

A consumer–resource approach to the density-dependent population dynamics of mutualism

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Abstract. Like predation and competition, mutualism is now recognized as a consumer–resource (C–R) interaction, including, in particular, bi-directional (e.g., coral, plant–mycorrhizae) and uni-directional (e.g., ant–plant defense, plant–pollinator) C–R mutualisms. Here, we develop general theory for the density-dependent population dynamics of mutualism based on the C–R mechanism of interspecific interaction. To test the influence of C–R interactions on the dynamics and stability of bi- and uni-directional C–R mutualisms, we developed simple models that link consumer functional response of one mutualistic species with the resources supplied by another. Phase-plane analyses show that the ecological dynamics of C–R mutualisms are stable in general. Most transient behavior leads to an equilibrium of mutualistic coexistence, at which both species densities are greater than in the absence of interactions. However, due to the basic nature of C–R interactions, certain density-dependent conditions can lead to C–R dynamics characteristic of predator–prey interactions, in which one species overexploits and causes the other to go extinct. Consistent with empirical phenomena, these results suggest that the C–R interaction can provide a broad mechanism for understanding density-dependent population dynamics of mutualism. By unifying predation, competition, and mutualism under the common ecological framework of consumer–resource theory, we may also gain a better understanding of the universal features of interspecific interactions in general.

Key words: consumer–resource interaction; context dependent; density dependent; equilibrium; functional response; indirect interaction; resource supply; stability; transient behavior.

INTRODUCTION

The consumer–resource (C–R) interaction was originally incorporated into the study of interspecific interactions to provide a mechanism for the ways by which individuals interact with one another (MacArthur and Levins 1967, MacArthur 1972). C–R interactions simply relate the process of energy and/or nutrient transfer between an organism (consumer) and a resource. A resource is any biotic or abiotic factor that increases the population growth of its consumer, at least over some range of the availability or supply of the resource; consumers simultaneously change (and typically deplete) the availability or abundance of the exploited resource. Though often treated synonymously with predator–prey interactions, C–R interactions are more general and do not always imply a (+ –) outcome. For example, while predation (+ –) is a direct C–R interaction in which a consumer (predator) exploits a resource (prey), exploitation competition (– –) is an indirect C–R interaction in which two or more

consumers (competitors) exploit a shared abiotic (nutrient) or biotic (prey) resource.

Through the careful elucidation of C–R interactions, great progress has been made in the study of interspecific interactions. In particular, the density-dependent response of consumers to the supply of resources has become a central, mechanistic foundation for the study of predation and competition (Murdoch et al. 2003, Turchin 2003). For example, the study of predation has been advanced by the formulation of nonlinear functional responses; that is, the density-dependent consumption by and satiation of predators as a function of prey density (Solomon 1949, Holling 1959, Rosenzweig and MacArthur 1963). Likewise, the study of exploitative competition has been advanced by the formulation of density-dependent relationships between competitors and the supply of their shared resources (Leon and Tumpson 1975, Tilman 1982). On the other hand, mutualism lags in becoming a third pillar in the study of interspecific interactions, due in part to there being few mechanistic theories that can transcend particular study systems.

Recently, however, mutualism has begun to be considered explicitly in terms of the C–R interaction (Agrawal and Fordyce 2000, Holland et al. 2005, Ferrière et al. 2007, Chamberlain and Holland 2008,

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Holland et al. 2009), in which a consumer (mutualist) exploits a resource (e.g., nutrient, nectar, shelter) supplied by another species (mutualist) and in the process provisions that species with another resource or a non-trophic service of dispersal or defense. Nearly all mutualisms can be classified as one of three general forms of C-R interaction, namely bi-directional, uni-directional, and indirect C-R mutualisms (Holland et al. 2005). Bi-directional C-R mutualisms entail each species functioning as both a consumer and a resource (Table 1). As depicted graphically (Fig. 1a), one mutualist (M_1) consumes (in the broad sense) resources supplied by another mutualist (M_2), while the latter also consumes resources supplied by the former. Consistent with traditional views of C-R interactions, uni-directional C-R mutualisms entail one species functioning as a consumer and the other as a resource, but neither functions as both (Table 1). Resources produced by a mutualistic species (M_1) attract and reward a consumer (M_2), which, in the process of exploiting the resource, provisions the former with a service of dispersal (Fig. 1b) or defense (Fig. 1c) (Table 1). Indirect C-R mutualisms occur when the effects of the species (M_1 , M_2) on one another are mediated entirely by the density or traits of a third species that is a consumer (predator, P) or resource (R) of one or both of them (Table 1, Fig. 1d-f).

To our knowledge, theory for the density-dependent population dynamics of mutualism has not yet been formulated in terms of the consumer-resource mechanism of species interactions. In this paper, we extend the consumer-resource framework of interspecific interactions to the study of the population dynamics of bi- and uni-directional C-R mutualisms. We do not study three-species indirect C-R mutualisms further here. In developing the C-R approach to the population dynamics of mutualism, we build general models with basic formulations of the interspecific linkage between consumer functional responses of one mutualistic species and the resources supplied by another. Specifically, we used a variation on the Rosenzweig-MacArthur (1963) model of predation, one of the most basic C-R models in ecology. Our goal was general theory development, not precise or realistic tests of particular species interactions (Levins 1966), with the aim that such theory development will stimulate future studies of more realistic models of specific systems in nature.

MODEL DEVELOPMENT FOR THE DYNAMICS OF BI- AND UNI-DIRECTIONAL C-R MUTUALISMS

Any general expression for the rate of population change of a mutualistic species should include both the positive and negative effects on the rate of population change that are associated with the consumption and supply of resources. Positive effects on population change arise from the consumption of resources or the acquisition of non-trophic services. Resources include food, nutrients, or space (e.g., nectar, nitrogen, shelter),

while non-trophic services include the dispersal of oneself, one's gametes, or one's progeny (e.g., seeds, pollination) or defense from natural enemies (e.g., ants guarding plants). Negative effects on population change may arise from the provision of resources that attract and reward the mutualists with which a species interacts.

Based on the above overarching biology of mutualism, a general model for the population growth rate of a mutualistic species can then be expressed as

$$\frac{dM_i}{dt} = M_i[r_i + c_i f_i(R_j) - q_i g_i(R_i) - d_i M_i] \quad (1)$$

where M_i represents the number or biomass density of mutualistic species i . This model can be extended to mutualistic communities of n species. The first and fourth terms represent effects on population change that are separate from mutualism. The first term, $r_i M_i$, is the intrinsic population growth rate in the absence of mutualists, which can be set equal to or greater than zero for obligate and facultative species, respectively. For simplicity, we have used a quadratic function in the fourth term, $d_i M_i^2$, to modify population growth through density-dependent self-limitation. We include self-limitation as a starting point, as species often require some resource beyond those supplied by mutualists, any one of which may be limiting.

The second term, $c_i f_i(R_j)$, describes positive effects on population change of species i due to its resource consumption or service acquisition from species j . $f_i(R_j)$ is the functional response of M_i , describing how resources or services acquired by M_i vary with R_j . We denote $f_i(R_j)$ as $f_i[R_j(M_i, M_j)]$ when it is a resource of species j and as $f_i[S_j(M_i, M_j)]$ when it is a service (S) of species j , either one or both of which may vary with M_i and/or M_j . $f_i(R_j)$ has dimensions of biomass, energy, or nutrients consumed per consumer per unit of time when $f_i[R_j(M_i, M_j)]$, and is a dimensionless quantity per individual per unit of time when $f_i[S_j(M_i, M_j)]$. The third term, $q_i g_i(R_i)$, describes negative effects on population change of species i due to supplying a resource to species j . In this term $g_i(R_i)$ is more fully $g_i[R_i(M_i, M_j)]$, which describes how resource supply to species j may reduce the biomass, nutrients, or energy of species i as a function of M_i and/or M_j . In the second and third terms, c_i and q_i are conversion rates that translate f_i and g_i into numerical responses, rates of change in the number or biomass density of species i .

We now develop general, pair-wise expressions of Eq. 1 for bi-directional and uni-directional C-R mutualisms between two interacting species, M_1 and M_2 . Population-dynamic equations for bi-directional C-R mutualisms can be expressed by appropriately modifying f_i and g_i in Eq. 1 to reflect the dual nature of resource consumption and resource supply:

$$\frac{dM_1}{dt} = M_1 \{r_1 + c_1 f_1[R_2(M_1, M_2)] - q_1 g_1[R_1(M_1, M_2)] - d_1 M_1\} \quad (2)$$

TABLE 1. Examples of bi-directional, uni-directional, and indirect consumer–resource mutualisms, with M_1 and M_2 (mutualistic species) corresponding to topological models of Fig. 1.

Mutualism	Species	Consumer	Resource
Bi-directional consumer–resource mutualisms			
Lichen	fungi, algae	fungi (M_2) algae (M_1)	algal photosynthates nutrients, water
Coral	coral, zooxanthellae	coral (M_2) zooxanthellae (M_1)	algal photosynthates nutrients, nitrogen
Mycorrhizal	plant, mycorrhizal fungi	plant (M_1) mycorrhizae (M_2)	nutrient, phosphorus root exudates, carbon
Nitrogen fixation	plant, rhizobial bacteria	plant (M_1) rhizobium (M_2)	nitrogen root, exudates, carbon
Myrmecotrophy	plants, ants	plant (M_1) ant (M_2)	nitrogen in debris plant food rewards
Ant agriculture	ant, fungus	ant (M_2) fungus (M_1)	fungus ant-collected leaves
Digestive	aphid–bacteria termite, protozoa	aphid (M_1) bacteria (M_2) termite (M_1) protozoa (M_2)	amino acids aphid-ingested food protozoa-digested food termite-ingested cellulose
Uni-directional consumer–resource mutualisms			
Dispersal	plant (pollen), animal fungus (spores), beetle plant (seed), vertebrate	animal (M_2) beetle (M_2) vertebrate (M_2)	plant (M_1) nectar/pollen tissue of fungus (M_1) plant (M_1) fruit
Defense	plant (seed), ant plant, ant ant–lycaenid caterpillar ant–homopteran plant, fungal endophytes	ant (M_2) ant (M_2) ant (M_2) ant (M_2) fungi (M_2)	plant (M_1) seed elaiosome plant (M_1) nectar/food body caterpillar (M_1) secretions homopteran (M_1) excretions plant (M_1) carbon
Indirect consumer–resource mutualisms via a third species			
Müllerian mimicry	two or more mimics	mimics predator (P)	mimics (M_1, M_2)
Mixed foraging	two or more vertebrates	predator (P)	foraging species (M_1, M_2)
Honey guide	honey guide bird, badger	bird (M_1), badger (M_2)	bee larvae and honey (R)
Cleaning	cleaner fish, client fish	cleaner fish (M_2)	client (M_1) ectoparasites(P)

Notes: M_1 and M_2 represent mutualistic species 1 and 2; R and P represent a resource or predator extrinsic to the pair-wise mutualism. The table represents a broad range of consumer–resource mutualisms but is not exhaustive.

$$\frac{dM_2}{dt} = M_2[r_2 + c_2 f_2[R_1(M_1, M_2)] - q_2 g_2[R_2(M_1, M_2)] - d_2 M_2]. \tag{3}$$

These equations depict interspecific linkages of consumers and resources through $R_2(M_1, M_2)$ in f_1 and g_2 and through $R_1(M_1, M_2)$ in f_2 and g_1 . For example, plants (M_1) produce photosynthates and root exudates (R_1) that are exploited by mycorrhizal fungi (M_2), while mycorrhizae harvest a nutrient such as phosphorus (R_2) from the soil, which is supplied as a resource to plants (Table 1, Fig. 1a). Likewise, population dynamics of uni-directional C–R mutualisms can be expressed by modifying f_i and g_i in Eq. 1 to reflect uni-directional consumption and resource supply:

$$\frac{dM_1}{dt} = M_1[r_1 + c_1 f_1[S_2(M_1, M_2)] - q_1 g_1[R_1(M_1, M_2)] - d_1 M_1] \tag{4}$$

$$\frac{dM_2}{dt} = M_2[r_2 + c_2 f_2[R_1(M_1, M_2)] - d_2 M_2]. \tag{5}$$

Eqs. 4 and 5 are coupled through the interspecific linkage of $R_1(M_1, M_2)$ in f_2 and g_1 ; and, $f_1(R_2)$ in Eq. 1 is

$f_1[S_2(M_1, M_2)]$ in Eq. 4, reflecting that during the uni-directional C–R interaction, the consumer provisions the resource-supplying species with a non-trophic service (S_2) of dispersal or defense. For example, as animals (M_2) consume nectar (R_1) of plants (M_1), they pollinate the plants’ flowers (S_2) (Table 1, Fig. 1b); as ants (M_2) consume food secretions (R_1) of lycaenid larvae (M_1), they increase larval survival through defense (S_2) from parasitoids (P) (Table 1, Fig. 1c).

Uni-directional C–R mutualisms differ from bi-directional C–R mutualisms in that Eq. 5 of M_2 does not include $g_2(R_2)$; that is, a decrease in population growth from supplying a resource to M_1 . This does not imply that there are never “costs” to M_2 for provisioning a service of dispersal or defense to M_1 . Rather, it indicates that there are no apparent reductions in population growth associated with the provision of a resource. Other such costs can certainly occur, such as those imposed on ant foraging time for the defense of lycaenid larvae, but these costs would likely just modify M_2 ’s functional response (e.g., via handling time), as opposed to necessitating new model terms. Collectively, these models of bi- and uni-directional C–R mutualisms resemble predator-prey interactions with the interspe-

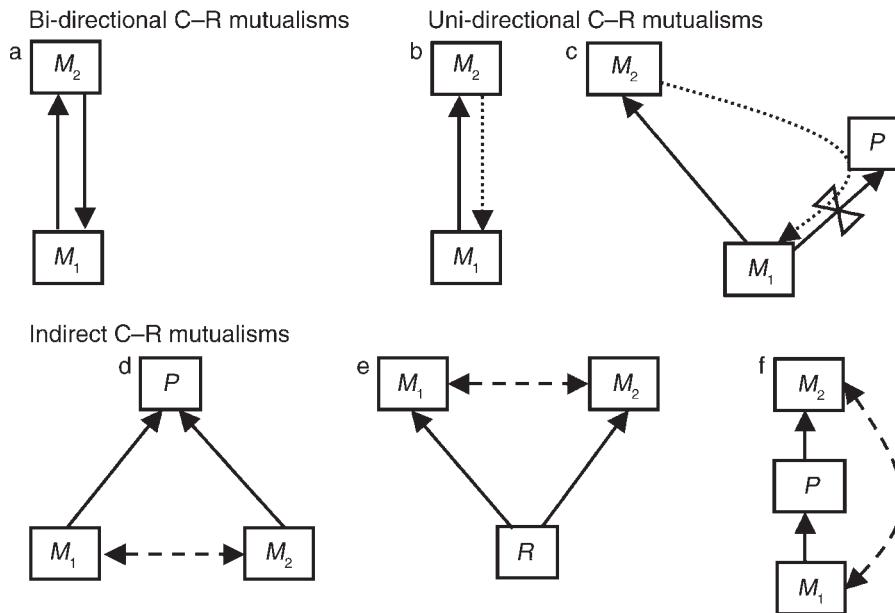


FIG. 1. Graphical models of (a) bi-directional, (b, c) uni-directional, and (d-f) indirect consumer-resource (C-R) mutualisms involving interactions between two populations, M_1 and M_2 , and in some cases a third population that is a natural enemy (P) or resource (R) of one or both of M_1 and M_2 . As with food webs, trophic levels are depicted based on energy flow, such that if M_2 is above M_1 , then it is on a higher trophic level. Solid one-directional arrows depict C-R interactions, directed from the resource to the consumer in the direction of energy flow or nutrient movement. Dotted one-directional arrows depict a non-trophic service of dispersal or defense, directed from the population providing the service to the one receiving it. Dashed two-directional arrows depict indirect C-R interactions between M_1 and M_2 . In panel (c) the joined triangles represent a rate modifier; in this case M_2 modifies the rate at which P attacks M_1 .

cific linkage of C-R interactions coupled through f_1 and g_2 and through f_2 and g_1 .

The above equations provide a modelling framework for general theory development, but quantitative analysis can only be performed when specific mathematical forms are substituted. As a first step in testing the influences of C-R interactions on the density-dependent population dynamics of mutualism, we begin with the following formulations of bi-directional and uni-directional C-R mutualisms:

$$\frac{dM_1}{dt} = M_1 \left[r_1 + c_1 \left(\frac{\alpha_{12}M_2}{h_2 + M_2} \right) - q_1 \left(\frac{\beta_1M_2}{e_1 + M_1} \right) - d_1M_1 \right] \tag{6}$$

$$\frac{dM_2}{dt} = M_2 \left[r_2 + c_2 \left(\frac{\alpha_{21}M_1}{h_1 + M_1} \right) - q_2 \left(\frac{\beta_2M_1}{e_2 + M_2} \right) - d_2M_2 \right] \tag{7}$$

and

$$\frac{dM_1}{dt} = M_1 \left[r_1 + c_1 \left(\frac{\alpha_{12}M_2}{h_2 + M_2} \right) - q_1 \left(\frac{\beta_1M_2}{e_1 + M_1} \right) - d_1M_1 \right] \tag{8}$$

$$\frac{dM_2}{dt} = M_2 \left[r_2 + c_2 \left(\frac{\alpha_{21}M_1}{h_1 + M_1} \right) - d_2M_2 \right]. \tag{9}$$

We used Eqs. 6 and 7 and Eqs. 8 and 9 as an explicit formulation of Eqs. 2 and 3 and Eqs. 4 and 5, respectively, as this model is a simple extension of the Rosenzweig-MacArthur model, an often employed and well understood model of C-R interactions in theoretical ecology. In the hyperbolic functional response, α_{ij} is the saturation level and h_j is the half-saturation density of species j . We used a similar saturating function for resource supply by species i , for which β_i is the saturation level and e_i the half-saturation constant. The functional response and resource supply of M_i saturates with M_j , which is perhaps the simplest starting assumption that can be made in the development of general C-R models of mutualism. Moreover, it is consistent with some biological examples, including for example seed/fruit consumption by larvae in pollinating seed-eating mutualisms (Holland 2002, Holland and DeAngelis 2006). Of course, this assumption may be inadequate for particular systems, but it does provide a first broad picture of what possible dynamics may be for mutualism based on C-R interactions.

PHASE-PLANE ANALYSES OF THE POPULATION DYNAMICS OF C-R MUTUALISMS

We conducted phase-plane analyses of the transient dynamics and stability properties of bi- and uni-directional C-R (consumer-resource) mutualisms through analytical and numerical solutions of Eqs. 6

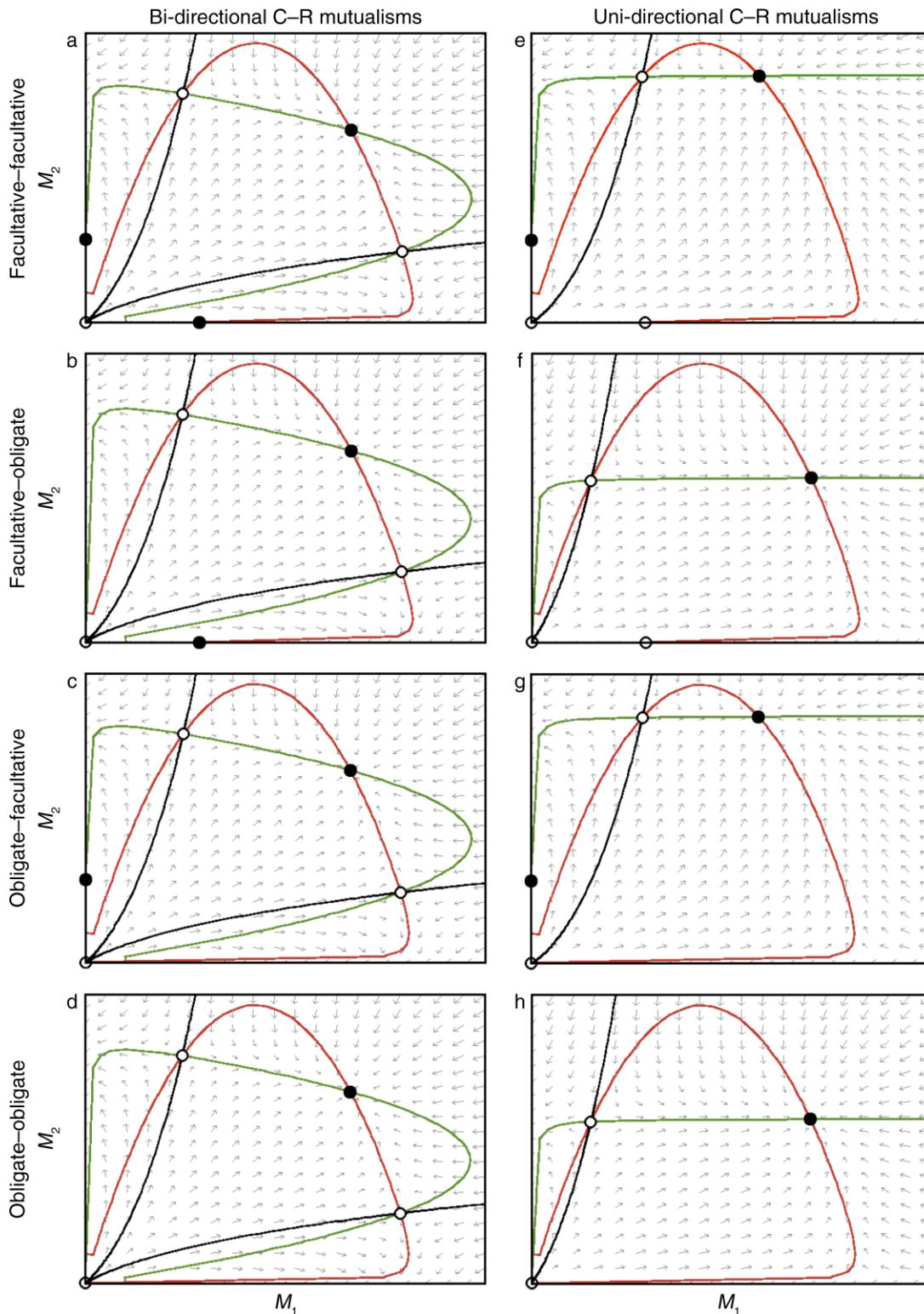


FIG. 2. Phase-plane diagrams for the population dynamics of (a–d) bi-directional and (e–h) uni-directional consumer–resource (C–R) mutualisms between facultative–facultative (a, e), facultative–obligate (b, f), obligate–facultative (c, g), and obligate–obligate (d, h) species with population densities of M_1 and M_2 , respectively. Red and green lines are zero-growth isoclines ($dM_i/dt = 0$) for M_1 and M_2 , respectively. Vector fields throughout phase-plane space are shown with pale gray arrows. Stable and unstable equilibria (nodes) are identified by solid and open circles, respectively. Saddle points have a black line (separatrix) passing through them to the origin, subdividing phase-plane space into different basins of attraction that correspond to a particular node.

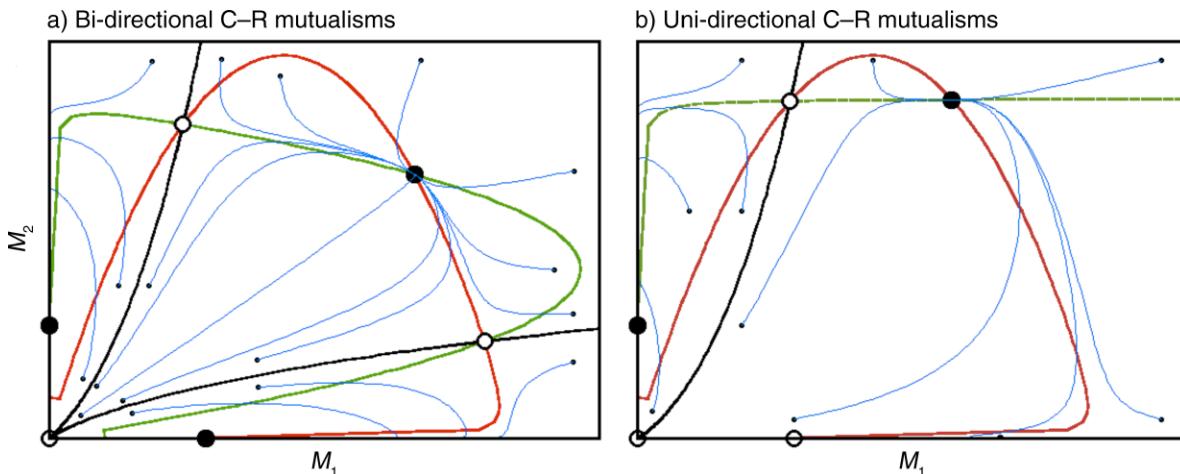


FIG. 3. Transient dynamics of some population trajectories (blue lines) in phase-plane space for facultative-facultative scenarios of the (a) bi-directional and (b) uni-directional consumer-resource (C-R) mutualisms in Fig. 2. Initial conditions for M_1 and M_2 of each trajectory are represented by solid back circles. Parameter values, zero-growth isoclines, equilibria, and separatrices are identified as in Fig. 2a, e.

and 7 and Eqs. 8 and 9 using MATLAB R2007b (MathWorks 2007) (Edelstein-Keshet 2005). We evaluated facultative-facultative (F-F), facultative-obligate (F-O), obligate-facultative (O-F), and obligate-obligate (O-O) interactions between M_1 and M_2 by setting one, both, or neither of r_1 and r_2 to 0. Results are reported for constant parameter values of c_i , q_i , d_i , h_i , and e_i , though we did test for their robustness to a wide range of values for which $f_i > g_i$.

Dynamical properties of the various facultative-obligate scenarios of bi-directional and uni-directional C-R mutualisms have some important features in common (Figs. 2 and 3). First, individually, populations grow logistically. Second, in the absence of mutualistic interactions, facultative species persist at the equilibrium density (M_i^*) of the positive node on their axis in phase-plane space, that is $M_i^* > 0$ when $M_j^* = 0$. Obligate species, on the other hand, do not persist in the absence of mutualism, as they go extinct when the density of the mutualist with which they interact is 0, that is $M_i^* \rightarrow 0$ when $M_j^* = 0$. Thus, obligate species do not have an

equilibrium state on their axis in phase-plane space that is distinct from the node of extinction at the origin. Lastly, a central stable node of mutualistic coexistence occurs in the middle to upper right of phase-plane space despite the facultative-obligate nature of interactions. At this stable equilibrium of coexistence, densities of the mutualistic species (M_1^* , M_2^*) are greater than those of each species at its respective node in the absence of mutualistic interactions. C-R interactions between M_1 and M_2 commonly lead to the central stable node of mutualistic coexistence, but, depending on the bi-directional/uni-directional and facultative/obligate nature of the C-R mutualism, a variety of dynamical properties may occur, ranging from stable and unstable nodes to saddle and spiral points (Figs. 2 and 3).

For facultative-facultative (F-F) bi-directional C-R mutualisms (Fig. 2a), six equilibria occur. (Additional equilibria may occur under certain circumstances, but they do not change the basic nature of the population dynamics, and so will not be discussed further here.) In a clockwise order, the equilibria include an unstable node

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Starting with the origin and moving clockwise, the equilibria (and parameter values) for each panel include: (a) unstable node, stable node, saddle point, stable node, saddle point, stable node ($r_1 = r_2 = 0.3$, $\alpha_{21} = \alpha_{12} = 0.6$, $q_1 = q_2 = 1.0$); (b) unstable node, saddle point, stable node, saddle point, stable node ($r_1 = 0.3$, $r_2 = 0$, $\alpha_{21} = 0.9$, $\alpha_{12} = 0.6$, $q_1 = q_2 = 1.0$); (c) unstable node, stable node, saddle point, stable node, saddle point ($r_1 = 0$, $r_2 = 0.3$, $\alpha_{21} = 0.6$, $\alpha_{12} = 0.9$, $q_1 = q_2 = 1.0$); (d) unstable node, saddle point, stable node, saddle point ($r_1 = r_2 = 0$, $\alpha_{21} = \alpha_{12} = 0.9$, $q_1 = q_2 = 1.0$); (e) unstable node, stable node, saddle point, stable node, saddle point ($r_1 = r_2 = 0.3$, $\alpha_{21} = \alpha_{12} = 0.6$, $q_1 = 1.0$, $q_2 = 0$); (f) unstable node, saddle point, stable spiral point, saddle point ($r_1 = 0.3$, $r_2 = 0$, $\alpha_{21} = \alpha_{12} = 0.6$, $q_1 = 1.0$, $q_2 = 0$); (g) unstable node, stable node, saddle point, stable node ($r_1 = 0$, $r_2 = 0.3$, $\alpha_{21} = 0.6$, $\alpha_{12} = 0.9$, $q_1 = 1.0$, $q_2 = 0$); (h) unstable node, saddle point, stable spiral point ($r_1 = r_2 = 0$, $\alpha_{21} = 0.6$, $\alpha_{12} = 0.9$, $q_1 = 1.0$, $q_2 = 0$). Other parameter values remained constant ($\beta_1 = \beta_2 = 0.2$, $c_1 = c_2 = 1.0$, $d_1 = d_2 = 0.01$, $h_1 = h_2 = 0.3$, $e_1 = e_2 = 0.3$).

Symbol key: r_i is the intrinsic population growth rate; d_i is density-dependent self-limitation; α_{ij} is the saturation level of the hyperbolic functional response, while h_j is the half-saturation density of species j ; β_j is the saturation level, and e_i the half-saturation constant of the resource supply function; c_i and q_i are conversion rates that, respectively, translate f_i and g_i into numerical responses.

at the origin; a stable node at $M_2^* > 0$, $M_1^* = 0$; a saddle point; a central, stable node of mutualistic coexistence; a saddle point; and a stable node at $M_1^* > 0$, $M_2^* = 0$. Associated with each saddle point is a separatrix that passes from the origin through the saddle point (Fig. 2a). The two separatrices subdivide phase-plane space into three basins of attraction. The larger central basin of attraction corresponds with transient dynamics that lead to the stable node of mutualistic coexistence. The two smaller peripheral basins of attraction correspond with the stable nodes on M_1 and M_2 axes (i.e., $M_i^* > 0$, $M_j^* = 0$), which lead to dynamics and outcomes more typical of predator-prey interactions.

The peripheral basins of attraction govern transient dynamics when the density of one species, M_i , is large relative to that of the other, M_j , and when the density of the latter is low. M_i overexploits and drives M_j to extinction, as the increase in M_j 's population growth rate from its functional response saturates with M_i , whereas its decrease in population growth from supplying resources to M_i does not. M_i persists at the stable node on its axis in phase-plane space in the absence of interactions with M_j ($M_i^* > 0$, $M_j^* > 0$), but at a lower density than that of the stable node of mutualistic coexistence. Overexploitation may enhance population densities of M_i in the short term, but both species attain greater densities in the long term in the absence of overexploitation. When the particular density-dependent conditions of peripheral basins of attraction dominate, population dynamics and interaction outcomes between M_1 and M_2 more closely resemble those of predator-prey (or parasite-host) relationships. For F-F cases, the overexploiting species persists in the absence of the overexploited species (Fig. 2a), but both species go to extinction for O-O cases (Fig. 2d). For F-O and O-F cases, either one mutualist species persists or both go extinct, depending on whether the obligate or facultative species is overexploiting the other (Fig. 2b, c).

Uni-directional C-R mutualisms exhibit similar dynamics and stability properties as bi-directional C-R mutualisms, but with some key differences associated with M_2 not supplying a resource to M_1 . For the F-F case (Fig. 2e), five equilibria occur, including, in a clockwise order, an unstable node at the origin; a stable node at $M_2^* > 0$, $M_1^* = 0$; a saddle point; a central, stable node of mutualistic coexistence; and a saddle point at $M_1^* > 0$, $M_2^* = 0$ (Fig. 2e). One separatrix occurs for uni-directional C-R mutualisms, which subdivides phase-plane space into two (rather than three) basins of attraction, the central basin of attraction that corresponds with the stable node of coexistence and a peripheral basin of attraction that corresponds with the stable node on M_2 's axis ($M_2^* > 0$, $M_1^* = 0$) (Fig. 2e). As with bi-directional C-R mutualisms, most transient dynamics lead to the central stable node of coexistence (Fig. 3b). A greater range of density-dependent conditions lead to the central node of coexistence for uni-

directional than bi-directional C-R mutualisms, given the lack of the second separatrix in uni-directional C-R mutualisms. Depending on the point of intersection of M_2 's zero-growth isocline with that of M_1 , the equilibrium of coexistence may be either a stable node (Fig. 2e, g) or a stable spiral point (Fig. 2f, h), though this does not depend on the facultative-obligate status of M_2 as suggested by Fig. 2. When the equilibrium is a stable spiral point, rather than an asymptotically approached stable node, population dynamics can involve cycles and damped oscillations toward the equilibrium (Edelstein-Keshet 2005).

The peripheral basin of attraction of uni-directional C-R mutualisms governs transient behavior under the same particular density-dependent conditions as those of bi-directional C-R mutualisms. In this case, overexploitation occurs when the density of M_2 is greater than M_1 , whose density is low. Unlike bi-directional C-R mutualisms, density-dependent overexploitation in uni-directional C-R mutualisms may only occur by M_2 , because M_1 cannot overexploit M_2 as M_2 does not supply resources that are exploited by M_1 . Similar population dynamics as described for F-F uni-directional C-R mutualisms occur for O-F uni-directional C-R mutualisms (Fig. 2g), although, because M_1 is obligate, it does not persist in the absence of M_2 . However, for F-O and O-O uni-directional C-R mutualisms, M_2 's overexploitation of M_1 results in both M_1 and M_2 going to extinction, as M_2 does not persist in the absence of M_1 (Fig. 2f, h). These results suggest that the facultative-obligate status of M_1 do not alter the dynamics of uni-directional C-R mutualisms like that of M_2 . Overexploitation by obligate consumers in uni-directional and bi-directional C-R mutualisms is predicted to be uncommon.

DISCUSSION

Central to advancing the study of mutualistic interactions is mechanistic theory for and empirical tests of their density-dependent population dynamics. Despite its critical shortcomings (May 1976, Holland et al. 2006), theory for the population dynamics of mutualism is still often based on phenomenological Lotka-Volterra models in which the negative signs for competition are replaced by positive signs for mutualism (e.g., Bascompte et al. 2006). Such models predict that mutualism is unstable, leading to unbounded population growth due to the endless positive feedback of linear functional responses, or stable only under limited conditions of weak, asymmetric interaction strengths (Gause and Witt 1935). We now know that mutualism is not intrinsically unstable, as predicated by Lotka-Volterra models, but we have few mechanistic theories for the population dynamics of mutualism that can guide empirical studies, and which empirical studies can validate, refute, or help refine (but see Holland et al. 2002, Stanton 2003, Thompson et al. 2006). In our present study we have taken a first step in extending the consumer-resource

(C-R) framework of predation and competition to mutualism in an effort to build a conceptual and mechanistic approach that may guide future empirical and theoretical studies. To test the influence of C-R interactions on the short-term transient dynamics and long-term stability properties of bi- and uni-directional C-R mutualisms, we built population-dynamic models that link consumer functional responses of one mutualistic species with resources supplied by another. Phase-plane analyses show that, while typically associated with predation and competition, C-R interactions can also lead to mutualism. This may seem like an empirically obvious point, but it is the first theory to show that a C-R interaction can actually enhance the population growth rates of both interacting species, and lead to a stable equilibrium of mutualistic coexistence in which both species have enhanced densities.

While models with saturating functional responses for the benefits of mutualism are an important advance over Lotka-Volterra models, showing mutualism is not inherently unstable (May 1976, Kot 2001, Holland et al. 2006), they nonetheless predict little fluctuation in the short-term population dynamics or the long-term stability of mutualistic interactions, regardless of the density dependence or obligate-facultative nature of the interacting species. In contrast, the C-R approach reveals a diverse range of population dynamics, all of which were not well recognized by prior theory of mutualism. For instance, phase-plane plots entail multiple equilibria, ranging from stable and unstable nodes to saddle points and spiral points. Associated with the separatrices of the saddle points are peripheral basins of attraction in which density-dependent overexploitation of one mutualist by another shifts C-R dynamics from mutualism to predator-prey relationships (Fig. 2). Such theoretical results predict that density-dependent C-R interactions can explain when and how mutualism transitions into parasitism, an empirical phenomenon that has largely been disjoint from theory. The results also make the novel prediction that overexploitation may be beneficial to a species in the short-term, but densities of both species are greater in the absence of overexploitation in the long term. Moreover, depending on the facultative-obligate nature of the interaction, overexploitation can lead to the extinction of one or both species. Though not thoroughly explored in the present study, the C-R approach also predicts the occurrence of population fluctuations, as seen by (weak) stable spiral points in the phase-plane plots (Fig. 2f, h). Though the oscillatory properties in the examples shown are very weak, this theoretical prediction is new and indicates that mutualisms may entail population cycles and damped oscillations. Such fluctuations are key empirical and theoretical phenomena of predation that are just being recognized of mutualism (Holland et al. 2002, McGill 2005).

Though similar in ways to the benefit-cost approach to the dynamics of mutualism (e.g., Holland and

DeAngelis 2002, Holland et al. 2002), the consumer-resource approach is different and represents a step forward for the population ecology of mutualism. The benefit-cost approach is based on many diverse currencies, depending on the system of study, some of which are intangible and lack correspondence with currencies of other mutualisms, not to mention other species interactions. The C-R approach builds on the common currency of resource intake/supply that has been so fundamental to decades of progress in the study of other species interactions. Most notably, the benefits and costs of mutualism are often simply the acquisition of resources (or services) by one mutualist and the supply of resources by another. The benefit-cost approach includes a functional response for the net benefits (gross benefits minus costs) of mutualism. The C-R approach has terms for the consumption and supply of resources, thereby distinguishing bi-directional C-R mutualisms from uni-directional C-R mutualisms that lack a $g_i(R_i)$ term for M_2 . This suggests that disparate mutualisms in nature (Table 1) may encompass similar or contrasting dynamical properties, depending on the exact nature of their C-R interactions. The benefit-cost approach has utility for studying the dynamics of particular systems, but the C-R framework is more mechanistic, leading to some of the aforementioned novel insights into population dynamics not recognized by prior theory.

Despite these insights and the potential to advance our understanding of the population ecology of mutualism, this study represents only the first of many steps needed to extend the C-R framework to mutualism. As a starting point for the development of general theory, we used formulations of $f_i(R_j)$ and $g_i(R_i)$ according to the Rosenzweig-MacArthur model of predation. Our results show some of the broad types of possible dynamics that may emerge from mutualism under the C-R approach. Of course, the specific functional formulations of the models used here may not apply well to some specific cases, and, in fact, neither these nor any other formulations of $f_i(R_j)$ and $g_i(R_i)$ will be generally appropriate for all mutualistic systems in nature. For example, it is unlikely that increasing frugivore densities will ever lead plant populations to extinction, as predicted by the models. Nevertheless, from such general theory, precise and more realistic models of such specific systems can be developed. Models of mutualisms in Table 1 should incorporate the empirically appropriate functional shapes (e.g., Types I, II, and III) of $f_i(R_j)$ and $g_i(R_i)$ and whether they are donor- or recipient-controlled.

Interplay between this general theory and empirical research is crucial. Empirical studies of mutualisms can extend methods of examining predator functional responses (Juliano 2001) to that of consumer density responses of one mutualistic species to the resources supplied by others. In particular, studies are needed that evaluate whether consumer functional responses [$f_i(R_j)$] and resource supply rates [$g_i(R_i)$] vary with M_i and/or

M_j (see Abrams and Ginzburg 2000). In general, we hope the large body of theoretical and empirical work developed for consumer–resource interactions of predation and competition will be extended to the population ecology of mutualism in an effort to provide new insights into their dynamics.

Because mutualistic interactions have often been considered to be non-trophic, mutualism has been perceived as an eccentric case of interspecific interaction with little importance to population dynamics in general. This view may stem simply from a lack of general theory and principles of mutualism that can transcend the particular natural histories of the many diverse systems in nature. To this end, we propose that the consumer–resource approach can unify the population ecology of mutualism by providing a broad mechanistic basis for understanding density-dependent population dynamics of mutualism. The C–R approach suggests that diverse mutualisms in nature may have similar or contrasting dynamics, depending on the bi- or uni-directional and the facultative/obligate nature of their interactions. More generally, because predation, competition, and mutualism can all be unified under the common ecological framework of consumer–resource theory, the various types of interspecific interactions may have more in common than previously thought. The recognition of mutualism as a C–R interaction can also aid in its theoretical and empirical inclusion into food chains and food webs, which itself will aid in advancing food-web ecology, which largely lacks multiple forms of interspecific interaction, including mutualism. Lastly, while our ecological analyses for overexploitation raise questions for the evolution of mutualism, future studies of adaptive dynamics are needed to explore the ramifications of C–R interactions for evolutionary dynamics.

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LITERATURE CITED

- Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent, or neither. *Trends in Ecology and Evolution* 15:337–341.
- Agrawal, A. A., and J. A. Fordyce. 2000. Induced indirect defence in a lycaenid–ant association: the regulation of a resource in a mutualism. *Proceedings of the Royal Society of London B* 267:1857–1861.
- Bascompte, J., P. Jordano, and J. M. Olesen. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312:431–433.
- Chamberlain, S. A., and J. N. Holland. 2008. Density-mediated, context-dependent consumer–resource interactions between ants and extrafloral nectar plants. *Ecology* 89:1364–1374.
- Edelstein-Keshet, L. 2005. *Mathematical models in biology*. Society for Industrial and Applied Mathematics (SIAM), Philadelphia, Pennsylvania, USA [Reprint of Random House edition].
- Ferrière, R., M. Gauduchon, and J. L. Bronstein. 2007. Evolution and persistence of obligate mutualists and exploiters: competition for partners and evolutionary immunization. *Ecology Letters* 10:115–126.
- Gause, G. F., and A. A. Witt. 1935. Behavior of mixed populations and the problem of natural selection. *American Naturalist* 69:596–609.
- Holland, J. N. 2002. Benefits and costs of mutualism: Demographic consequences in a pollinating seed–consumer interaction. *Proceedings of the Royal Society of London B* 269:1405–1412.
- Holland, J. N., S. A. Chamberlain, and K. Horn. 2009. Optimal defence theory predicts investment in extrafloral nectar resources in an ant–plant mutualism. *Journal of Ecology* 97:89–96.
- Holland, J. N., and D. L. DeAngelis. 2002. Ecological and evolutionary conditions for fruit abortion to regulate pollinating seed-eaters and increase plant reproduction. *Theoretical Population Biology* 61:251–263.
- Holland, J. N., and D. L. DeAngelis. 2006. Interspecific population regulation and the stability of mutualism: fruit abortion and density-dependent mortality of pollinating seed-eating insects. *Oikos* 113:563–571.
- Holland, J. N., D. L. DeAngelis, and J. L. Bronstein. 2002. Population dynamics and mutualism: functional responses of benefits and costs. *American Naturalist* 159:231–244.
- Holland, J. N., J. H. Ness, A. L. Boyle, and J. L. Bronstein. 2005. Mutualisms as consumer–resource interactions. Pages 17–33 in P. Barbosa and I. Castellanos, editors. *Ecology of predator–prey interactions*. Oxford University Press, New York, New York, USA.
- Holland, J. N., T. Okuyama, and D. L. DeAngelis. 2006. Comment on “Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance.” *Science* 313:1887.
- Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist* 91:293–320.
- Juliano, S. A. 2001. Nonlinear curve fitting: predation and functional response curves. Pages 178–196 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Oxford University Press, New York, New York, USA.
- Kot, M. 2001. *Elements of mathematical ecology*. Cambridge University Press, New York, New York, USA.
- Leon, J. A., and D. B. Tumpson. 1975. Competition between two species for two complementary or substitutable resources. *Journal of Theoretical Biology* 50:185–201.
- Levins, R. 1966. The strategy of model building in population biology. *American Scientist* 54:421–431.
- MacArthur, R. H. 1972. *Geographical ecology*. Harper and Row, New York, New York, USA.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–385.
- MathWorks. 2007. *MATLAB R2007b*. MathWorks, Natick, Massachusetts, USA.
- May, R. M. 1976. Models of two interacting populations. Pages 78–104 in R. M. May, editor. *Theoretical ecology: principles and application*. Saunders, Philadelphia, Pennsylvania, USA.
- McGill, B. 2005. A mechanistic model of a mutualism and its ecological and evolutionary dynamics. *Ecological Modelling* 187:413–425.
- Murdoch, W. M., C. J. Briggs, and R. M. Nisbet. 2003. *Consumer–resource dynamics*. Princeton University Press, Princeton, New Jersey, USA.

- Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. *American Naturalist* 97:209–223.
- Solomon, M. E. 1949. The natural control of animal populations. *Journal of Animal Ecology* 18:1–35.
- Stanton, M. L. 2003. Interacting guilds: moving beyond the pairwise perspective on mutualisms. *American Naturalist* 162:S10–S23.
- Thompson, A. R., R. M. Nisbet, and R. J. Schmitt. 2006. Dynamics of mutualist populations that are demographically open. *Journal of Animal Ecology* 75:1239–1251.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.
- Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press, Princeton, New Jersey, USA.