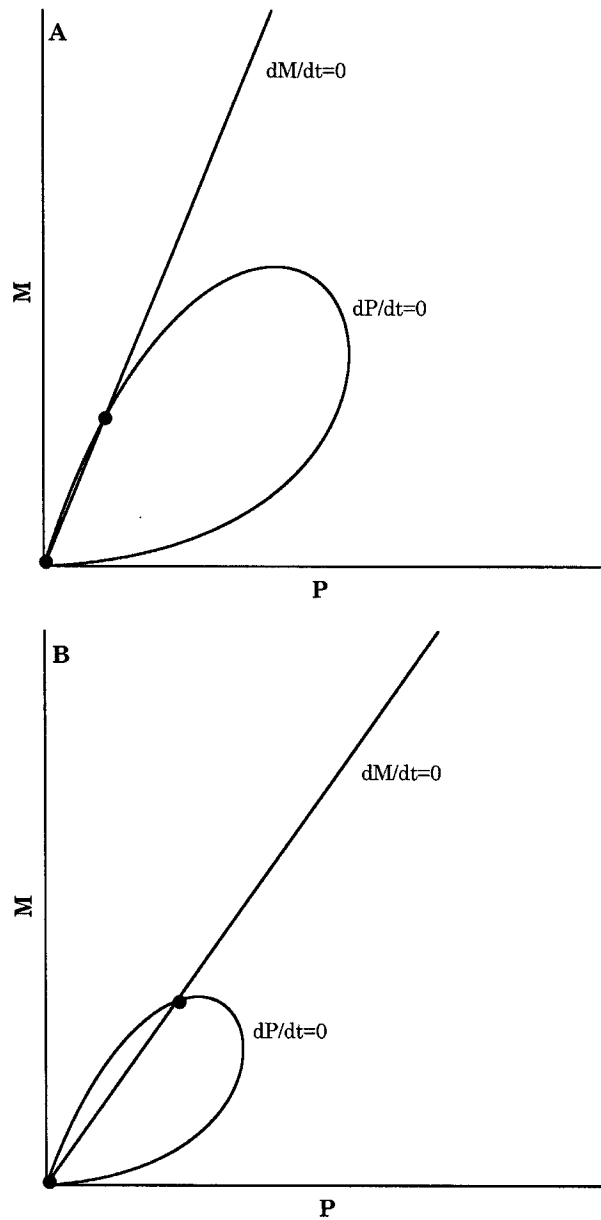
Figure 5: Diagram of the *P*, *M* state plane for variation 1, showing zero isoclines of plants and moths formed by plotting *M* versus *P* for $dP/dt = 0$ and $dM/dt = 0$, respectively. There is only one stable equilibrium point (*solid circle*) in addition to the singular point at the origin $(0, 0)$. *A*, There are no fruit abortions, or $a = 0.0$. *B*, There are fruit abortions, with $a = 0.3$. The other parameter values are $F = 20$, $\alpha = 0.13$, $\gamma_1 = 4.0$, $\gamma_2 = 2.0$, $d_1 = 0.1$, $d_2 = 1.0$, and $g = 0.001$.

$dP/dt > 0$ is substantial enough that there is also a shift in the stable equilibrium point toward a smaller equilibrium value for the cactus population. However, this reduction in the equilibrium number of cacti is accompanied by increased population persistence because the lower moth

zero isocline drops to the *P*-axis (fig. 5*B*), which reduces the likelihood of the mutualism from going to extinction. Furthermore, as was the case in the original model, fruit abortion increases the equilibrium number of cacti in the population compared to the equilibrium when there is no fruit abortion (fig. 5*A*, 5*B*).

Variation 2. A basic assumption of the functional responses in the original model and variation 1 is that both pollination and oviposition occur as Poisson processes in the space of pollinated flowers so that some flowers have many eggs while others have few to none at all. However, senita moths do not oviposit randomly; instead, they distribute their eggs evenly among flowers (Holland and Fleming 1999*b*).

An even distribution of eggs among flowers changes the functional responses for both mutualists. To simulate this change mechanistically, we leave pollination in the form given in variation 1 but assume that moths apportion their eggs evenly across pollinated flowers. Recall that the Poisson model assumed that an effective mean number of eggs γ_2 were laid by each moth and that "effective" signifies that the survival of eggs to pupae is incorporated into γ_2. Here, we assume that γ_2 is the product of two factors, γ_3 and γ_4, where γ_3 is the actual mean number of eggs laid per moth and γ_4 is the probability of an egg surviving to the pupal stage. If $\gamma_3 M < FP$, then $\gamma_3 M$ flowers have one egg each, and the remaining flowers have none. A mean total of $\gamma_3\gamma_4 M$ larvae survive to the pupal stage. If $FP < \gamma_3 M < 2FP$, then every flower has one egg, and $\gamma_3 M - FP$ flowers have two eggs. The expected number of pupae is then $\gamma_3\gamma_4 FP + (FP - \gamma_3\gamma_4 M)\gamma_4$. This process can be continued to estimate the number of pupae as $\gamma_3 M$ increases beyond $3FP$, $4FP$, and so forth. As *M* increases, the number of pupae expected approaches *FP*, as in the Poisson search case, although with the present mechanism, *FP* is approached faster as a function of *M*.

In the original model, it was unlikely that all fruit would be destroyed by larvae because of the decaying exponential rate of larval seed eating associated with the Poisson distribution of ovipositions. This is not the case when ovipositions are even among flowers. The state-plane diagram for this functional response of oviposition behavior has no stable equilibrium point unless the death rate, d_2, of moths is exceptionally high (fig. 6*A*, no fruit abortion). In figure 6*A*, the moth population grows very large such that all flowers receive enough ovipositions that all fruit are eventually destroyed. This leads to the extinction of first the cactus population and then the moth population. However, when fruit set is <1.0 and fruit abortion does occur ($a = 0.45$; fig. 6*B*), the slope of the moth isocline decreases, resulting in a stable equilibrium point. This is because fruit abortion can function as a mechanism that
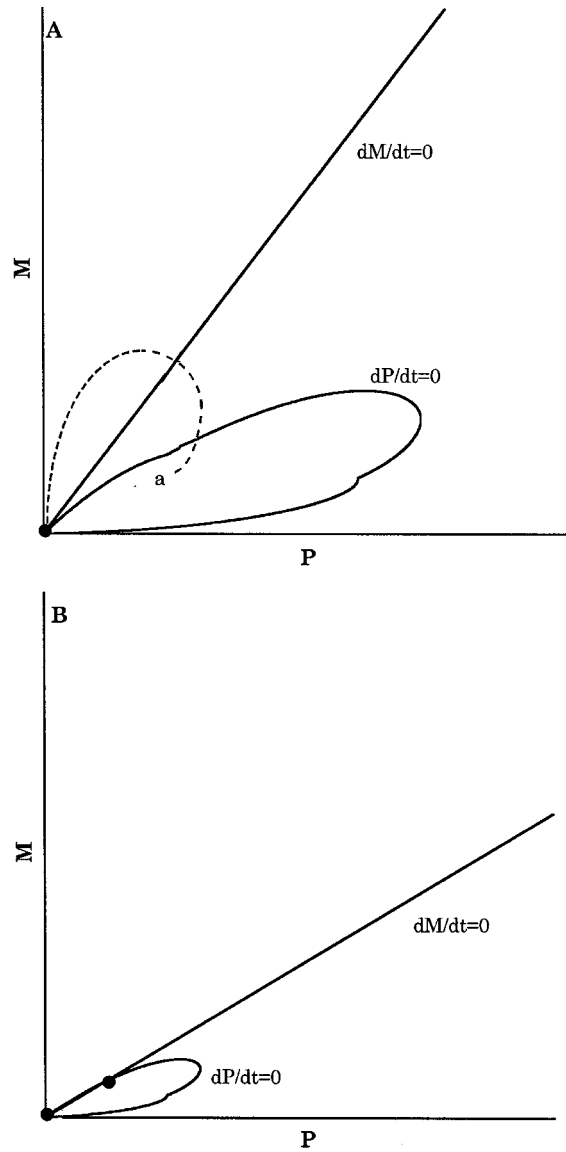
Figure 6: Diagram of the *P*, *M* state plane for variation 2, showing zero isoclines of plants and moths formed by plotting *M* versus *P* for $dP/dt = 0$ and $dM/dt = 0$, respectively. *A*, No stable equilibrium occurs other than at the origin (0, 0). All trajectories, including the shown trajectory, *a*, go to extinction. There are no fruit abortions ($a = 0.0$). *B*, Only one stable equilibrium (*solid circle*) occurs in addition to the singular point at the origin (0, 0). There are fruit abortions, with $a = 0.45$. The other parameter values are $F = 20$, $\alpha = 0.13$, $\gamma_1 = 4.0$, $\gamma_2 = 2.0$, $d_1 = 0.1$, $d_2 = 1.0$, and $g = 0.001$.

prevents overexploitation of senita cacti by limiting the growth of the moth population. Thus, by increasing costs to pollinator recruitment, reduced fruit set and the existence of fruit abortion can stabilize the mutualism and prevent plant and pollinator populations from going to extinction.

Discussion

Mutualisms range from obligate to facultative, from species specific to highly generalized, and from symbiotic to nonsymbiotic. They involve diverse taxa occurring in habitats worldwide, often with complex natural histories (Boucher et al. 1982; Janzen 1985; Herre et al. 1999; Bronstein 2001*b*). This diversity has limited the development of the kind of general theory that has characterized predator-prey and competitive interactions. Although different equations are needed to explore the growth and dynamics of mutualistic species that vary considerably in their ecology and natural history, we suggest that functional responses in terms of benefits and costs can provide a general theory for reaching a mechanistic understanding of how mutualism affects the growth, stability, and dynamics of populations. For example, functional responses inherent to mutualisms may provide a general mechanism for understanding what limits the positive feedback of mutualism on population growth and thereby maintaining some stability of populations and preventing unbounded population growth.

In addition to the mechanistic explanation for the long-standing problem of why mutualistic populations do not grow unbounded, the functional response approach to mutualisms suggests that different mutualisms with different functional responses should have different stability properties. Conversely, mutualisms differing greatly in ecology and natural history may have very similar dynamical properties, if they have similar functional responses. This is because linear, saturating, and unimodal functional responses can be expected to have characteristic effects on the growth, limitation, and dynamics of mutualists (fig. 2). For example, a mutualistic interaction in which both interacting species have saturating functional responses can have different stability properties from a mutualism in which one species has a unimodal functional response and the other a linear functional response.

The outcome of mutualistic interactions can be variable and conditional on factors such as the community and environmental context in which the interaction occurs, size/age/stage classes of mutualists, and the distribution and density of mutualists (Thompson 1988; Bronstein 1994). Functional responses in terms of benefits and costs can provide some insight into one reason why the strength and outcome of interspecific interactions can vary. If densities occur for which costs exceed gross benefits, then the outcome of an interaction will be antagonistic (fig. 1). At other densities where gross benefits are greater than costs, the net outcome will be mutualism. Thus, it is feasible for one "mutualistic" species to have positive net effects on its partner for some population densities, while at other densities it may have a commensalistic or parasitic net effect.

Despite the advantages of the functional response approach, there are certain potential drawbacks that may impede its general application to mutualisms. Unlike the senita pollination mutualism, in many mutualisms both the benefits and costs do not affect either reproduction or recruitment of both mutualists. Furthermore, the benefits and costs to a given partner cannot always be quantified in the same units, such as seeds for senita cacti or recruitment of new moths for senita moths. It may be difficult to quantify functional responses when benefits and costs are not in the same currency or when they accrue in currencies of time or energy. Finally, unlike the obligate species-specific mutualism between senita cacti and senita moths, many mutualisms are diffuse and facultative. For such multispecies facultative interactions, one or more of these mutualists may be functionally redundant, such that the effect of one mutualist on the benefits its partner receives may vary depending on its abundance relative to other mutualists interacting with that partner. Nevertheless, it should be possible to extend the functional response approach to multispecies facultative mutualisms, although it may require more complex models.

Despite these potential limitations, a functional response approach to mutualism can cut across mutualisms differing in natural history, generating new insights and highlighting underlying similarities and differences in population dynamics. The senita pollination mutualism, for example, parallels the better-known pollinating seed-eater mutualism between yucca and yucca moths (Addicott 1986*b*; Pellmyr et al. 1996; Pellmyr 1997; Pellmyr and Leebens-Mack 2000). Functional responses for these two mutualisms are likely to be similar, given that in both cases moths pollinate and oviposit into flowers, and larvae consume the fruit that result; oviposition is behaviorally associated with active pollination, which is a behavioral and morphological adaptation that facilitates directed placement of pollen on stigmas of flowers; and fruit abortion reduces recruitment of moths because eggs and larvae invariably die in aborting fruit. Furthermore, the natural history of both of these mutualisms suggests that gross benefits and costs to plants result in a unimodal net effect functional response.

The functional response approach yields new insights into the function and consequence of certain evolved traits common to the yucca and senita pollination mutualisms. Active pollination, for example, has apparently evolved under strong selection for moths to increase the likelihood of a flower setting fruit because this reduces the chances of flower abscission and hence increases the likelihood of larval survival (Pellmyr et al. 1996). Recall from variation 1 of our original model that the behavioral association of

oviposition with active pollination causes the costs of seed eating to increase at a greater rate, such that greater exploitation of the plant population occurs for a smaller pollinator population size (cf. figs. 3, 5). Nevertheless, the association of oviposition with active pollination can reduce the likelihood that plant and pollinator populations will become extinct (fig. 5).

Another trait of both senita and yucca moths is the strategy of not randomly distributing their eggs among flowers (Wilson and Addicott 1998; Holland and Fleming 1999*b*; Huth and Pellmyr 1999). Because aborting fruit with many eggs imposes a greater cost on pollinator recruitment than does aborting fruit with few to no eggs, moths can increase the likelihood that any one of their offspring will survive by distributing eggs evenly among flowers, as in senita moths (Holland and Fleming 1999*b*), or by laying eggs less frequently in flowers that have already been oviposited into, as in yucca moths (Wilson and Addicott 1998; Huth and Pellmyr 1999). Recall from variation 2 that an even distribution of eggs can destabilize the mutualism and prevent a nonzero stable equilibrium from occurring. This is because the cost functional response of seed eating to plants changes to the point where even a moderate abundance of moths can result in excessive exploitation of the plant population (fig. 6*A*). However, if senita cacti and yucca plants abort fruit, then senita moths and yucca moths can be limited below the abundance at which excessive exploitation occurs (fig. 6*B*). In fact, both senita and yucca populations are known to consistently have low fruit set, despite sufficient pollination, and to abort fruit (see Holland and Fleming 1999*a*; Holland and DeAngelis 2001).

For mutualisms in which costs increase with the abundance of a mutualist's partner, as in senita and yucca mutualisms, we hypothesize that mutualists, particularly those involved in obligate interactions, will have some mechanism for limiting their partner's abundance. Mechanisms analogous to fruit abortion apparently occur in diverse kinds of mutualisms. For plants defended by myrmecophytic ants, costs of providing ants with food sources, such as extrafloral nectaries and lipid-rich food bodies, can increase with increased ant abundance. However, plants can limit the abundance of ants by limiting the ants' nesting space within hollow thorns (Fonseca 1993, 1999). Similarly, for plant–mycorrhizal fungus mutualisms, the cost to plants of carbon loss to fungi can increase with increased abundance or colonized root length by fungi. Although the exact mechanism remains poorly understood, plants can limit mycorrhizal growth (Smith and Read 1997). Empirical studies of mutualisms with different-shaped gross benefit and cost curves are needed to test whether and when organisms do in fact have mechanisms to limit mutualist population sizes.

In conclusion, virtually all mutualisms involve both benefits and costs to each species. A fundamental question for any mutualism is how gross benefits, costs, and net effects to each mutualist vary as a function of the population size of its mutualistic partner. These functional responses, and traits associated with them, can lead to insights into the growth and limitation of populations, and their dynamics and stability resulting from mutualism. Deriving functional responses empirically, and investigating them theoretically, therefore holds great potential to reveal broad ecological and evolutionary parallels among mutualisms whose differences in natural history have, until now, obscured any similarities.

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