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interaction α -function defined**

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Dynamics of transitions between population interactions: a nonlinear interaction α -function defined

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In nature, two populations may interact in different ways during their lifetime, and even undergo transitions from one type of interaction to another. A model for the dynamics of these transitions has been developed in this study. The interaction coefficients α_{ij} in the Lotka–Volterra equations are re-interpreted as nonlinear functions of population densities N_i , N_j , modulated by environmental parameters, which offers the possibility of a change in sign. Transitions can take place owing to variations in population density (endogenous effect), or in the environmental parameters (exogenous effect). Models for both facultative and obligate associations are examined. Graphical stability analyses show that multiple density equilibria are possible, accounting for the occurrence of the transitions.

Keywords: population interactions; variable interaction coefficients; transitions between interactions; conditional interactions; symbiosis; Lotka–Volterra models

1. INTRODUCTION

Biological examples of the different symbiotic interactions that have been described for two or more populations are frequently reported in the literature (e.g. mutualism, competition, parasitism, etc.). Very rarely, though, we read about populations showing one kind of interaction at one moment of time—or space—and then switching to another; that is, undergoing transitions between different interactions. But in nature this occurs often.

Associations between some ant and aphid species can be beneficial at low aphid densities, but either detrimental or just neutral as this density increases; the interaction depends also on other external conditions (Addicott 1979; Cushman & Addicott 1991).

Wahl & Hay's (1995) study of epibiotic associations between host seaweed and some plant and animal epibionts showed that associations included both positive and negative effects. The outcome, 'associated resistance' or 'shared doom', was highly influenced by the relative densities of the species involved.

Phillips *et al.* (1995) reported that seaweed flies, *Coelopa frigida* and *C. pilipes*, can interact either as competitors or as amensalists; in addition, the direction of the amensalism depends upon environmental conditions. Hodge & Arthur (1997) described how according to the resource presented to these fly populations the interaction can either be (+, –) or (0, –).

At low densities, interactions between Mullerian mimics are mutualistic as they facilitate the training of predators in recognizing unpalatable prey. At higher densities they become competitors because they share resources (Gilbert 1983).

Thompson (1988) presents a comprehensive review on the subject. He focuses on the variation in the outcome of interactions depending on individual traits—rather than population attributes—and on environmental gradients. Bronstein (1994) regards interactions as 'occupying potentially dynamic positions along a continuum of possible outcomes', set by the balance of costs and benefits for each partner.

Although some experimental work has been done on the occurrence of these transitions, and plenty of discussion has followed about the inadequacy of the static classification of interactions, there is a lack of theoretical work to represent and understand this phenomenon.

Many models for the interactions of populations exist in the literature, mostly based on modified Lotka–Volterra equations (for reviews, see Gillman & Hails (1997) and May (1981)). Although most of the models are concerned mainly with only one type of association, those by Addicott (1981) and Wolin & Lawlor (1984) consider variation in the outcome of the interaction. Addicott compared three different mutualistic models, one of which was suggested by his work with the aphid–ant mutualism mentioned above. He studied stability properties after perturbations to equilibrium, in terms of return time and persistence. Wolin & Lawlor explored density-dependent effects in mutualistic interactions. One of their models, also connected to Addicott's work, considers that the mutualistic benefit decreases linearly with the

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recipient density, so that at high densities the partner behaves as a competitor or a parasite.

In this paper, a model is developed to study the stability properties of two-species systems that can undergo transitions between different population interactions. The model shows that the system can have multiple stable equilibria, and that under certain conditions these correspond to different types of interactions.

It is important to recognize two distinct approaches to the problem. First, there is a situation in which the interacting populations can coexist under one type of interaction or another, in the same environment. This is an ‘endogenous effect’, as the transition between interactions is driven by intrinsic features of the biological system. On the other hand, one can think of interacting populations that coexist under one form of interaction or another, depending on a specific environment. This is an ‘exogenous effect’, as the difference is imposed by an extrinsic factor.

2. THE BASIC MODEL

In the mathematical representation, transitions between all kinds of population interactions must be allowed to take place. Hence, the model must comply with being general and comprehensive. A Lotka–Volterra system of equations is used as a basic starting point. In a general sense, for a two-species interaction this can be expressed by a system of two equations of the form:

$$\frac{dN_i}{dt} = r_i N_i \left[1 - \frac{N_i}{K_i} + \alpha_{ij} \frac{N_j}{K_i} \right], \quad (1)$$

where $i, j=1, 2$ for $i \neq j$; r_i , N_i and K_i are the intrinsic rate of increase, population density and carrying capacity of species i , respectively; N_j is the population density of species j ; and α_{ij} is the interaction coefficient between species i and j . In the rest of the paper, species $i, j, 1$ and 2 will be referred to as sp_i , sp_j , sp_1 , and sp_2 , respectively. Some classical forms of the models for two interacting populations are represented by this system of equations depending on the signs of α_{ij} and α_{ji} , namely: competition, if both are negative; mutualism, if both are positive; and a victim–exploiter interaction, if one is positive and the other is negative. This last interaction includes all herbivory, predator–prey and parasite–host relationships. In this paper I will be referring to these as ‘parasitism’ in general.

According to equation (1), if sp_j is absent, then sp_i reaches the equilibrium value K_i from any initial density, and persists. This means two things. First, the interaction with sp_j is ‘facultative’; that is, sp_i can exist with or without being associated to sp_j . Second, density-dependent mechanisms govern the dynamics of the sp_i when being alone.

However, it is well known that some symbionts are biologically incapable of existing without a partner, be it a mutualist, a parasite or a predator. In this case the interaction is ‘obligate’. If sp_i cannot persist alone, then N_i is expected to decrease exponentially down to zero if sp_j is no longer present. To account for this situation, equation (1) is modified to:

$$\frac{dN_i}{dt} = r_i N_i [-1 + \alpha_{ij} N_j]. \quad (2)$$

Both facultative and obligate interactions will be considered in the analysis of the model as they correspond to essentially different biological phenomena.

3. DEFINITION OF AN α -FUNCTION

I now introduce the concept of an interaction α -function. In the classical model the parameter α_{ij} (as in equations (1) and (2)) actually measures what an individual of sp_j is worth to an individual of sp_i . Expressed differently, α_{ij} measures how many sp_j individuals (either an integer or a fractional number) make one sp_i individual in terms of its performance in the interaction. When this value is constant, it means that any new individual of sp_j which joins the system is worth the same to sp_i individuals as any one of those who were already in. But this might not always be so. Rather, let us say that α_{ij} is not constant but a nonlinear function of, in the widest terms, both population densities N_i and N_j , and of some environmental parameters (biotic and abiotic). That is, $\alpha_{ij} \equiv \alpha_{ij}(N_i, N_j; b_i, c_i, d_i)$. A very important feature is that α_{ij} can change sign. This allows the transitions to take place. Let us define the particular α -functions that will be used in the forthcoming analysis.

(a) The ‘ $\alpha(+)$ ’ α -function

Consider a symbiotic relationship that is beneficial to sp_i at low sp_j densities but detrimental when N_j is high. The values for α_{ij} are described by an α -function that grows positively with N_j —from zero or from a threshold value—up to a maximum, then declines down to $\alpha_{ij}=0$, meaning that the positive and negative effects of sp_j on sp_i compensate. Then, as N_j grows further, α_{ij} take negative values levelling asymptotically. A general formula to obtain this behaviour is:

$$\alpha_{ij} = \frac{b_i N_j - c_i N_j^2}{1 + d_i N_j^2}. \quad (3)$$

This is illustrated in figure 1a. The parameters b_i , c_i and d_i modify the general shape (the intensity of change and threshold values) and represent the environmental influence on α_{ij} , that is, the ‘exogenous effect’. The fundamental shape and the dependence on N_j portray the effect of the ‘endogenous’ element.

(b) The ‘ $\alpha(-)$ ’ α -function

Now suppose that the effect of sp_j on sp_i is always negative but with an asymptotically decreasing intensity as N_j increases. There is no change in sign involved, but a nonlinear α -function imposes. In this case, the appropriate formula is:

$$\alpha_{ij} = -\frac{g_i N_j}{1 + h_i N_j}. \quad (4)$$

The general shape is depicted in figure 1b. The parameters, g_i and h_i , represent the environmental effect.

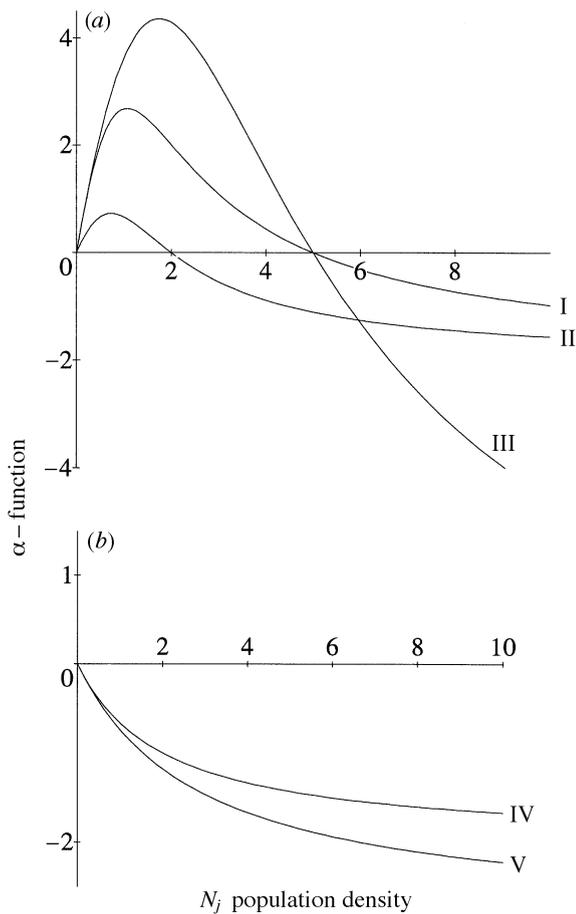


Figure 1. α -functions used in the model. (a) The $\alpha(+ -)$ function. Parameters b_i, c_i, d_i : [I] = (5, 1, 0.5); [II] = (2, 1, 0.5); [III] = (5, 1, 0.1). (b) The $\alpha(-)$ function. Parameters g_i, h_i : [IV] = (1, 0.5); [V] = (1, 0.35).

4. STABILITY ANALYSIS

The models to be analysed here are finally obtained by substituting the α_{ij} parameters in equations (1) and (2) by the α -functions defined in equations (3) and (4). Many combinations are possible: the associations can be facultative or obligate for both populations, or just one of each kind. With a facultative interaction, any sort of α -function, $\alpha(+ -)$ or $\alpha(-)$, can be expected; but in an obligate interaction only an $\alpha(+ -)$ type has biological meaning. Each combination represents a different biological situation, but all pertain to the phenomenon of transitions between interactions.

Four particular situations will be explored. The stability analysis will be presented with explicit details for the first case. This provides an outline of reasoning for the other cases, which will be dealt with in a more concise manner.

Stability properties are studied mainly with graphical analysis, which offers the attractive possibility of visualizing global solutions. These results are supported with local stability analysis at equilibria, which gives more accurate answers. The interpretation and applicability of these results on ecological grounds follows in § 5.

(a) Case I. Both facultative; both $\alpha(+ -)$ functions

Consider an interaction where both α -functions are of the $\alpha(+ -)$ type. Then, at low densities the association is mutualistic, but at higher densities it is competitive. Depending on the threshold values where α_{12} and α_{21} are equal to zero, there might be intermediate density values where a parasitic interaction can also occur. If we assume that both species can exist either alone or in association, then the appropriate model to represent this situation is, from equations (1) and (3):

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} + \left(\frac{b_1 N_2 - c_1 N_2^2}{1 + d_1 N_2^2} \right) \frac{N_2}{K_1} \right],$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} + \left(\frac{b_2 N_1 - c_2 N_1^2}{1 + d_2 N_1^2} \right) \frac{N_1}{K_2} \right].$$

Figure 2 shows the graphical analysis. In an N_1, N_2 phase space graph, the nullclines for each equation in the system are plotted. These are the isoclines corresponding to density values at which there is no population growth ($dN_i/dt=0$). Thus, the intersection points correspond to equilibrium values of the system. These are referred to as $\mathbf{X}^* = (N_1^*, N_2^*)$. If multiple equilibria exist these are labelled \mathbf{X}^* , \mathbf{Y}^* and \mathbf{Z}^* . Only non-negative solutions are discussed.

Figure 2a displays the situation where the α -function parameters b_i, c_i, d_i and K_i are identical for both species. For this particular set there are multiple equilibria. The vector field indicates that \mathbf{X}^* and \mathbf{Y}^* are stable, and \mathbf{Z}^* is unstable. This is confirmed by performing local stability analysis. This relies on the calculation of the eigenvalues associated with the 2×2 Jacobian matrix of the system of equations. These are numerically evaluated at each equilibrium point. If both are real and negative, or complex with negative real parts, then the equilibrium is stable. If both are real and positive, or complex with positive real parts, then it is unstable. If one is positive and the other is negative, it is a saddle point. If not in equilibrium, N_1 and N_2 move towards stable—or away from unstable—equilibrium, monotonically if the eigenvalues are real, or in an oscillatory fashion if they are complex. In the figure legend these values are shown for each equilibrium point. According to these, \mathbf{X}^* and \mathbf{Y}^* are oscillatory stable (damped oscillations) and \mathbf{Z}^* is a saddle point.

Both \mathbf{X}^* and \mathbf{Y}^* correspond to mutualistic interactions, as the N_1^* and N_2^* values are greater than the K_1 and K_2 values in both cases. In addition, it can be checked that α_{12} and α_{21} are positive for these density values.

Each N_i nullcline crosses the N_i axis at ($N_i=K_i, N_j=0$). These are obviously equilibrium points for the biological system. In figure 2, all $(0, K_2)$, and $(K_1, 0)$ are unstable (saddle points), and $(0, 0)$ is asymptotically unstable.

Taking figure 2a as reference, it can be shown that variation of the parameters in the model may have a pronounced effect on the outcomes. Increasing both K_1 and K_2 symmetrically, the situations in figure 2b are obtained (see K_i labels on axes to follow discussion). For an increment of 1 to 4, there are again the two stable \mathbf{X}^* and \mathbf{Y}^* equilibrium points. It must be observed, however, that now the species coexist in a parasitic fashion ($N_i^* > K_i$ and $N_j^* < K_j$ in both cases). A transition from

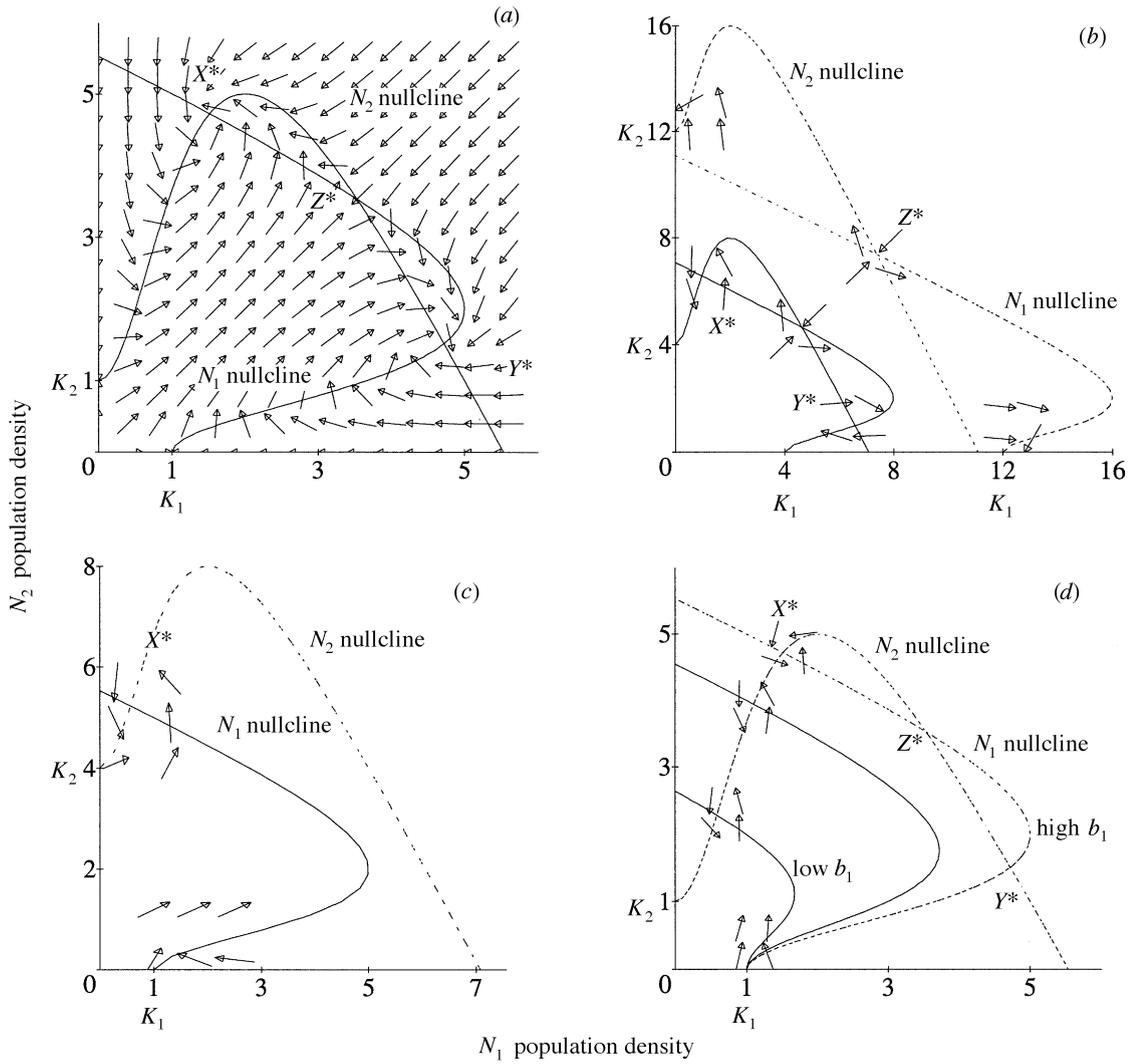


Figure 2. Case I: both facultative; $\alpha_{12}(+ -)$, $\alpha_{21}(+ -)$. (a) $K_1=K_2=1$, $b_1=b_2=5$, $c_1=c_2=1$, $d_1=d_2=0.5$. (b) $K_1=K_2=4$ (solid line) and $K_1=K_2=12$ (dashed line), other parameters as in (a). (c) $K_1=1$, $K_2=4$, other parameters as in (a). (d) Parameters as in (a) (dashed line), $b_1=4$ and $b_1=2$ (solid line). Eigenvalues of Jacobian matrix in (a), at X^* and Y^* : $(-3.12 \pm i3.66)$; at Z^* : $(-8.92, 1.86)$; at $(0, 0)$: $(1, 1)$; at $(0, K_2)$ and $(K_1, 0)$: $(-1, 3.67)$.

mutualism to parasitism has occurred. When the K 's are further increased to 12, the nullclines 'outgrow' the possibility of crossing at any stable point. Only the saddle point Z^* stays. Thus, no stable coexistence for the populations is now feasible. If only K_2 is increased (figure 2c), the N_2 nullcline 'moves upwards' and only the stable X^* remains. The association is a parasitism, sp1 being the victim ($N_1^* < K_1$).

Figure 2d shows the effect of varying parameter b_1 . Only variations in b_i are displayed here because for the other α parameters the results are not qualitatively different. The N_1 nullcline 'moves leftwards' as b_1 is decreased and only a stable parasitism at X^* remains. The transition from mutualism to parasitism occurs when the equilibrium point falls below K_1 . At exactly $N_1^* = K_1$ the interaction should be identified as a commensalism ($\alpha_{12} = 0$).

(b) Case II. Both facultative; one $\alpha(+ -)$ function, one $\alpha(-)$ function

Now suppose that sp1 can benefit from the interaction with sp2, provided that N_2 is low, but the presence of sp1

is always detrimental for sp2, increasingly as N_1 increases. Thus, the α_{12} function is of the $\alpha(+ -)$ kind, whereas α_{21} is an $\alpha(-)$. If the association is facultative for both populations, we use equations (1) and (3) for sp1, and equations (1) and (4) for sp2, so that:

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} + \left(\frac{b_1 N_2 - c_1 N_2^2}{1 + d_1 N_2^2} \right) \frac{N_2}{K_1} \right],$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - \left(\frac{g_2 N_1}{1 + h_2 N_1} \right) \frac{N_1}{K_2} \right].$$

Figure 3 displays the graphical and local stability analyses for different sets of parameters. Figure 3a shows there are two asymptotically stable equilibrium points: X^* , where the species compete; and Y^* , where the interaction is parasitic, sp2 being the host. Z^* is a saddle point, and all equilibria involving zero densities are unstable.

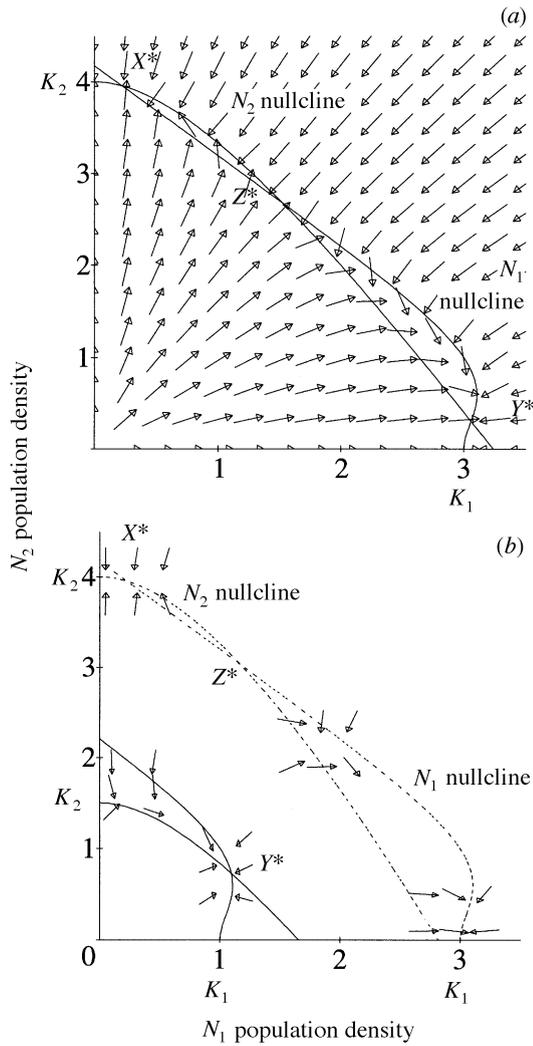


Figure 3. Case II: both facultative; $\alpha_{12}(+ -)$, $\alpha_{21}(-)$. (a) $K_1=3$, $K_2=4$, $b_1=1$, $c_1=1$, $d_1=1$, $g_2=1$, $h_2=0.5$. (b) $h_2=0.35$ (dashed line) and $K_1=1$, $K_2=1.5$ (solid line), other parameters as in (a). Eigenvalues of Jacobian matrix in (a), at \mathbf{X}^* : $(-1.02, -0.04)$; at \mathbf{Y}^* : $(-0.98, -0.11)$; at \mathbf{Z}^* : $(-1.30, 0.10)$; at $(0, 0)$: $(1, 1)$; at $(0, K_2)$: $(-1, 0.06)$; at $(K_1, 0)$: $(-1, 0.10)$. In (b), at $(K_1=3, 0)$: $(-1, -0.10)$.

Fundamental variation is introduced by changing parameters as illustrated in figure 3b. For a smaller h_2 (dashed lines) the possibility of parasitic coexistence disappears, and only a competitive association at \mathbf{X}^* is feasible. But $(K_1, 0)$ is now a stable point, which offers the possibility of extinction of sp2. Decreases in K_1 and K_2 (solid lines) lead to a unique parasitic stable association at \mathbf{Y}^* . If only one K_i was lowered the nullclines would not cross and no coexistence would be possible (not shown).

(c) **Case III. One obligate, one facultative; both $\alpha(+ -)$ functions**

Consider that the interaction is obligate for sp1 and facultative for sp2. Thus, sp1 can only exist in association and there is no K_1 value; but if sp2 is alone it is expected to eventually attain $N_2=K_2$. The α -functions are both assumed $\alpha(+ -)$ type. Substituting equation (3) into equations (2) (for sp1) and (1) (for sp2), the model becomes:

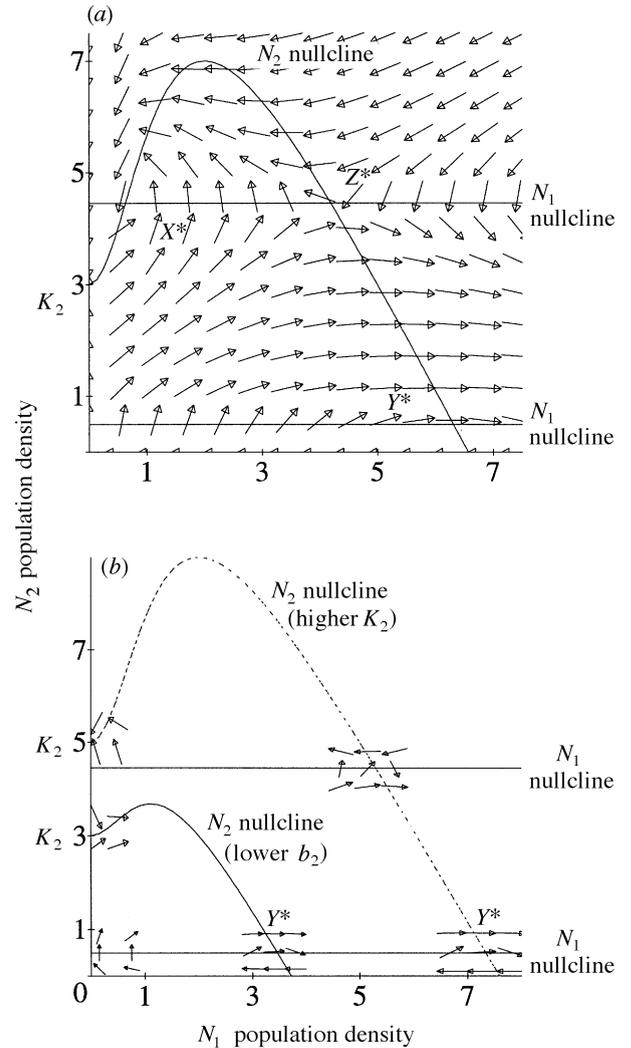


Figure 4. Case III: one obligate, one facultative; $\alpha_{12}(+ -)$, $\alpha_{21}(+ -)$. (a) $K_2=3$, $b_1=b_2=5$, $c_1=c_2=1$, $d_1=d_2=0.5$. (b) $K_2=5$ (dashed line) and $b_2=2$ (solid line), other parameters as in (a). Eigenvalues of Jacobian matrix in (a), at \mathbf{X}^* : $(-0.74 \pm i2.3)$; at \mathbf{Y}^* : $(-0.08 \pm i2.61)$; at \mathbf{Z}^* : $(-5.17, 3.68)$; at $(0, K_2)$: $(2.28, -1)$. In (b), at $(0, K_2=5)$: $(-1, -1)$.

$$\frac{dN_1}{dt} = r_1 N_1 \left[-1 + \left(\frac{b_1 N_2 - c_1 N_2^2}{1 + d_1 N_2^2} \right) N_2 \right],$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} + \left(\frac{b_2 N_1 - c_2 N_1^2}{1 + d_2 N_1^2} \right) \frac{N_1}{K_2} \right].$$

The stability features are displayed in figure 4. The nullclines for N_1 are two horizontal lines, which is not surprising because no positive N_1 value should exist for $N_2=0$. The situation presented in figure 4a exhibits a saddle point, \mathbf{Z}^* , and two oscillatory stable equilibrium points: \mathbf{X}^* where the species coexist as mutualists, and \mathbf{Y}^* where the interaction is parasitic, and in which, obviously, the facultative species is the host. $(0, K_2)$ is an unstable saddle point. But for a higher K_2 , as shown in figure 4b (dashed line), the $(0, K_2)$ point becomes asymptotically stable. The parasitic association \mathbf{Y}^* is still a possibility also. In the same graph, the effect of a smaller b_2 is shown. In this case the hump in the N_2 nullcline is below the upper line of the N_1 nullcline. This leads to

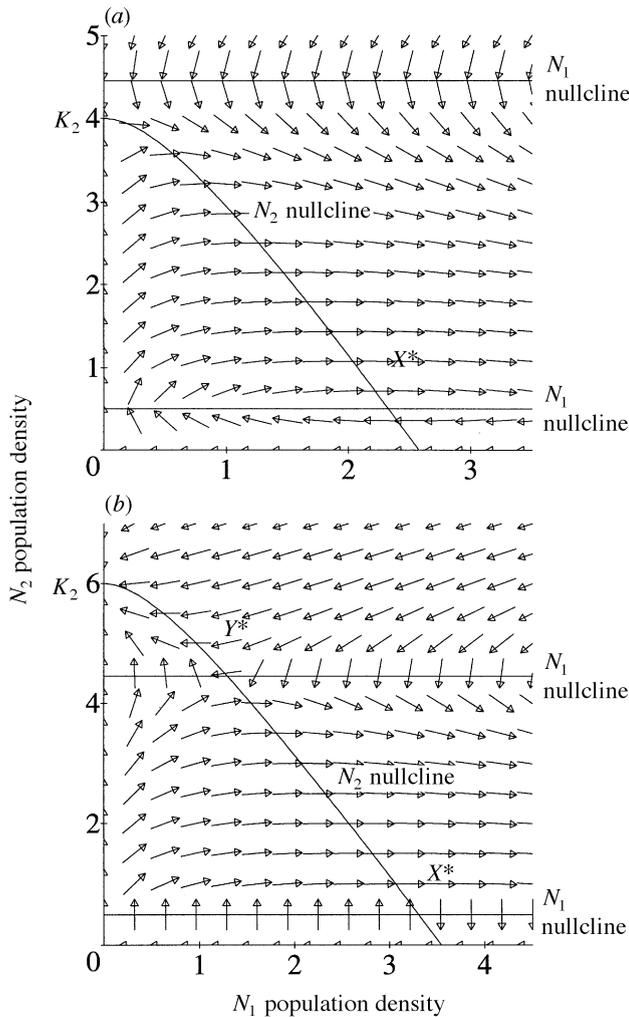


Figure 5. Case IV: one obligate, one facultative; $\alpha_{12}(+ -)$, $\alpha_{21}(-)$. (a) $K_2=4$, $b_1=5$, $c_1=1$, $d_1=0.5$, $g_2=2$, $h_2=0.9$. (b) $K_2=6$, other parameters as in (a). Eigenvalues of Jacobian matrix in (a), at X^* : $(-0.06 \pm i1.40)$; at $(0, K_2)$: $(-1, 0.80)$. In (b), at Y^* : $(-2.14, 1.40)$; at $(0, K_2)$: $(-2.90, -1)$.

a unique stable parasitic coexistence at Y^* . It can be gathered that the same effect could be accomplished if K_2 , instead of b_2 , is decreased; and if it is further reduced below the lower horizontal line, the possible outcomes are as in figure 4a (not shown). In addition, variations in the α_{12} function parameters make the position of the horizontal nullclines change; thus the same patterns can also be obtained this way.

(d) Case IV. One obligate, one facultative; one $\alpha(+ -)$ function, one $\alpha(-)$ function

Finally, consider the situation where the association is obligate for spl, being beneficial for low N_2 densities but becoming detrimental for larger N_2 , and is facultative and always detrimental for sp2. Thus, substituting equation (3) into (2), and equation (4) into (1), the model becomes:

$$\frac{dN_1}{dt} = r_1 N_1 \left[-1 + \left(\frac{b_1 N_2 - c_1 N_2^2}{1 + d_1 N_2^2} \right) N_2 \right],$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - \left(\frac{g_2 N_1}{1 + h_2 N_1} \right) \frac{N_1}{K_2} \right].$$

The stability graphics depicted in figure 5a exhibit one oscillatory stable point X^* , which indicates that stable coexistence is only possible in a parasitic fashion. The equilibrium point at $(0, K_2)$ is unstable. If K_2 is higher, as in figure 5b, an intermediate saddle equilibrium point Y^* now exists, and the $(0, K_2)$ equilibrium point becomes asymptotically stable, leading to extinction of spl. The same patterns can also be obtained changing the α_{12} parameters, which produces variation in the position of the horizontal nullclines. However, changes in the α_{21} parameters does not make fundamental transformations in the variety of outcomes.

5. DISCUSSION

(a) The concept of a nonlinear dependence of the interaction coefficient α_{ij} on population densities and on environmental parameters allows a theoretical representation of the often-observed transitions between population interactions. The models interpret the occurrence of different associations between the same two species, either in different or in identical environments, or in formerly different environments. Some general trends emerge from the preceding stability analysis. Two categories may be distinguished:

(i) Transitions induced by perturbation of population densities; no environmental change involved

These can be visualized as the system moving within an N_1, N_2 phase space graph, from one equilibrium point to another, its direction being dependent on which domain of attraction the system is in. The ‘endogenous effect’, as formerly defined, accounts for the dynamic response of the system. Trajectories between two equilibrium points might involve a transition between different kinds of interactions (as in figures 3a and 4a), or might not (as in figure 2a,b).

This reveals the fact that no environmental changes are necessary to induce transitions. The system can be led from one domain of attraction to the other by a substantial variation in density numbers, as could happen after a natural catastrophe, or by culling in population management or biological control. On the other hand, it would be interesting to analyse the behaviour of these systems under stochastic perturbations causing them to jump between different domains of attraction.

A common feature in these transitions is that going from one equilibrium point to another involves a decrease in one of the population densities and an increase in the other, as if suggesting a sort of general carrying capacity for the system, which can be fulfilled with adequate combinations of N_1 and N_2 . This is a consequence of the particular closed shape of the nullclines that cut both N_1 and N_2 axes, a result of the interaction coefficient nonlinearly changing with density. This is an unusual shape for a nullcline, especially in mutualistic models, and it permits bounded self-regulatory systems, with no extrinsic agents needed to account for its limitation. This has been a classical problem in models of mutualism, usually solved by incorporating external (biotic or abiotic) conditions. Dean (1983), however, also provides a self-regulated model of mutualism. He considers that the

carrying capacities of the populations show diminishing returns as their densities increase. His model shows one possible stable equilibrium.

(ii) Transitions induced by environmental changes

These can be visualized between graphs of the same case but with different parameters. The nullclines are displaced with respect to each other, and so are the corresponding equilibria. In most cases, the system goes from one to multiple stable equilibria, and vice versa. However, two different conditions must be recognized according to the way the environmental variation affects the biological system.

1. Inducing alterations in the α -functions via the b_i , c_i , d_i , g_i and h_i parameters. The 'exogenous effect' leads the dynamics in this case. Extrinsic conditions (biotic or abiotic) have changed in a manner that causes variations in the nonlinear response to the presence of the other species.
2. Causing changes in the carrying capacity values, K_i . These can be interpreted as variations in environmental quality for sp_i . It is an extrinsic factor, but the α -function remains unchanged.

Again, variations in the type of interaction might occur or not.

It is obvious that in a realistic environment all endogenous and exogenous effects are expected to be present simultaneously. Each phase space graph is just an instantaneous picture of the biotic system and its external conditions. A sequence of these put together represents the long-term dynamics, the biological system trying to follow the directions indicated at each step.

(b) Matching ecology and models

In the absence of specific data, it is not possible to explicitly represent any of the many examples of transitions between interactions, or variation in outcomes, as those mentioned in § 1. However, we can explore some cases where the model and the ecological situation seem to correspond. For instance, the case depicted in figure 2*b* (solid lines) shows the possibility of two stable parasitic interactions, with the peculiarity that each species can play both the victim and exploiter roles interchangeably. Could this be the situation found by Phillips *et al.* (1995) in the *C. frigida* and *C. pilipes* association? Figure 3 provides a situation where both competition and parasitism are feasible under identical or under different environments. This model might be helpful in the study of associations like epibiosis or mullerian mimetism.

Ant-aphid associations are very well documented in the literature, and provide a clear example of interactions that depend on ecological conditions (Addicott 1979; Cushman & Addicott 1991; Bronstein 1994). Under limiting environments, some aphid species can greatly benefit from mutualism with ants. However, under better conditions for the aphids, the presence of the ants becomes either negative or just neutral. If the association is obligate for the ant population, the situation can be followed in figure 4*a,b*. When environmental conditions for the aphids (sp_2) become better (higher K_2), a transition from mutualism to parasitism, or to the extinction of the ants population (sp_1) occurs. On the other hand, if

the association is facultative for both species, figure 2*d* provides an appropriate illustration. Changes in the α -interaction function for the aphid population (now sp_1), causes transitions from mutualism to parasitism. The ants (sp_2) always gain benefits. Notice that the actual shape of the α -function is the result of the cost-benefit balance in the association. A lower b_1 means that the association is beneficial to aphids for a smaller range of ant population density N_2 (see figure 1*a*).

The models also provide a framework for the analysis of species invasion or colonization, and the persistence of the biological systems. Situations where the 'borders' are unstable (e.g. figures 2*a-c* and 3*a*) mean that the association between the species is persistent. That is, densities will positively increase from zero upon re-invasion, and any of the species can invade a site occupied by the other. This is particularly illuminating for those cases where the sequence of arrival of colonizing species determines the outcome of the relationships, as those reported for seaweed flies by Hodge & Arthur (1996, 1997). For instance, in figures 3*a* and 3*b* (dashed line), the outcome depends on which species arrives first. On the other hand, environmental changes may lead to the possibility of extinction of one of the species, with no re-invasion possible, as in figures 2*b*, 3*b*, 4*b* (dashed line) and 5*b*. This makes the system no longer persistent. Important insights can also be gathered in cases where the relationship is obligatory for one of the species (figures 4 and 5). The carrying capacity of the facultative partner (always the species being invaded) plays a determinant role, as the invasion will only be successful if K_2 is below a certain threshold. This supports the ideas of the 'paradox of enrichment' in Rosenzweig's (1971) predator-prey nonlinear model, where the importance of the prey carrying capacity in controlling the stability of the association is stressed.

The mechanism behind this is clear from the model. For an invading sp_1 (i.e. low N_1), α_{21} is certainly positive if it is an $\alpha(+ -)$ type, or negative but weak if it is an $\alpha(-)$ type (see figure 1). This expresses what the invading species 'has to offer' on its arrival. But for the sp_2 being invaded, and assuming it had reached its carrying capacity, the sign of α_{12} —what the invader gets in return—is determined by K_2 . For an $\alpha(+ -)$ function, it is positive if K_2 is low; otherwise it is negative. If α_{12} is an $\alpha(-)$ type, it is always negative, although weaker at lower K_2 .

(c) Some general remarks

Broadly comparing the four biological systems studied, it is interesting to observe that only for case II is a stable competitive coexistence possible. However, this is not surprising. In case I, the association is facultative for both populations and both α -functions can take positive values. Intuitively the competition solution would be that of the lowest fitness. In cases III and IV, the obligate character of the association for sp_1 eliminates this possibility, and by inspection of the equations of the models it can be shown that N_2^* can never be such that the α_{12} function takes negative values. The general results agree with Bronstein's (1994) prediction that the 'outcomes of facultative mutualisms should be more variable than outcomes of more obligate mutualisms'.

Further theoretical work needs to be done regarding the α -function concept; many other forms of α -functions can be thought of. Those considered here depend only on the partner's density, i.e. $\alpha_{ij}(N_j)$. It would be interesting to analyse α_{ij} as a function of both N_i and N_j , and also of K_i and K_j . For instance, in Addicott's (1981) model III, and Wolin & Lawlor's (1984) model IF, the interaction coefficients are multiplied by a factor $(1 - N_i/K_i)$. However, the decrease with N_i is linear and never gets negative values. The isoclines in such cases do not yield multiple equilibria. Predator-prey models such as those by Holling (1965) and Tanner (1975) include nonlinear predator functional responses in the equations. This is in some sense conceptually similar to the nonlinear α -function here. Again, the difference is in the possibility of the latter of taking both negative and positive values, which allows the variation in the outcome of the interactions. Another option is to consider variable 'intra-specific interaction coefficients' $\alpha_{ii}(N_i)$ and $\alpha_{jj}(N_j)$, which in this model are considered equal to one. This would account for variation in what one individual of the same species is worth as its own density changes.

The model developed in this study presents a comprehensive and integrative approach, which makes it amenable for evolutionary analysis (Hernandez 1998). Thompson (1988) states: 'Just as variation in traits in populations is the raw material traits to the evolution of the species, variation in outcome is the raw material for the evolution of interactions'. Bronstein (1994) comments briefly on the possibility of net benefits within mutualistic interactions being related to the way in which interactions evolve. The model presented here suggests that some interactions between populations can be 'explained by a single paradigm', as Matsuda & Shimada (1993) have proposed in their cost-benefit evolutionary model of symbiotic interactions. Perhaps not every population association can be conceived this way, but what is indeed clear is that the borderline between some symbiotic associations might be surprisingly thin, a blurred frontier.

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