

LETTER

Consumer-resource theory predicts dynamic transitions between outcomes of interspecific interactions

J. Nathaniel Holland^{1*} and Donald L. DeAngelis²

¹*Department of Ecology and Evolutionary Biology, Rice University, Houston, TX 77005, USA*

²*US Geological Survey/Florida Integrated Science Center and Department of Biology, University of Miami, Coral Gables, FL 33124, USA*

*Correspondence: E-mail: jholland@rice.edu

Abstract

Interactions between two populations are often defined by their interaction outcomes; that is, the positive, neutral, or negative effects of species on one another. Yet, signs of outcomes are not absolute, but vary with the biotic and abiotic contexts of interactions. Here, we develop a general theory for transitions between outcomes based on consumer–resource (C–R) interactions in which one or both species exploit the other as a resource. Simple models of C–R interactions revealed multiple equilibria, including one for species coexistence and others for extinction of one or both species, indicating that species' densities alone could determine the fate of interactions. All possible outcomes [(+ +), (+ −), (− −), (+ 0), (− 0), (0 0)] of species coexistence emerged merely through changes in parameter values of C–R interactions, indicating that variation in C–R interactions resulting from biotic and abiotic conditions could determine shifts in outcomes. These results suggest that C–R interactions can provide a broad mechanism for understanding context- and density-dependent transitions between interaction outcomes.

Keywords

Conditionality, consumer–resource interaction, context dependent, density dependent, interaction outcome, mutual predation, mutualism, parasitism, resource supply, stability, theory.

Ecology Letters (2009) 12: 1357–1366

INTRODUCTION

Interspecific interactions affect biological processes when the actions, traits, or density of individuals of one population change some attribute (e.g., density, size, abundance, demographic rate, fitness, trait values) of another species' population. Arising from their positive (+), neutral (0), or negative (−) effects on such attributes, interspecific interactions are differentiated into six discrete forms based on the pairwise signs (+, 0, −) of their interaction outcomes, including, for example, predation/parasitism (+ −), competition (− −), mutualism (+ +) and commensalism (+ 0). Yet, interaction outcomes are not static in space or time, as depicted by an interaction grid of their pairwise signs. Instead, species interactions vary on a continuum along which the strengths and signs of interaction outcomes grade into one another (Haskell 1949; Paine 1980; Thompson 1988; Bronstein 1994, 2001; Berlow *et al.* 2004; Wootton & Emmerson 2005).

Originally proposed by Haskell (1949) and later improved upon by Bronstein (2001), the interaction compass (Fig. 1) describes continuous transitions and shifts back and forth between the six basic forms of species interaction by varying the sign of the effect of one or both species on the other. For example, intraguild predation (+ −) may transition to competition with (− −) interaction outcomes depending on the supply of the shared resources; or alternatively, to mutual predation with (− −) outcomes if the predator-prey relationship is bi-directional and detrimental to both species (Polis *et al.* 1989). Competition (− −) can become highly asymmetric and shift to amensalism with (− 0) or (0 −) outcomes, depending on which species is the superior competitor. As a final example, mutualism can transition to commensalism (+ 0) or parasitism (+ −) as one species diminishes its supply of resources to and/or overexploits the other species. This latter case of the mutualism-parasitism continuum is the foundational example from which has arisen the principle of the context dependency of species

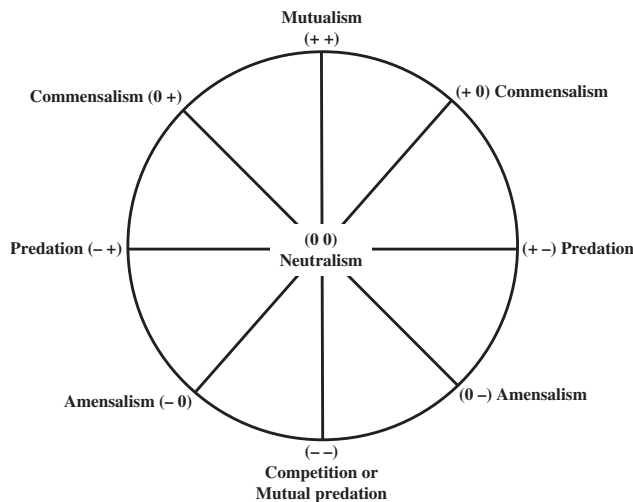


Figure 1 The interaction compass for the classification of interspecific interactions based on interaction outcomes, for which the positive (+), neutral (0), or negative (–) signs represent the effect of one species on the other. The first sign represents the effect of species *i* on species *j*, and the second sign represents the effect of species *j* on species *i*. Unlike the discrete characterization of interspecific interactions by the interaction grid, the interaction compass depicts how changes in the sign of species *i* and/or *j* reflects a continuum of transitions among the six basic forms of interspecific interaction. Interaction outcomes with (+ –) signs are termed predation here, but also includes parasitism, herbivory, and the like.

interactions (Cushman & Whitham 1989; Cushman 1991; Cushman & Addicott 1991; Bronstein 1994).

Now recognized as a key area of study for advancing population and community ecology (Agrawal *et al.* 2007), context dependency (or conditionality) refers to a change in the outcome of an interspecific interaction through a shift in the sign (+, 0, –) of one or both species due to variation in the local biotic or abiotic conditions of the community. There is a growing body of literature on the various biotic and abiotic factors that contribute to variation in the outcomes of many diverse species interactions, a few of which include the identity, behaviour, and densities of the interacting species; the age, size and stage classes of the individuals; the presence, absence, and densities of other species and exploited resources; and environmental factors such as rainfall and nutrient availability (Del-Claro & Oliveira 2000; Offenberg 2001; Daugherty & Juliano 2002; van Ommeren & Whitham 2002; Schmitt & Holbrook 2003; Westerbergh 2004; Kersch & Fonseca 2005; Callaway 2007; Heath & Tiffin 2007; Chamberlain & Holland 2008; Goldenheim *et al.* 2008; Lee *et al.* 2009). These and other studies show that species interactions may often rest somewhere between the six pure forms, and that they may grade into one another

and routinely transition back and forth between different interaction outcomes.

Important attention is being given to the evolutionary transitions between interaction outcomes (Herre *et al.* 1999; Hochberg *et al.* 2000; Sachs & Simms 2006), and specific models have been developed for the ecological transitions of particular species interactions (Johnstone & Bshary 2002; Kokko *et al.* 2003; Neuhauser & Fargione 2004), but basic theory is largely lacking for the dynamics of ecological transitions between interaction outcomes. In this study, we modelled population interactions and tested whether merely varying parameters of density-dependent consumer–resource (C–R) interactions can contribute to transitions between interaction outcomes. Although C–R interactions are usually assumed to be identical with the (+ –) outcomes of predator–prey or parasite–host relations, C–R interactions are also central to competitive and mutualistic interactions (Holland *et al.* 2005). Indeed, our results suggest that C–R interactions can provide a broad mechanistic basis for understanding context- and density-dependent transitions between different outcomes of species interactions.

CONSUMER–RESOURCE MODELS OF SHIFTS IN INTERACTION OUTCOMES

Originally integrated into the study of species interactions as a means to describe the mechanism or ways by which individuals of different species interact (MacArthur 1972), the C–R interaction has become a central principle for understanding interspecific interactions (Murdoch *et al.* 2003; Turchin 2003). Resources are biotic or abiotic factors that increase population growth of consumers over some range of the availability or supply of the resource. Resources can be entire individuals of an exploited species, such as in predator–prey interactions; a portion of exploited species, such as leaves in herbivore–plant interactions; or a food provisioned for a consumer, such as nectar in pollination mutualisms. Consumers change (and typically deplete) the availability or supply of the exploited resource. In this way, species interactions are recognized as bi-directional, uni-directional, and indirect C–R interactions. Bi-directional C–R interactions occur when each species functions as both a consumer and a resource of the other, such as mutual predation (Polis *et al.* 1989) and plant–rhizobial mutualisms (Holland *et al.* 2005). Uni-directional C–R interactions occur when one species functions as a consumer and the other as a resource, but neither functions as both. Indirect C–R interactions occur when the effects of the two species on one another are mediated entirely by the density or traits of a third species that is a consumer or resource of one or both of them. While indirect C–R interactions are important and widespread in ecological communities (Wootton 1994; Werner & Peacor 2003), we do not consider them further

here, as their dynamics and outcomes arise from three-species interactions, which goes beyond this initial study of dynamic transitions between the outcomes of two species bi- and uni-directional C–R interactions.

Equations for the population dynamics of bi-directional C–R interactions include, for each species, increases in population growth from consumer functional responses and decreases in population growth from being exploited as a resource by the other species. In this way, the population dynamics of bi-directional C–R interactions can be depicted by:

$$\frac{dN_1}{dt} = N_1[r_1 + c_1 f_1(N_1, N_2) - q_1 g_1(N_1, N_2) - d_1 N_1] \quad (1)$$

$$\frac{dN_2}{dt} = N_2[r_2 + c_2 f_2(N_1, N_2) - q_2 g_2(N_1, N_2) - d_2 N_2], \quad (2)$$

where N_i represents the number or biomass density of species i . The first term, r_i , on the right-hand side of eqns 1 and 2 represents population growth independent of interspecific interactions, which can be set equal to or greater than zero for obligate and facultative species, respectively. Specifically, when $r_i = 0$, then a positive growth rate of species i occurs only as a result of its functional response with species j , whereas when $r_i > 0$, then a positive growth rate of species i occurs in the absence of interactions with species j . The second and third terms describe the bi-directional C–R interaction. The second term, $c_j f_i(N_i, N_j)$, describes increases in the growth of species i due to its consumption of resources obtained from species j , of which $f_i(N_i, N_j)$ is the functional response for how resources acquired by N_i vary with N_j and/or N_i . The third term, $q_j g_i(N_i, N_j)$, describes decreases in population growth of species i from being consumed by or supplying resources to species j , of which $g_i(N_i, N_j)$ describes how resource consumption by species j reduces biomass or energy of species i . Coefficients c_i and q_i convert $f_i(N_i, N_j)$ and $g_i(N_i, N_j)$ into rates of numerical change in the number or biomass density of species i . Both equations for N_1 and N_2 have terms for $c_j f_i(N_i, N_j)$ and $q_j g_i(N_i, N_j)$ because each species functions as a consumer and a resource. The fourth term, $d_i N_i^2$, modifies population growth through density-dependent self-limitation.

The population dynamics of uni-directional C–R interactions can be portrayed by:

$$\frac{dN_1}{dt} = N_1[r_1 + c_1 f_1(N_1, N_2) - q_1 g_1(N_1, N_2) - d_1 N_1] \quad (3)$$

$$\frac{dN_2}{dt} = N_2[r_2 + c_2 f_2(N_1, N_2) - d_2 N_2], \quad (4)$$

where the parameters and variables are the same as in eqns 1 and 2. In this case, C–R interactions are uni-directional, with N_2 provisioning a non-trophic beneficial service of dispersal

or defense in the other direction (Holland *et al.* 2005). As defined here, uni-directional C–R interactions differ from bi-directional C–R interactions in that N_2 's population growth rate does not decrease from being exploited as a resource by N_1 .

These models entail interspecific linkage of C–R interactions coupled through f_1 and g_2 and f_2 and g_1 in bi-directional C–R interactions (eqns 1, 2) and through f_2 and g_1 in uni-directional C–R interactions (eqns 3 and 4). To test influences of C–R interactions on transitions between outcomes, we used the following specific formulations of the models:

$$\frac{dN_1}{dt} = N_1 \left[r_1 + c_1 \left(\frac{\alpha_{12} N_2}{b_2 + N_2} \right) - q_1 \left(\frac{\beta_1 N_2}{e_1 + N_1} \right) - d_1 N_1 \right] \quad (5)$$

$$\frac{dN_2}{dt} = N_2 \left[r_2 + c_2 \left(\frac{\alpha_{21} N_1}{b_1 + N_1} \right) - q_2 \left(\frac{\beta_2 N_1}{e_2 + N_2} \right) - d_2 N_2 \right] \quad (6)$$

and

$$\frac{dN_1}{dt} = N_1 \left[r_1 + c_1 \left(\frac{\alpha_{12} N_2}{b_2 + N_2} \right) - q_1 \left(\frac{\beta_1 N_2}{e_1 + N_1} \right) - d_1 N_1 \right] \quad (7)$$

$$\frac{dN_2}{dt} = N_2 \left[r_2 + c_2 \left(\frac{\alpha_{21} N_1}{b_1 + N_1} \right) - d_2 N_2 \right]. \quad (8)$$

In the hyperbolic functional response, α_{ij} is the per-capita interaction strength of species j on i (the saturation level of the functional response), and b_j is the half-saturation density of species j . We used a similar saturating function for resources exploited of species i , for which β_i is the saturation level and e_i the half-saturation constant. These formulations of bi- and uni-directional C–R interactions are a simple extension of the Rosenzweig–MacArthur model of predator–prey interactions, one of the most commonly employed C–R models in ecology.

PHASE-PLANE ANALYSES OF UNI- AND BI-DIRECTIONAL C–R INTERACTIONS

We conducted phase-plane analyses of uni- and bi-directional C–R interactions between facultative species ($r_i > 0$) through solutions of eqns 5–8 with Matlab R2007b (Mathworks Inc., Natick, MA, USA) (Edelstein-Keshet 2005). Each species has logistic growth, such that, in the absence of interactions with the other, population growth ($r_i N_i$) and self-limitation ($d_i N_i^2$) determine an equilibrium density (N_i^*) at a node along its positive axis in phase-plane space ($N_i^* > 0, N_j^* = 0$). By comparing species' densities at equilibria of coexistence ($N_i^* > 0, N_j^* > 0$) with equilibrium densities of each species in the absence of interactions with the other ($N_i^* > 0, N_j^* = 0$), we were able to assess the positive (+), neutral (0), and negative (–) effects of C–R interactions on interaction outcomes. In this way, interaction outcomes

are based on density effects of each species on the other (Abrams 1987). We tested the influence of C–R interactions on transitions between outcomes by varying the saturation levels of increases in population growth from consumer functional responses [i.e., α_{ij} in $f_i(N_i, N_j)$] and decreases in population growth from being exploited as a resource [i.e., β_i in $g_i(N_i, N_j)$]. An increase in α_{ij} increases the saturation level of the consumer functional response of species i , and hence the positive effects of species j on population growth of species i . An increase in β_i increases the magnitude of the resources of species i that can be exploited by species j , and hence decreases the population growth of species i . Aside from α_{ij} and β_i , other parameter values in this study remained largely unchanged.

Transitions between outcomes of uni-directional C–R interactions

Equations (7, 8) and (5, 6) are sufficient to explain all possible interaction outcomes for uni- and bi-directional C–R interactions. Consider uni-directional C–R interactions, for which five equilibria occurred for each phase-plane portrait regardless of the interaction outcome (Fig. 2). The equilibria, N_{ij}^* , are henceforth labelled with two subscripts, i to number the equilibrium point and j to number the species. In c order (Fig. 2), the equilibria include an unstable node at the origin ($N_{1,1}^* = 0, N_{1,2}^* = 0$); a stable node ($N_{2,1}^* = 0, N_{2,2}^* = r_2/d_2$); a saddle point ($N_{3,1}^* > 0, N_{3,2}^* > 0$); a central, stable node of species coexistence ($N_{4,1}^* > 0, N_{4,2}^* > 0$); and another saddle point ($N_{5,1}^* = r_1/d_1, N_{5,2}^* = 0$). We first describe how the interior saddle point within each phase-plane portrait can lead to shifts in outcomes without varying the C–R interaction.

Associated with the interior saddle point in each of the six phase-plane portraits is a separatrix that passes from the origin through the saddle point, subdividing phase-plane space into a central and a peripheral basin of attraction. The separatrix divides the system between the basin where trajectories lead to species coexistence at the central, stable equilibrium ($N_{4,1}^* > 0, N_{4,2}^* > 0$) and the basin where all trajectories lead to extinction of species 1 and persistence of species 2 at its carrying capacity in the absence of interactions ($N_{2,1}^* = 0, N_{2,2}^* = r_2/d_2$). As shown in the six panels of Fig. 2, there are six possible outcomes for the central, stable attractor for species coexistence ($N_{4,1}^* > 0, N_{4,2}^* > 0$), depending on the interaction parameter values (α_{ij}, β_i) of eqns 7 and 8. The first is predation (+ –) (Fig. 2a), in which the density of species 2 is increased above its carrying capacity in the absence of interspecific interactions ($N_{4,2}^* > N_{2,2}^* = r_2/d_2$) and the density of species 1 is reduced below its carrying capacity in the absence of interspecific interactions ($N_{4,1}^* < N_{5,1}^* = r_1/d_1$). The second is commensalism (+ 0) (Fig. 2b), in which the density of

species 2 is increased and species 1 remains the unchanged. The third is a mutualism (+ +) (Fig. 2c), in which the densities of both species increase above their carrying capacities in the absence of interspecific interactions. The fourth is commensalism (0 +) (Fig. 2d), in which the density of species 2 remains the same and species 1 increases above its carrying capacity in the absence of interactions. The fifth case is neutralism (0 0) (Fig. 2e), in which the densities of both species remain unchanged relative to their carrying capacities in the absence of interactions. And, the sixth case is amensalism (0 –) (Fig. 2f), in which the density of species 2 remains the same as its carrying capacity in the absence of interactions, while species 1 is reduced (Fig. 2f).

The other part of the phase-plane, the peripheral basin of attraction, has a stable attractor ($N_{2,1}^* = 0, N_{2,2}^* = r_2/d_2$) representing a predator–prey (+ –) outcome, by which N_2 overexploits and drives N_1 to extinction. A transition from the stable node of coexistence in the central basin of attraction can occur if there is a sufficiently positive fluctuation in the density of N_2 , or negative fluctuation in N_1 , or a combination of both. Thus, even without changes in the functional forms of the C–R interactions themselves, that is $f_i(N_i, N_j)$ or $g_i(N_i, N_j)$, ecological variation in the species' densities alone can lead N_2 to shift from coexisting with N_1 as a predator (Fig. 2a), commensalist (Fig. 2b), mutualist (Fig. 2c), or neutralist (Fig. 2d, e, f), to being a predator that drives N_1 extinction.

Increasing and decreasing the saturation levels of the interaction parameter values of α_{ij} in the consumer functional response [$f_i(N_i, N_j)$] or of β_i in resource supply function [$g_i(N_i, N_j)$] also lead to transitions in interaction outcomes by causing stable nodes of coexistence to shift to new equilibrium densities with different stability properties. For example, when the zero-growth isocline of N_2 asymptotes at a large value ($N_{4,2}^* = (r_2 + c_2\alpha_{21})/d_2$), such that it intersects near the peak of N_1 's isocline, but with ($N_{4,1}^* < N_{5,1}^* = r_1/d_1$), then stable predator–prey coexistence occurs with a (+ –) interaction outcome for species 2 and 1, respectively (Fig. 2a). This stable predator–prey interaction can be destabilized by increasing α_{21} to the point where the N_2 zero-growth isocline does not intersect with the N_1 zero-growth isocline (i.e., the point $N_{4,1}^* > 0, N_{4,2}^* > 0$ disappears), leading N_2 to overexploit and drive N_1 to extinction. On the other hand, decreasing α_{21} causes the N_2 zero isocline to intersect lower on the hump of the N_1 zero isocline at a larger density of N_1 . Hence, the stable node of coexistence shifts to commensalism with (+ 0) outcomes for N_2 and N_1 , respectively (Fig. 2b). A further reduction in α_{21} leads its isocline to intersect yet lower on the hump for even larger densities of N_1 , and hence a stable node of mutualistic (+ +) coexistence (Fig. 2c).

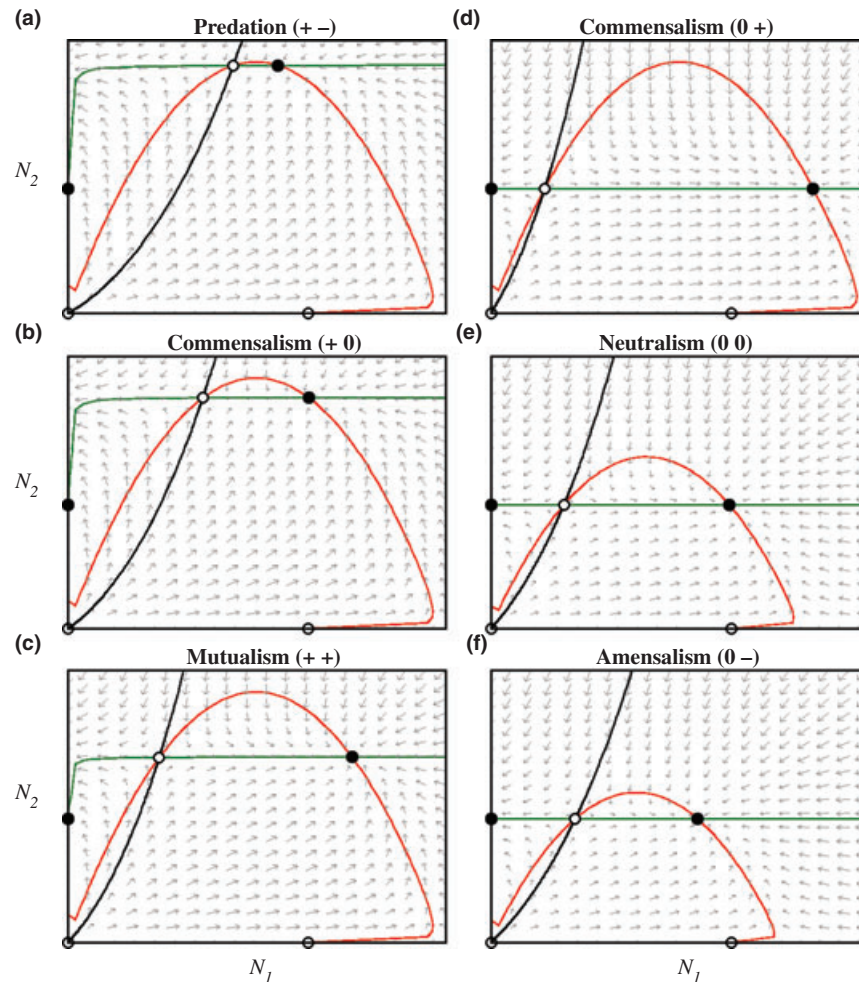


Figure 2 Phase-plane diagrams for the population dynamics of uni-directional consumer–resource interactions between two species with population densities of N_1 and N_2 . The sequence of panels shows how changes in the interaction strengths (α_{ij} , saturation level) of functional responses and saturation levels (β_i) of supplying resources lead to dynamic transitions between (a) predation (+ –) ($r_1 = 0.7$, $r_2 = 0.5$, $\alpha_{12} = 0.4$, $\alpha_{21} = 0.5$, $\beta_1 = 0.3$), (b) commensalism (+ 0) ($r_1 = 0.7$, $r_2 = 0.5$, $\alpha_{12} = 0.4$, $\alpha_{21} = 0.435$, $\beta_1 = 0.3$), (c) mutualism (+ +) ($r_1 = 0.7$, $r_2 = 0.5$, $\alpha_{12} = 0.4$, $\alpha_{21} = 0.25$, $\beta_1 = 0.3$), (d) commensalism (0 +) ($r_1 = 0.7$, $r_2 = 0.5$, $\alpha_{12} = 0.4$, $\alpha_{21} = 0$, $\beta_1 = 0.3$), (e) neutralism (0 0) ($r_1 = 0.7$, $r_2 = 0.5$, $\alpha_{12} = 0.21$, $\alpha_{21} = 0$, $\beta_1 = 0.3$), and (f) amensalism (+ –) ($r_1 = 0.7$, $r_2 = 0.5$, $\alpha_{12} = 0.15$, $\alpha_{21} = 0$, $\beta_1 = 0.3$). The red and green lines are zero-growth isoclines for N_1 and N_2 , respectively. Vector fields in phase-plane space are shown with grey arrows, which show the direction and speed (size/length of arrow) of population trajectories for particular points throughout phase-plane space. Stable and unstable nodes are identified by filled and open circles, respectively. Saddle points have a black line (separatrix) passing through them to the origin, subdividing the phase-plane space into different basins of attraction that correspond with a particular node. Starting with the origin and moving clock-wise, the equilibria for each panel are unstable node, stable node, saddle point, stable node, and a saddle point. Signs (+,0,–) of interaction outcomes are based on the effect of the interaction on equilibrium densities of the interacting species, compared to their equilibrium densities in the absence of interactions (i.e., the node on each species axis). Other parameter values remained unchanged ($c_1 = c_2 = 1.0$, $q_1 = q_2 = 1.0$, $d_1 = d_2 = 0.01$, $b_1 = b_2 = 0.3$, $e_1 = e_2 = 0.3$) and the scales of axes are fixed among panels.

Eliminating the effect of N_1 on N_2 by setting $\alpha_{21} = 0$ leads to a linear isocline for N_2 , which then intersects N_1 's isocline at densities of N_2 equal to N_2 's stable node on its axis, and for certain choices of the parameters, at ($N_{4,1}^* > r_1/d_1$, $N_{4,2}^* = r_2/d_2$). Thus, N_1 has no effect on the density of N_2 , but N_1 still increases with N_2 relative to

$N_{5,1}^* = r_1/d_1$, producing a stable commensalism with (0 +) outcomes for N_2 and N_1 , respectively (Fig. 2d). Although α_{21} cannot be reduced further, other parameters of the C–R interaction can be adjusted, such that either a stable node of neutralism (0 0) (Fig. 2e) or a stable node of amensalism (0 –) (Fig. 2f) occurs for N_2 and N_1 . We do not show the

results, but transitions in the outcomes of uni-directional C–R interactions also occur with the facultative status of N_1 . For example, as N_1 shifts from being facultative (large r_1) to nearly obligate (small r_1), its equilibrium in the absence of interactions with N_2 ($N_1^* = r_1/d_1$, $N_2^* = 0$) shifts from a high to a low density value, as obligate species do not have a node on their axis separate from that of extinction. In turn, the stable node of predator–prey (Fig. 2a) and commensalistic (Fig. 2b) coexistence can shift to one of mutualistic coexistence.

Transitions between outcomes of bi-directional C–R interactions

As with uni-directional C–R interactions, varying the parameters α_{ij} of $f_i(N_b, N_j)$ and/or β_i of $g_i(N_b, N_j)$ changed the stability properties and interaction outcomes of bi-directional C–R interactions. However, unlike the case of uni-directional C–R interactions, here the number of equilibria (along with their stability properties) varied with changes in the parameters of interspecific interactions. Most phase-plane portraits of bi-directional C–R interactions resulted in six equilibria (e.g., Fig. 3a, d, e, f), including the one with a central stable attractor with a mutualistic (+ +) outcome. In this case, the equilibria include, in clock-wise order, an unstable node at the origin ($N_{1,1}^* = 0$, $N_{1,2}^* = 0$); a stable node ($N_{2,1}^* = 0$, $N_{2,2}^* = r_2/d_2$); a saddle point ($N_{3,1}^* > 0$, $N_{3,2}^* > 0$); a central, stable node of mutualistic coexistence ($N_{4,1}^* > 0$, $N_{4,2}^* > 0$); a saddle point ($N_{5,1}^* > 0$, $N_{5,2}^* > 0$); and a stable node ($N_{6,1}^* = r_1/d_1$, $N_{6,2}^* = 0$). The separatrices associated with the saddle points split the system into three basins of attraction, a central basin of attraction and two peripheral basins of attraction (Fig. 3a), each with a different outcome: coexistence of the two species at the central, stable node of mutualistic coexistence ($N_{4,1}^* > 0$, $N_{4,2}^* > 0$), extinction of species 1 and persistence of species 2 at its carrying capacity in the absence of interactions ($N_{2,1}^* = 0$, $N_{2,2}^* = r_2/d_2$), and extinction of species 2 and persistence of species 1 at its carrying capacity in the absence of interactions ($N_1^* = r_1/d_1$, $N_2^* = 0$). The peripheral basins of attraction correspond to predator–prey interactions of (+ –) or (– +) outcomes for N_2 and N_1 , respectively. Transition from the stable node of mutualistic coexistence in the central basin of attraction can occur for the same density conditions of uni-directional C–R interactions; that is, if there is a sufficiently positive fluctuation in the density of N_b or negative fluctuation in N_j or both; in this case, however, either N_i or N_j can overexploit the other, as both species are exploited as resources by the other. As with uni-directional C–R interactions, ecological variation in species' densities alone can lead to shifts in interaction outcomes.

For stable mutualistic coexistence (+ +) to occur, the pair of parameters α_{12} and α_{21} (set to $\alpha_{12} = \alpha_{21}$ here for

convenience) of the functional response $f_i(N_b, N_j)$ must be sufficiently large relative to β_1 and β_2 (set to $\beta_1 = \beta_2$ again for convenience) of the exploited resources $g_i(N_b, N_j)$. If the pair of parameters $\alpha_{12} = \alpha_{21}$ are decreased relative to $\beta_1 = \beta_2$, then the three points ($N_{3,1}^* > 0$, $N_{3,2}^* > 0$), ($N_{4,1}^* > 0$, $N_{4,2}^* > 0$), and ($N_{5,1}^* > 0$, $N_{5,2}^* > 0$) coalesce into a single fixed point. In this case, the bi-directional C–R interaction shifts from mutualistic (+ +) coexistence (Fig. 3a) to unstable mutualism (+ +) (Fig. 3b). Four (rather than six) equilibria now occur, with the densities of N_1 and N_2 at the central equilibrium point being greater than those of the stable nodes on N_1 and N_2 axes (i.e., $N_{3,1}^* > N_{6,1}^* = r_1/d_1$, $N_{3,2}^* > N_{2,2}^* = d_2/r_2$) (Fig. 3b). While N_1 and N_2 can attain higher densities in the presence rather than absence of interactions with the other, the mutualistic effect is unstable, as the central equilibrium is a saddle point (Fig. 3b). Predator–prey dynamics ensue, in which, depending on the initial densities associated with the separatrix, either N_1 or N_2 overexploits the other and causes it to go to extinction (Fig. 3b). If we continue to reduce the $\alpha_{12} = \alpha_{21}$ parameters of functional responses relative to the $\beta_1 = \beta_2$ parameters, to the point that $\alpha_{12} = \alpha_{21} = \beta_{12} = \beta_{21}$ (e.g. to 0.30), so that $f_i(N_{k,i}^*, N_{k,j}^*) = g_i(N_{k,i}^*, N_{k,j}^*)$ (where $k = 3, 4, 5$), then this leads to the same dynamics as unstable mutualism (Fig. 3b), but in this case N_1 and N_2 at the saddle point are equal to the densities of their carrying capacities in the absence of interactions (i.e. $N_{3,1}^* = N_{6,1}^* = r_1/d_1$, $N_{3,2}^* = N_{2,2}^* = d_2/r_2$), and hence unstable neutralism (Fig. 3c). Reducing $\alpha_{12} = \alpha_{21} = \beta_1 = \beta_2$ further (e.g., to 0.15), leads to a stable node of neutralism (0 0) (Fig. 3d). The phase-plane configuration in Fig. 3d looks similar to that of the stable mutualism (Fig. 3a), but it is a stable neutral outcome rather than a stable mutualistic outcome.

Bi-directional C–R interactions can also shift to mutual (or reciprocal) predation with outcomes ranging from (+ –) to (– –) (Polis *et al.* 1989). Bi-directional C–R interactions shift to mutual predation when trophic loops are relatively weak compared to facultative growth ($r_i N_i$) and self-limitation ($d_i N_i^2$) (Fig. 3e, f). Specifically, shifts to stable mutual predation with (+ –) outcomes for N_1 and N_2 occur when $f_1(N_1, N_2) > g_1(N_1, N_2)$ and $f_2(N_1, N_2) = g_2(N_1, N_2)$ (e.g., when α_{12} is increased from its value of 0.15 in Fig. 3d to 0.26 and other parameters are kept the same) (Fig. 3e). In this case, the stable node of coexistence entails an increase in one species' density (N_1) and a decrease in the other's density (N_2), compared with their carrying capacities in the absence of interactions ($N_{4,1}^* > N_{6,1}^* = r_1/d_1$, $N_{4,2}^* < N_{2,2}^* = d_2/r_2$). Alternatively, transitions to stable mutual predation with (– –) outcomes (Fig. 3f) occur when $f_i(N_b, N_j) < g_i(N_b, N_j)$ for both species (e.g., when $\alpha_{12} = \alpha_{21} = 0.05$, $\beta_1 = \beta_2 = 0.15$). In this case, population growth of both species is reduced more as a result of their being a resource than it is increased from being a consumer

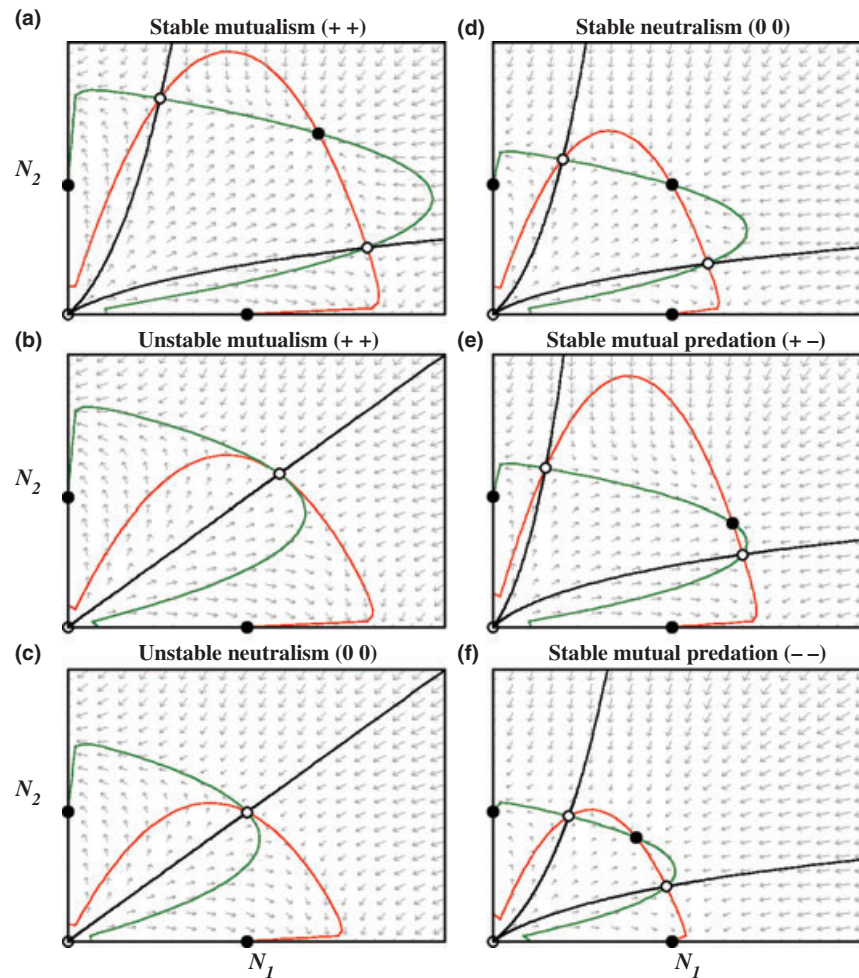


Figure 3 Phase-plane diagrams for the population dynamics of bi-directional consumer–resource interactions between two species with population densities of N_1 and N_2 . The sequence of panels shows how changes in the interaction strengths (α_{ij} , saturation level) of functional responses and saturation levels (β_i) of supplying resources can lead to dynamic transitions between (a) stable mutualism (+ +) ($\alpha_{21} = \alpha_{12} = 0.4$, $\beta_1 = \beta_2 = 0.2$), (b) unstable mutualism (+ +) ($\alpha_{21} = \alpha_{12} = 0.39$, $\beta_1 = \beta_2 = 0.3$), (c) unstable neutralism (0 0) ($\alpha_{21} = \alpha_{12} = 0.3$, $\beta_1 = \beta_2 = 0.3$), (d) stable neutralism (0 0) ($\alpha_{21} = \alpha_{12} = 0.15$, $\beta_1 = \beta_2 = 0.15$), (e) stable mutual predation with (+ –) outcomes ($\alpha_{21} = 0.15$, $\alpha_{12} = 0.26$, $\beta_1 = \beta_2 = 0.15$), and (f) stable mutual predation with (– –) outcomes ($\alpha_{21} = \alpha_{12} = 0.05$, $\beta_1 = \beta_2 = 0.15$). As in Fig. 2, red and green lines are zero-growth isoclines for N_1 and N_2 ; vector fields are denoted with grey arrows; stable and unstable equilibria are identified by filled and open circles; saddle points have a black line (separatrix) passing through them to the origin, subdividing phase-plane space into different basins of attraction; and signs (+, 0, –) of interaction outcomes are based on interaction effects on equilibrium densities of the species, compared to the equilibrium densities in the absence of interactions. Starting with the origin and moving clock-wise, the equilibria for panels (a), (d), (e), and (f) are unstable node, stable node, saddle point, stable node, saddle point, stable node, and for panels (b) and (c) are unstable node, stable node, saddle point, stable node. Other parameter values remained constant ($r_1 = r_2 = 0.5$, $c_1 = c_2 = 1.0$, $q_1 = q_2 = 1.0$, $d_1 = d_2 = 0.01$, $b_1 = b_2 = 0.3$, $e_1 = e_2 = 0.3$) and the scales of axes are fixed among panels.

of the other. The stable node of coexistence entails a decrease in the density of both species compared with their densities in the absence of interactions ($N_{4,1}^* < N_{6,1}^* = r_1/d_1$, $N_{4,2}^* < N_{2,2}^* = d_2/r_2$) (Fig. 3f). Consistent with decreasing functional responses and increasing exploited resources, the area under the isoclines in which $dN/dt > 0$ becomes smaller as outcomes shift from mutualism to mutual predation (compare Fig. 3a–f).

DISCUSSION

With growing appreciation of the context dependency of species interactions in nature (Bronstein 1994; Agrawal *et al.* 2007), it is ever more essential to develop theory for dynamic transitions between outcomes of interspecific interactions. For good reasons, species interactions with different outcomes have been studied with models of

contrasting structure and underlying biological principles. As such, population dynamic models of species interactions have been understandably poor in describing transitions in interaction outcomes. In this study, we modified an underlying biological principle inherent to most species interactions, namely the C–R interaction, to build general population dynamic models of two species interactions. We incorporated interspecific linkages between increases in population growth from consumer functional responses and decreases in population growth from being exploited as a resource. Using phase-plane analyses, we tested whether shifts in interaction outcomes could be predicted by changes in the saturation levels of the consumer functional responses [i.e., α_{ij} in $f_i(N_b, N_j)$] and resource supply functions [i.e., β_i of $g_i(N_b, N_j)$]. Analyses show that, without altering the structure of the models, the C–R interaction can provide a broad mechanism for understanding transitions back and forth between pure forms of predation/parasitism (+ –), mutual predation [(+ –) or (– –)], mutualism (+ +), commensalism (+ 0), neutralism (0 0), and amensalism (0 –).

Transitions between interaction outcomes arose from two general processes associated with the C–R mechanism of interspecific interaction. First, species interactions transitioned to different outcomes simply through fluctuations in the densities of the interacting species that pushed the system into a new basin of attraction. Specifically, phase-plane topologies included central basins of attraction in which interaction outcomes of a variety of forms of species coexistence (e.g., predation, mutualism, amensalism, commensalism, mutual predation) were stable. Peripheral basins of attraction also occurred in which these stable outcomes of coexistence shifted to pure predator-prey interactions (Figs 2, 3). Due to the basic nature of C–R interactions, when the densities of the interacting species are perturbed into certain zones in the phase-plane, such that one species is very abundant and compared with the other that is relatively rare, then the former overexploits and drives the latter to extinction. In this way, ecological perturbations that results in such changes in the relative densities of the interacting species can in turn alter their interaction outcomes. Thus, without changing the nature of the C–R interaction itself [i.e., without altering the interaction parameters in the consumer functional response, $f_i(N_b, N_j)$, or the resource supply function $g_i(N_b, N_j)$], fluctuations in species' densities alone may often account for shifts in the outcomes of species interactions.

Second, transitions between interaction outcomes arose from changes in the saturation levels of consumer functional responses [i.e., α_{ij} in $f_i(N_b, N_j)$] and/or resource supply functions [i.e., β_i of $g_i(N_b, N_j)$], which shifted the equilibrium points themselves to densities with different stability properties and interaction outcomes. Without altering the overall structure or biological principles of the models, merely changing the strengths of density-dependent C–R

interactions resulted in the equilibria of species coexistence transitioning between predation, commensalism, mutualism, neutralism, amensalism and mutual predation. Context-dependent interaction outcomes in nature may commonly arise from biotic and abiotic conditions that alter the strengths of the density dependence of the C–R interactions that are inherent to most species interactions. Yet, some changes in α_{ij} of $f_i(N_b, N_j)$ and β_i of $g_i(N_b, N_j)$ can just strengthen or weaken a particular outcome of coexistence, without shifting its signs. Though variance occurs around mean outcomes, and interaction strengths can vary from weak to strong (Berlow *et al.* 2004), context dependency does not occur unless there is a change in the signs of the outcomes resulting from the C–R interactions. While it is well-recognized that discrete interaction outcomes vary along a continuum of interaction strengths (Paine 1980; Berlow *et al.* 2004; Wootton & Emmerson 2005), these results demonstrate how the signs of interaction outcomes may vary with interaction strengths.

Take as an example of transitions between the outcomes of C–R interactions pollinating seed-eating interactions between yucca and yucca moths and senita cacti and senita moths (Holland & DeAngelis 2002, 2006; Holland *et al.* 2004). Adult insects lay eggs in flowers they pollinate, from which larvae that consume the seeds and fruit develop. First, outcomes can shift via fluctuations in the densities of moths to flowers. If pollinators become abundant relative to flowers, then enough eggs can be laid that larval seed consumption (plant resource supply function) outweighs the reproductive functional response of plants, which can shift the interaction from mutualism to parasitism. Second, changes in the relative magnitudes of α_{ij} of $f_i(N_b, N_j)$ and β_i of $g_i(N_b, N_j)$ for the plants may shift the strength and outcome of interactions. For example, short-term environmental conditions may favour larval survival, thereby reducing the discrepancy between the pollination functional response and the seed consumption functional response [resource supply (seeds, fruit) function]. This will reduce the strength of the mutualism and/or shift it to parasitism depending upon the relative magnitudes of $f_i(N_b, N_j)$ and $g_i(N_b, N_j)$. While the theory goes well beyond this example, it is in need of empirical and theoretical exploration, especially in the context of specific study systems. Carefully controlled experiments and survey's of natural populations will be useful for evaluating how and when interaction strengths and outcomes vary with $f_i(N_b, N_j)$ and $g_i(N_b, N_j)$.

In this study, we have shown that variation in C–R interactions can provide a general means for understanding dynamic transitions between interaction outcomes. While this is to our knowledge one of the first mechanistic theories for variation in interaction outcomes, a few other theoretical studies are yielding similar results. For example, in a series of thoughtful analyses, Hernandez 1998, 2008; (Hernandez &

Barradas 2003) explicitly examined transitions in interaction outcomes by replacing static interaction coefficients in Lotka-Volterra models with nonlinear density-dependent interaction functions which span the range of positive to negative values (see also Zhang 2003; Zhang *et al.* 2007). The results of her theoretical studies led to conclusions similar to ours, with the exception that the underlying biological mechanism for the density-dependent interaction functions, and hence the transitions between interaction outcomes, was largely absent. We have tried to take a step forward in this direction by incorporating the biological principle of variation in C–R interactions. Our results entail greater variation in the shapes of the zero-growth isoclines, along with dynamical properties of species interactions.

Despite well-recognized variation in species interactions (Thompson 1988), few theories explain transitions in their interaction outcomes. As C–R interactions are universal to nearly all species interactions, we suggest that variation in the outcomes of species interactions may be more fully understood by studying bi- and uni-directional linkages between consumer functional responses and the exploited resources. Our results are consistent with interspecific interactions lying along a continuum of outcomes, as depicted by the interaction compass (Fig. 1), which under changing contexts of local biotic and abiotic conditions, may phase from one to another (Figs 2, 3). Of course, one may ask whether interspecific interactions with particular outcomes are distinct and happen to share the C–R mechanism of interaction, or alternatively, whether they are simply different forms of the C–R interaction differing in their outcome. Though semantic to some extent, having a clear hierarchical basis for understanding the patterns and processes of interest can influence how we perceive and study them. Thus, pure forms of species interaction may share more in common with one another than previously thought, and consequently, the study of interspecific interactions may greatly benefit from focusing on their similarities, rather than discrepancies associated different interaction outcomes. In either case, this study suggests that the C–R interaction is a general mechanism of interspecific interaction, from which we can gain a better understanding of the universal features of interspecific interactions, and in turn the context- and density-dependent transitions between pure forms of interaction outcome.

ACKNOWLEDGEMENTS

We thank J.L. Bronstein, A.E. Dunham, V.H.W. Rudolf, E. Siemann, and three anonymous referees for discussion of this study and/or comments on an earlier version of the manuscript. The work was supported by National Science Foundation grant DEB-081423. DLD also acknowledges support of the U.S.G.S. Florida Integrated Science Centres.

REFERENCES

- Abrams, P.A. (1987). On classifying interactions between populations. *Oecologia*, 73, 272–281.
- Agrawal, A.A., Ackerly, D.D., Adler, F., Arnold, A.E., Cáceres, C., Doak, D.F. *et al.* (2007). Filling key gaps in population and community ecology. *Front. Ecol. Environ.*, 5, 145–152.
- Berlow, E.L., Neutel, A.-M., Cohen, J.E., de Ruiter, P.C., Ebenman, B., Emmerson, E. *et al.* (2004). Interaction strengths in food webs: issues and opportunities. *J. Anim. Ecol.*, 73, 585–598.
- Bronstein, J.L. (1994). Conditional outcomes in mutualistic interactions. *Trends Ecol. Evol.*, 9, 214–217.
- Bronstein, J.L. (2001). Mutualisms. In: *Evolutionary Ecology* (eds Fox, C., Fairbairn, D. & Roff, D.). Oxford University Press, New York, pp. 315–330.
- Callaway, R.M. (2007). *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht, Netherlands.
- Chamberlain, S.A. & Holland, J.N. (2008). Density-mediated, context-dependent consumer-resource interactions between ants and extrafloral nectar plants. *Ecology*, 89, 1364–1374.
- Cushman, J.H. (1991). Host–plant mediation of insect mutualisms: variable outcomes in herbivore–ant interactions. *Oikos*, 61, 138–143.
- Cushman, J.H. & Addicott, J.F. (1991). Conditional interactions in ant–plant–herbivore mutualisms. In: *Ant–Plant Interactions* (eds Huxley, C.R. & Cutler, D.F.). Oxford University Press, Oxford, pp. 92–103.
- Cushman, J.H. & Whitham, T.G. (1989). Conditional mutualism in a membracid–ant association: temporal, age-specific, and density-dependent effects. *Ecology*, 70, 1040–1047.
- Daugherty, M.P. & Juliano, S.A. (2002). Testing for context-dependence in a processing chain interaction among detritus-feeding aquatic insects. *Ecol. Entomol.*, 27, 541–553.
- Del-Claro, K. & Oliveira, P.S. (2000). Conditional outcomes in a neotropical treehopper–ant association: temporal and species-specific variation in ant protection and homopteran fecundity. *Oecologia*, 124, 156–165.
- Edelstein-Keshet, L. (2005). *Mathematical Models in Biology*. Society for Industrial and Applied Mathematics (SIAM), Philadelphia (reprinting of Random House edition).
- Goldenheim, W.M., Irving, A.D. & Bertness, M.D. (2008). Switching from negative to positive density-dependence among populations of a cobble beach plant. *Oecologia*, 158, 473–483.
- Haskell, E.F. (1949). A clarification of social science. *Main Curr. Mod. Thought*, 7, 45–51.
- Heath, K.D. & Tiffin, P. (2007). Context dependence in the coevolution of plant and rhizobial mutualists. *Proc. Roy. Soc. B-Biol. Sci.*, 274, 1905–1912.
- Hernandez, M.-J. (1998). Dynamics of transitions between population interactions: a nonlinear interaction α -function defined. *Proc. R. Soc. Lond. B*, 265, 1433–1440.
- Hernandez, M.-J. (2008). Spatiotemporal dynamics in variable population interactions with density-dependent interaction coefficients. *Ecol. Model.*, 214, 3–16.
- Hernandez, M.-J. & Barradas, I. (2003). Variation in the outcome of population interactions: bifurcations and catastrophes. *J. Math. Biol.*, 46, 571–594.
- Herre, E.A., Knowlton, N., Mueller, U.G. & Rehner, S.A. (1999). The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends Ecol. Evol.*, 14, 49–53.

- Hochberg, M.E., Gomulkiewicz, R., Holt, R.D. & Thompson, J.N. (2000). Weak sinks could cradle mutualistic symbioses – strong sources should harbour parasitic symbioses. *J. Evol. Biol.*, 13, 213–222.
- Holland, J.N. & DeAngelis, D.L. (2002). Ecological and evolutionary conditions for fruit abortion to regulate pollinating seed-eaters and increase plant reproduction. *Theor. Pop. Biol.*, 61, 251–263.
- Holland, J.N. & DeAngelis, D.L. (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., DeAngelis, D.L. & Schultz, S.T. (2004). Evolutionary stability of mutualism: interspecific population regulation as an evolutionarily stable strategy. *Proc. R. Soc. Lond. B*, 271, 1807–1814.
- Holland, J.N., Ness, J.H., Boyle, A.L. & Bronstein, J.L. (2005). Mutualisms as consumer–resource interactions. In: *Ecology of Predator–Prey Interactions* (eds Barbosa, P. & Castellanos, I.). Oxford University Press, New York, pp. 17–33.
- Johnstone, R.A. & Bshary, R. (2002). From parasitism to mutualism: partner control in asymmetric interactions. *Ecol. Lett.*, 5, 634–639.
- Kersch, M.F. & Fonseca, C.R. (2005). Abiotic factors and the conditional outcome of an ant–plant mutualism. *Ecology*, 86, 2117–2126.
- Kokko, H., Mappes, J. & Lindstrom, L. (2003). Alternative prey can change model-mimic dynamics between parasitism and mutualism. *Ecol. Lett.*, 6, 1068–1076.
- Lee, J.H., Kim, T.W. & Choe, J.C. (2009). Commensalism or mutualism: conditional outcomes in a branchiobdellid–crayfish symbiosis. *Oecologia*, 159, 217–224.
- MacArthur, R.H. (1972). *Geographical Ecology*. Harper and Row, New York, NY.
- Murdoch, W.M., Briggs, C.J. & Nisbet, R.M. (2003). *Consumer–Resource Dynamics*. Princeton University Press, Princeton, NJ.
- Neuhauser, C. & Fargione, J.E. (2004). A mutualism–parasitism model and its application to plant–mycorrhizae interactions. *Ecol. Model.*, 177, 337–352.
- Offenberg, J. (2001). Balancing between mutualism and exploitation: the symbiotic interaction between *Lasius* ants and aphids. *Behav. Ecol. Sociobiol.*, 49, 304–310.
- van Ommeren, R.J. & Whitham, T.G. (2002). Changes in interactions between juniper and mistletoe mediated by shared avian frugivores: parasitism to potential mutualism. *Oecologia*, 130, 281–288.
- Paine, R.T. (1980). Food webs: linkage, interaction strength, and community infrastructure. *J. Anim. Ecol.*, 49, 667–685.
- Polis, G.A., Myers, C.A. & Holt, R.D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Ann. Rev. Ecol. Syst.*, 20, 297–330.
- Sachs, J.L. & Simms, E.L. (2006). Pathways to mutualism breakdown. *Trends Ecol. Evol.*, 21, 585–592.
- Schmitt, R.J. & Holbrook, S.J. (2003). Mutualism can mediate competition and promote coexistence. *Ecol. Lett.*, 6, 898–902.
- Thompson, J.N. (1988). Variation in interspecific interactions. *Annu. Rev. Ecol. Syst.*, 19, 65–87.
- Turchin, P. (2003). *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton, USA.
- Werner, E.E. & Peacor, S.D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100.
- Westerbergh, A. (2004). An interaction between a specialized seed predator moth its host plant shifting from parasitism to mutualism. *Oikos*, 105, 564–574.
- Wootton, J.T. (1994). The nature and consequences of indirect effects in ecological communities. *Ann. Rev. Ecol. Syst.*, 25, 443–466.
- Wootton, J.T. & Emmerson, M. (2005). Measurement of interaction strength in nature. *Ann. Rev. Ecol. Syst.*, 36, 419–444.
- Zhang, Z. (2003). Mutualism or cooperation among competitors promotes coexistence and competitive ability. *Ecol. Model.*, 164, 271–282.
- Zhang, B., Zhang, Z., Li, Z. & Tao, Y. (2007). Stability analysis of a two-species model with transitions between population interactions. *J. Theor. Biol.*, 248, 145–153.

Editor, Ferenc Jordan

Manuscript received 29 June 2009

First decision made 6 August 2009

Second decision made 27 August 2009

Manuscript accepted 29 August 2009