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Variation in the outcome of population interactions: bifurcations and catastrophes

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Abstract. The nature of the association between two species may vary depending on population abundances, age or size of individuals, or environmental conditions. Interactions may switch between beneficial and detrimental depending on the net balance of costs and benefits involved for each species. We study the repercussion of the ecological setting on the outcomes of conditional or variable interactions by means of a model that incorporates density-dependent interaction coefficients; that is, *interaction α-functions*. These characterize the responsiveness and sensitivity of the association to changes in partner's abundance, and can take positive and negative values. Variable outcomes – and transitions between them – are categorized as *homeo-* or *allo-environmental*, that is, occurring under the same ecological setting, or not, respectively. Bifurcation analyses show that these dynamics are moulded by ecological factors that are: *intrinsic* to the nature of the association (concerning the sensitivity of the interaction), and *extrinsic* to the association itself (the quality of the environment referred to each species alone). The influence of these factors may be conflicting; consequently, the dynamics involve *catastrophic* events. In a facultative variable association, stable *coexistence* is expected when environmental conditions are adverse; otherwise, the *exclusion of one species* is the likely outcome. Remarkable situations as the switching of victim-exploiter roles illustrate the theoretical perspective.

1. Introduction

Two, or more, populations can be found coexisting under different kinds of association. The static classification of interactions – mutualism, competition, predation, etc. – is therefore inadequate as the outcome may vary depending on densities, age or size of individuals, or environmental conditions (Abrams 1987; Thompson 1988). This has been referred to in the literature as *conditional or variable outcomes* (Bronstein 1994; Cushman 1991) or *conditional interactions* (Cushman & Addicott 1991).

The main feature among most of the cases of conditional interactions reported is that the presence of an associated species involves both costs and benefits to

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the partner species – measured in terms of depletion or enhancement of population growth rates – thus, the ultimate outcome depends on the net balance of these (Thompson 1988; Bronstein 1994; Herre *et al.* 1999; Hoeksema & Bruna 2000; Stachowicz 2001). Nature provides us with many examples; we illustrate with some particular situations:

In aquatic environments epibiotic associations are very common: epibionts (sponges, algae, etc) permanently, or facultatively, live and grow attached to hosts' surfaces (crabs, insects, algae, etc). The benefits for the epibionts are obvious; for instance, if attached to motile hosts they have an increased access to nutrients. However, phototropic epibionts may be impaired by attaching to negatively photoactic hosts. On the other hand, the presence of epibionts entails some costs for the hosts: mechanical harm to the surface, mobility impairment, lower nutrient and light availability, etc. Nevertheless, hosts may also benefit from the association because epibionts provide protection from predators by optical or chemical camouflage, or even by active defence. The degree of harm caused – or benefit obtained – largely depends upon the proportion of host surface covered by the epibiont (Vance 1978; Duffy 1990; Threlkeld *et al.* 1993; Wahl & Hay 1995). In addition, prey palatability to predators has to be considered: a potential predator either rejects or attacks the epibiont–host symbiont, depending on the epibionts being unpalatable, or a preferred prey: 'associational resistance', or 'shared doom' (Wahl & Hay 1995).

Ants benefit from their association with aphids and other homopteran herbivores because they provide excretions or secretions (honeydew) rich in sugars and aminoacids. In turn, herbivores get protection from ants against their natural predators. However, field and laboratory research has shown that the magnitude of these benefits depends on the relative densities of the two populations involved: at low aphid densities benefits for aphids are high; but at high density these are low, none, or even negative (Addicott 1979; Cushman & Addicott 1991) – conversely, Cushman & Whitman (1989) found a positive density-dependence. Environmental conditions can also influence the balance – at low predator densities less protection is needed by the herbivores (Del-Claro & Oliveira 2000) – or even reverse the outcome of the association: the higher the quality of the host plant phloem fluids, the higher the quality of the honeydew produced by the homopterans, thus, more ants are attracted and this ultimately means a higher herbivore fitness. However, when the quality of the fluids is low, so is the honeydew produced; and the ants may choose to predate on the herbivores! (Cushman 1991; Cushman & Addicott 1991; Stadler & Dixon 1998; Offenberg 2001). This case shows an obvious shift from a beneficial to a detrimental role in the association.

The switching of roles in victim-exploiter associations has been covered in the literature. A remarkable situation was reported in South Africa: at Malgas Island whelks are the favourite prey of an abundant population of rock lobsters; at Marcus Island – 4 Kms apart, same environmental conditions – rock lobsters are completely absent, whereas very high densities of whelks are present. When a thousand lobsters were transferred to Marcus Island, they were overwhelmed and consumed until complete exclusion by whelks within a week (Barkai & McQuaid 1988).

Apart from the fact that these species systems can be found under different associational regimes, they can also undergo transitions – in time, and space – between them. That is, populations can be at, or transit between, different combinations of stable equilibrium densities, and sometimes between different types of interactions. A general model for these dynamics was developed (Hernandez 1998) based on the assumption that the interaction coefficient, α_{ij}, between two species is not constant, as has been classically considered in the Lotka-Volterra type models, but a function (α-functions) of population density N_j that can take both positive and negative values. This means that the effect of each individual of species j on the population growth rate of species i depends on the partner's population; and, most importantly, α_{ij} can change sign. Graphical stability analyses of the model showed that multiple stable density equilibria occur under different kinds of associations for the same two species.

The paper by Hernandez (1998) presented an overview of a general model – including both facultative and obligatory associations. It inspected the potentiality of the theoretical approach, in particular, the possibility of re-interpreting interaction coefficients as functions which can shift from positive to negative; thus, shedding light on the representation of the dynamic behaviour of populations with conditional interactions. This could not be accomplished through former models in the literature. In the present paper we look deeper into the way in which the costs and benefits involved for each population in the association add up and yield either positive or negative outcomes for the interaction. We deal with the facultative situation only, but under a more formal and thorough approach. The main purpose is to explore the repercussion of ecological conditions on the possible outcomes of variable interactions; and specifically to unravel the relative significance of the extrinsic environmental conditions and the intrinsic properties of the association itself. This is accomplished by means of bifurcation analyses, which allow examining the essential properties of the model, and the relationship between equilibria and the relevant parameters, which are ultimately expressions of the general environmental conditions to which the association responds.

2. Population performances define types of interactions; costs and benefits mould interaction functions

Consider a facultative association between a species 1 (*sp1*) and a species 2 (*sp2*). Thus, if alone, populations reach densities N_1, N_2, equal to their corresponding carrying capacities K_1, K_2. A general model for the dynamics of these interacting populations is (Lotka-Volterra type)

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

where i, j=1,2, for $i \neq j$; r_i is the intrinsic rate of increase of *spi*, and $\alpha_{ij}$is the interaction coefficient between *spi* and *spj*.

The effect of the interaction between the two populations is expressed through the α_{ij} coefficient. If it is positive it means that the presence of *spj* has a positive contribution to the density-dependent factor in the per capita growth rate of *spi*, and conversely for the negative condition. The magnitude of α_{ij} expresses the intensity of this contribution. However, for associations that can be either beneficial or detrimental depending on certain ecological variables, α_{ij} may be reinterpreted as a function with the ability to shift from positive to negative (Hernandez 1998).

Two important issues set the basis for the analysis here: (i) a formal definition for the type of interaction or outcome of the association, and (ii) the actual shape and functional form of an interaction α-function.

(i) We consider that an interaction is *beneficial, neutral or detrimental* for a *species i*, if when associated with a *species j* it reaches an equilibrium density N_i^* which is *greater, equal or smaller* than its carrying capacity K_i, respectively. That is, it refers to a global comparison of the net or potential performances of the populations, with and without the presence of the other species, in ecological time. Mutualism, competition, and victim-exploiter associations are thus defined. No evolutionary processes are being considered here, so we use net effects on population performance as indicators of a positive or a negative association.

To follow conventional notation we use the symbols (+ +), (– –), (+ –), (– +), to denote types of interaction. The first sign refers to the effect of *sp1* on *sp2*, and vice-versa for the second sign. Thus, a *positive* or a *negative* sign in these symbols always correspond to $\alpha_{ij} > 0$ or < 0, respectively; that is, α_{21} for the first sign, and α_{12} for the second. This is a direct consequence of the definition of the outcome or type of interaction as used here, and is not to be confused with other classifications usually adopted in the literature that are based on the community (or Jacobian) matrix evaluated at equilibrium (e.g. Odum 1953; May 1973; Travis & Post 1979).

(ii) The functional form of the α_{ij}-function must reflect the biological circumstances of the natural situations presented above. According to these, for each population the presence of an associated species involves both benefits and costs, with magnitudes that increase with the partner's population density (we assume that this occurs at an ecological timescale). The outcome of the interaction – beneficial or detrimental – is set by the balance of these. Thus, the interaction α_{ij}-function can be visualized as the result of the algebraic sum of two functions inherent to the association; that is: 'benefits-to-*spi* vs. N_j', and 'costs-to-*spi* vs. N_j'. Figure 1 depicts some hypothetical examples of these functions and their corresponding α-function ($\equiv$benefits – costs). Figures 1(a,b) provide situations where α_{ij} values shift from positive to negative as N_j increases; for completeness and contrast, figures 1(c,d) show α-functions that do not change sign, even though α_{ij} values vary with N_j.

We confine our study to interactions that are cooperative at low population density, but become parasitic or competitive at higher densities. That is, to α_{ij}'s that change from positive to negative as in figures 1(a,b). The shift in sign occurs because benefits are greater than costs at lower N_j, but costs grow faster, thus, at higher N_j costs are higher than benefits. Visualize, for instance, epibionts that offer optical camouflage to hosts by covering their surfaces and they are more effective as surface coverage grows larger. However, at higher epibiont coverage, surface damage to the hosts may be large enough to outweigh the benefits of protection from predators, yielding a negative net effect (to consider the effect at population levels we implicitly assume average values among individuals in the populations). Figures 1(a,b) hint for different possibilities: curves may be linear or non-linear;

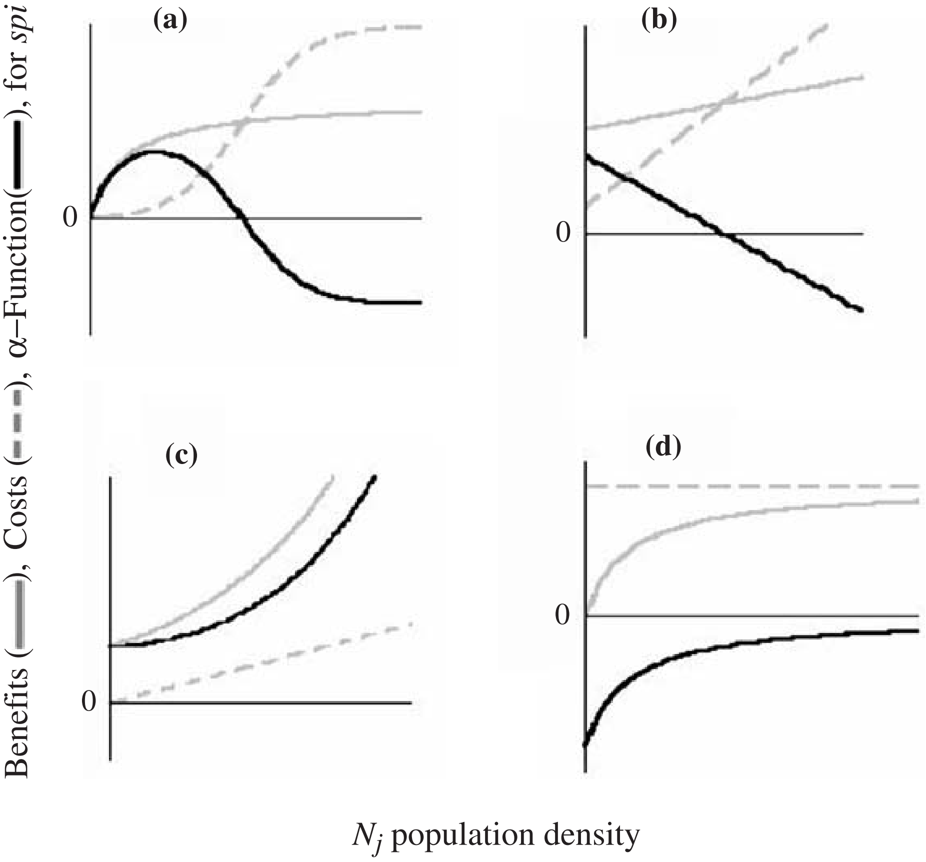

Fig. 1. Hypothetical relationships in variable interactions: benefits-to-*spi* vs. N_j (light solid); costs-to-*spi* vs. N_j (dashed); Interaction α-Function (dark solid) = benefits−costs. Equations used for costs and benefits curves: Linear (Ln) $Y = b + cX$; Concave (Cv) $Y = bX\big/(1 + cX)$; Convex (Cx) $Y = b + c\exp(dX)$; and Sigmoidal (Sg) $Y = (b + c\exp(dX))\big/(1 + f\exp(dX))$. **(a)** Cv–Sg; **(b)** Ln–Ln; **(c)** Cx–Ln; **(d)** Cv–Ln

may reveal saturation effects – as in (a), or not – as in (b); and also, depending on the relative gradients of the benefits and costs curves, the α-function may either first increase at low N_j and then decline, or just decrease from a starting positive value.

We want to study the dynamics of the associated populations under the net action of beneficial and detrimental effects. Therefore, instead of two separate costs and benefits functions, which would make the model unnecessarily cumbersome, we can use particular $\alpha(N_j)$ functional forms that comply with the main feature required: the ability to shift from positive to negative as N_j increases. Some possibilities are: *quadratic-ratio*, $\alpha_{ij} = \left(b_i N_j - N_j^2\right)\Big/\left(1 + c_i N_j^2\right)$; *parabolic*, $\alpha_{ij} = b_i N_j - c_i N_j^2$; *exponential*, $\alpha_{ij} = b_i \exp\left(-c_i N_j\right) - d_i$; and *linear*, $\alpha_{ij} = b_i - c_i N_j$.

2.1. The model

A preliminary graphical stability analysis of model (1) for the four α_{ij} functional forms outlined above, allows exploring relevant differences in their performance.

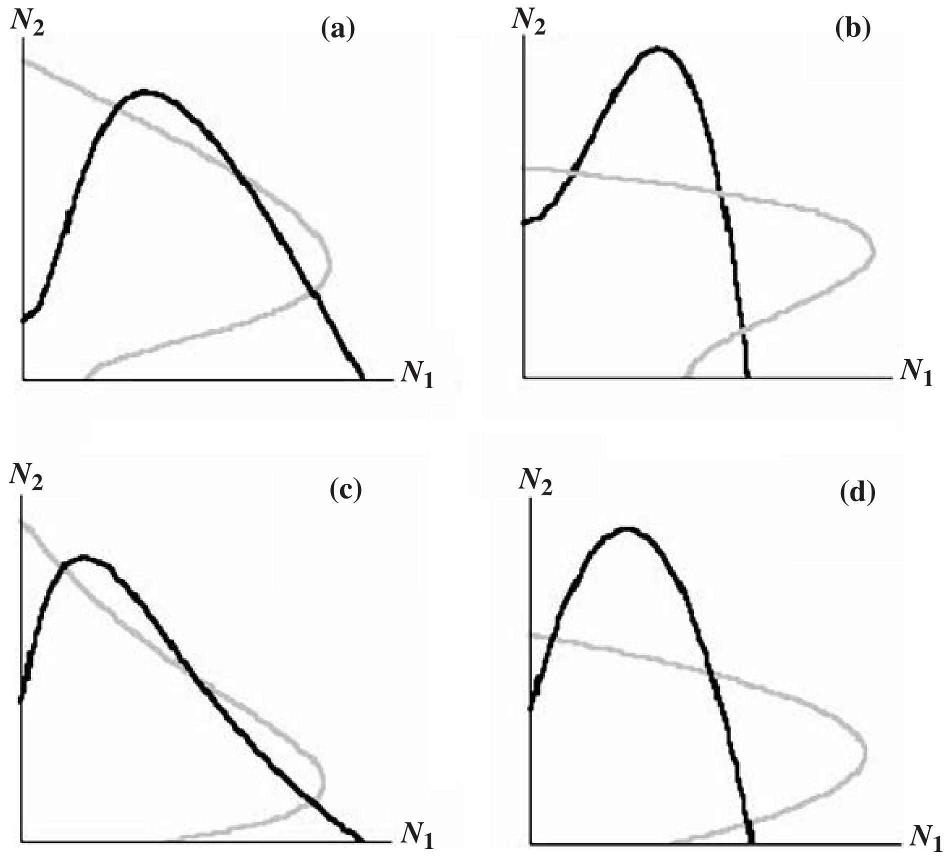

Fig. 2. Nullclines obtained for model (1) for four different interaction α-functions (see text for equations). N_1 nullcline: light; N_2 nullcline: dark. Parameter values used (for $i = 1, 2$): **(a)** $K_i = 1$, *quadratic-ratio* α_{ij}: $b_i = 5$, $c_i = 0.5$, **(b)** $K_i = 2$, *parabolic* α_{ij}: $b_i = 2.5$, $c_i = 1$, **(c)** $K_i = 2$, *exponential* α_{ij}: $b_i = 7$, $c_i = 1$, $d_i = 0.5$, **(d)** $K_i = 3$, *linear* α_{ij}: $b_i = 4$, $c_i = 1$. Software used: Maple V (Release 4, Waterloo Maple Inc.)

Figure 2 shows, for each case, the N_1 and N_2 nullclines; that is, curves of density values where there is no population growth (dN_1/dt=0, or dN_2/dt=0, respectively) plotted in a phase plane graph. Observe that regardless of the particular α-function used, the four resultant figures are structurally similar: all nullcline curves show a characteristic humped shape, which is a result of the α-functions being able to shift from positive to negative values (it can be checked that for α-functions that are always positive or always negative – as in figures 1(c,d) – the nullclines do not present this feature).

We choose to do further formal analysis using the *quadratic-ratio* α-function only:

$$\alpha_{ij} = \frac{b_i\, N_j - N_j^2}{1 + c_i N_j^2} \tag{2}$$

This function reproduces the form in figure 1(a). It provides a more general scope, and includes saturation effects, which is biologically more realistic. The equations of the model explicitly become:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left[1 - \frac{N_1}{K_1} + \left(\frac{b_1 N_2 - N_2^2}{1 + c_1 N_2^2}\right)\frac{N_2}{K_1}\right]\\ \frac{dN_2}{dt} &= r_2 N_2 \left[1 - \frac{N_2}{K_2} + \left(\frac{b_2 N_1 - N_1^2}{1 + c_2 N_1^2}\right)\frac{N_1}{K_2}\right]\end{aligned} \tag{3}$$

Unless stated otherwise, for the remaining of this article, '*the α-function*' and '*the model*' always refer to equations (2) and (3), respectively.

We have to study in turn: (i) the actual dynamics of the populations involved – i.e. the characterization of equilibria and their stability properties; and (ii) the possibilities of *variations in the outcome* of the association and how these are affected by the parameters.

3. Characterization of equilibria and stability properties of the model

Figure 3 shows all possible nullcline patterns that model (3) can yield for different parameter arrangements. Equilibrium points (N_1^*,N_2^*) are labelled $X*$,$Y*$,$Z*$, etc. The vector fields indicate trajectories of population densities from any point of the plane. Apart from the trivial (0,0), the system presents equilibria in two fashions: as *coexistence*, where both densities (N_1^*,N_2^*) are positive *internal* solutions; or as *exclusion*, where only one species survives at its carrying capacity and the other one goes extinct, that is, the *border* solutions (K_1,0) or (0,K_2).

In the appendix, we show that the eigenvalues, λ_1, λ_2, of the 2×2 Jacobian matrices of equation (3) evaluated at equilibria, are either both complex with negative real part or both real. In the latter case, one of them can be positive. This implies that if a steady state is unstable, it is always a saddle point. This in turn has further consequences. Since there is an invariant subset of the first quadrant, the Poincaré-Bendixon theorem implies that for this particular model no limit cycles are possible solutions, as these only exist if the unstable equilibrium is either a focus or a node (for a proof of this theorem see e.g. Jordan & Smith 1987). Furthermore, any solution with initial condition in the first quadrant tends to one of the stationary points.

Numerical and methodical calculation of eigenvalues λ_1,λ_2, allows the characterization of patterns in figure 3. Each case is distinguished by: (i) the number and stability properties of internal equilibrium solutions, and (ii) the stability properties at the borders; all this determined by the relative position of critical points K_i and N_{jC}.

(I) If both $K_i < N_{jC}$, as in figures 3(a,b,c), the system presents at least one *internal* stable equilibrium, and can have another one, or another two, stable-unstable *internal* pairs. The two *border* solutions are always unstable.

(II) If one $K_i > N_{jC}$, as in figures 3(d,e), there is either one stable-unstable *internal* pair, or none. The *border* solution where $K_i > N_{jC}$ is stable, the other one unstable.

(III) If both $K_i > N_{jC}$, as in figure 3(f), there is no stable *coexistence* possible. The two *border* solutions are stable.

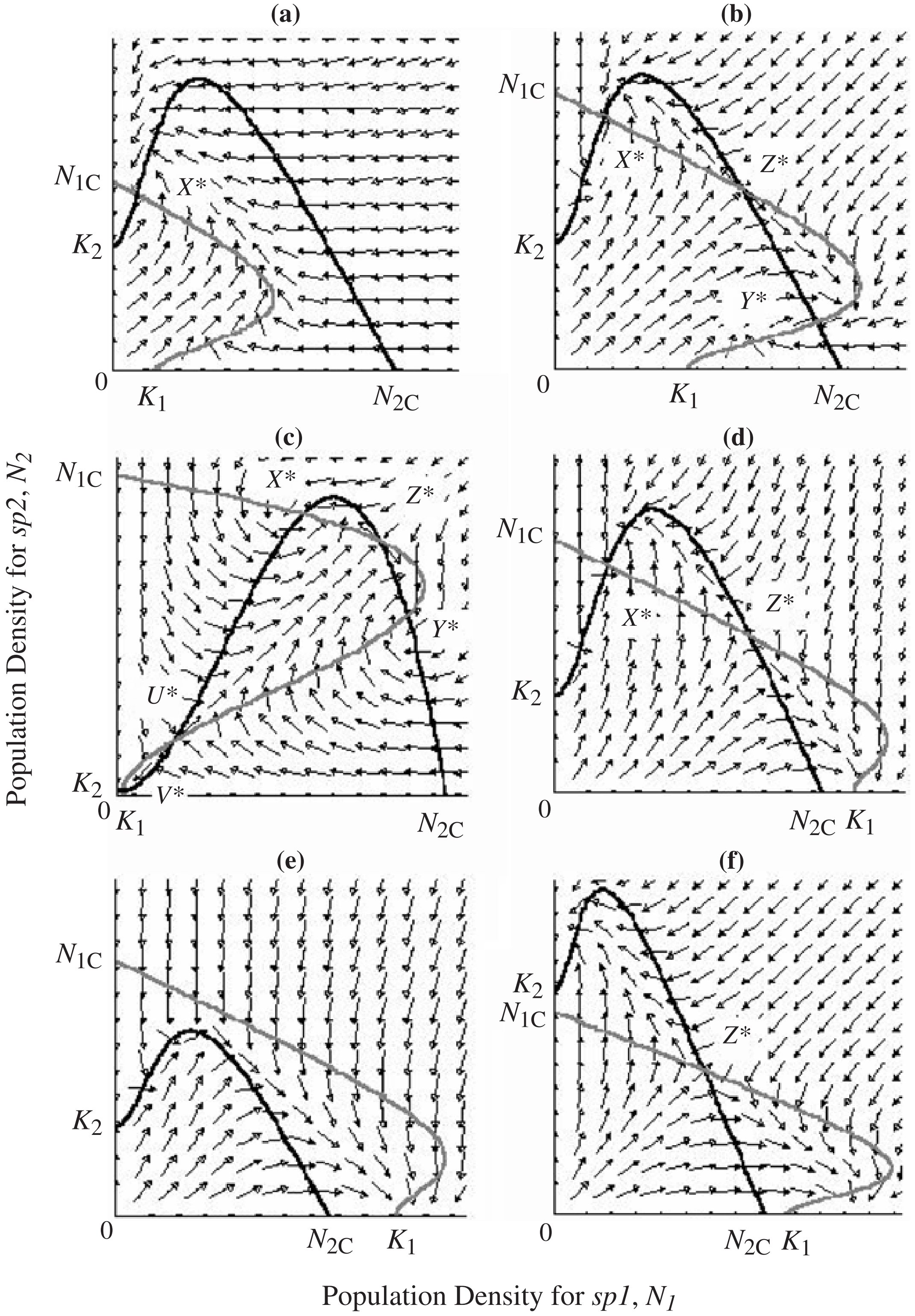

Fig. 3. Characterization of all possible nullcline patterns for model (3) in the N_1,N_2 phase space according to stability properties of internal and border solutions (see text). N_1 nullcline: light; N_2 nullcline: dark. Software used: Maple V (Release 4, Waterloo Maple Inc.)

In all cases, the *internal* stable points can be either nodes (λ_1,λ_2: real,< 0), or foci (λ_1,λ_2: complex, Re(λ)< 0), whereas, the stable *borders* are always nodes.

As in any theoretical–biological work, we must find a compromise between formal analysis and relevant ecological information. For example, we could re-scale the equations using $x_i = N_i \big/ K_i$ and the number of parameters would be reduced (K_1 and K_2 disappear). However, we purposely have chosen the K_i's to be explicitly shown in the equations since they represent an important environmental issue. K_i is the carrying capacity of *spi* and as expected is an equilibrium point (*spj* goes extinct). As seen above, it is the relative magnitudes of K_i and N_{jC} (for both $i = 1, 2$) what ultimately determines the outcome of different patterns. Furthermore, unstable border K_i goes stable when it becomes greater than N_{jC}; that is, N_{jC} represents the invasion boundary for *spj* – within a given domain of attraction.

4. The parameters of the model represent the ecological setting

K_i is the equilibrium density value for *spi* when there is no association; that is, K_i is an expression of the quality of the environment for *spi* – including biotic and abiotic elements – when *spj* is not part of this environment. The higher K_i is, the better performance the *spi* would have if alone; and this is modified – for better or for worse – by the presence of *spj*. Thus, the relative value of the performance of the species alone and in association provides relevant information on the net effect of the association.

The α-function parameters: b_i, c_i, – equation (2), determine the actual shape of the α_{ij} vs. N_j curve – see figure 4(a); they measure the sensitivity of the interaction to changes in the partner's density, and the threshold value between a positive and negative interaction. As shown in the figure, a higher b_1 provides an α-function with higher α_{12} magnitudes for all N_2 ranges, and also a larger N_2 range for which α_{12} is positive. On the other hand, a higher c_1 produces an α-function that is less sensitive to density variation (smaller α_{12} absolute magnitudes for all N_2), although N_2 ranges for positive and negative interactions remain the same. Furthermore, note that as c_1 tends to infinity, α_{12} tends to zero for all N_2. This would be a situation of a null interaction for *sp1* even in the presence of *sp2*.

Thus, α-function parameters are definitely the expression of the intrinsic properties of the *spi-spj* association in a particular ecological context. The interaction acknowledges environmental changes through the variation of parameters b_i and c_i. For instance, say that the main benefit that *sp1* receives from *sp2* is protection from predators – as in some aphid-ant associations, or certain epibiotic interactions – then, at environments where predator densities are low we expect α-functions with lower b_1 values. That is, α_{12} is lower for the same *sp2* density (furthermore, in an altogether predator-free environment, the association might even be negative for all density ranges, i.e. b_1=0).

Summing up, as a global appreciation it can be stated that higher b_i magnitudes translate into more efficient and better-valued contribution of *spj* to *spi* as a whole. Yet, c_i effects are contrasting: an increase in c_i is welcome at high N_j ranges, but it entails less positive α_{ij} values at low N_j. Additionally, if c_i is too high the interaction becomes very weak, or even null, for *spi*.

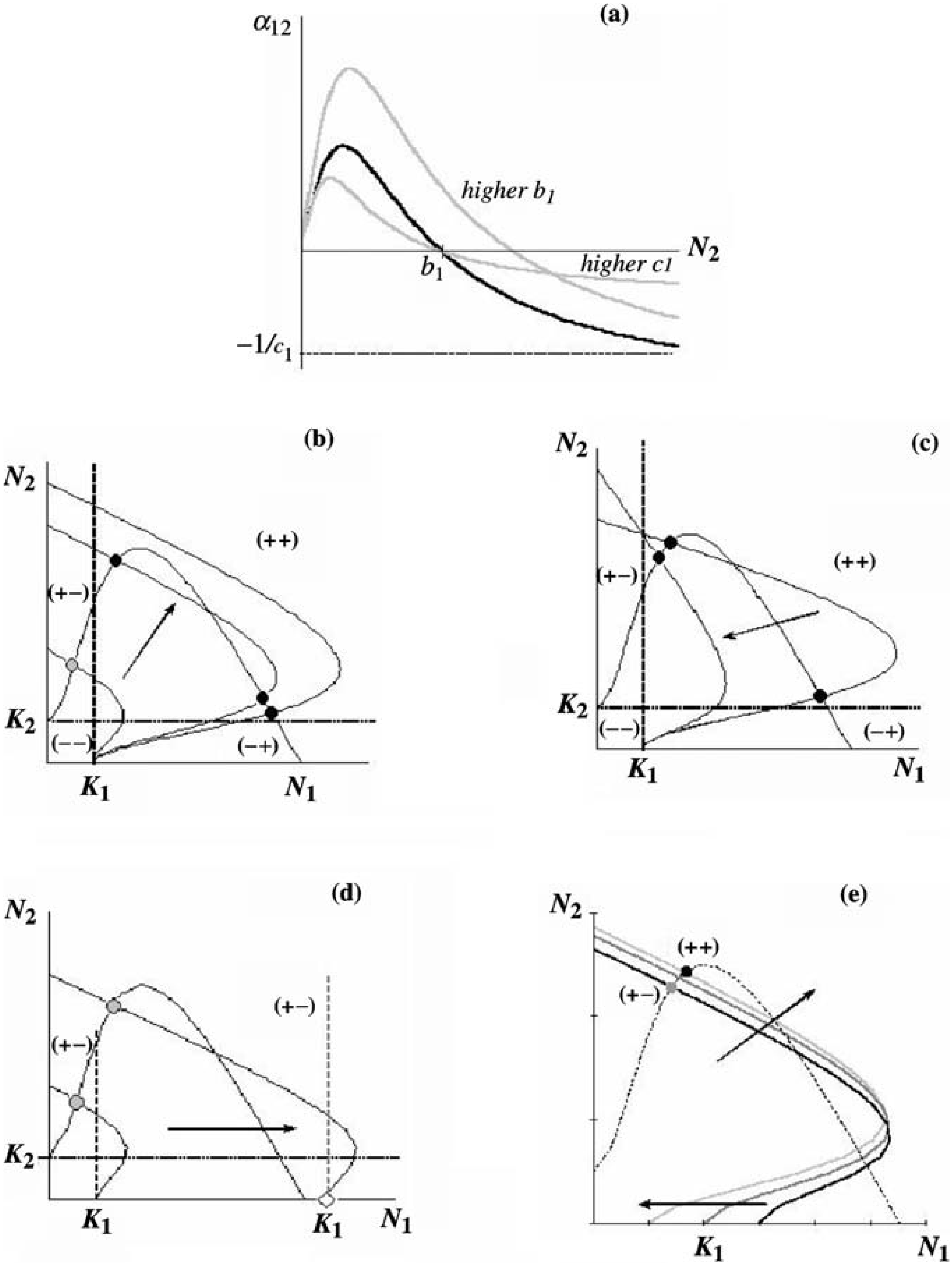

Fig. 4. **(a)** The *interaction* α_{12}*-function* – equation (2). Critical parameter values correspond to the dark line. Functions with higher parameters b_1 and c_1 (light lines) are shown for comparison; the other parameter kept constant. **(b)** and **(c)** depict the characterization of types of interaction, (+ +), (+ −), (− +), by quadrants delimited by lines at K_1 and K_2 in the N_1,N_2 phase space. Variations in the outcome may occur as parameters change. Arrows indicate shifts of N_1 nullcline as: **(b)** b_1 increases, **(c)** c_1 increases, **(d)** K_1 increases, **(e)** b_1 increases and K_1 decreases simultaneously. Other parameters constant. (●) mutualism, (⊗) victim-exploiter, (◇) exclusion of *sp2*.

5. Characterization of variations in the outcomes

Following the definition of type of interaction given in Section 2, constant lines at $N_1 = K_1$ and $N_2 = K_2$ define quadrants in the N_1,N_2 phase plane for the (+ –), (+ +), (+ –), (– –) types – see figures 4(b,c). All equilibrium points can be unequivocally characterized within. If parameters vary, the relative positions of the nullclines change so that annihilation and bifurcation of equilibria may occur, as well as changes in the outcomes of the interaction. Figures 4(b–e) show the effect of single or joint variation of parameters b_1, c_1, and K_1. These are best illustrated with ecological interpretations:

As stated in the previous section, an increase in parameter b_1 may be due to an increase in predators' pressure on a *sp1* that gets protection from a partner *sp2*. As figure 4(b) depicts, this may bring about a change from a parasitic to a mutualistic *sp2* (stable equilibrium goes from a (+ –) region to a (+ +) as b_1 increases). Hence, *sp1* may reach higher densities when associated than alone only if protection from predators is a real need. On the other hand, figure 4(d) shows that if the quality of the environment for *sp1* improves – say, for instance, that availability or nutritional quality of resources augments – then, its carrying capacity K_1 becomes higher and as a consequence, the association may vary from a parasitism on *sp1*, (+ –), to an *exclusion of sp2*, (K_1,0) – note that the point of reference for the definition of type of interaction changes.

Now consider the joint action of environmental changes: an increase in predator's abundance and a decrease in resource availability for *sp1* – i.e. b_1 increases and K_1 decreases simultaneously. Figure 4(e) shows that although the magnitudes of equilibrium population densities remain very similar, the outcome of the interaction may change from a parasitism (+ –) to a mutualism (+ +). Note that *sp1* goes from a victim to a mutualistic role because the relative magnitudes of potential densities alone and in association change for each case.

Rephrasing and expanding a previous categorization for transitions between types of interaction in Hernandez (1998), we generalize to the occurrence of variable outcomes in population interactions and distinguish two modes:

(i) Homeo-environmental variable outcomes. These occur under the same environmental conditions; that is, population densities show different stable configurations for the same set of parameters. Thus, the system presents multiple stable equilibria at coexistence and/or exclusion – e.g., X^* and Y^* in figure 3(b), or X^* and (K_1,0) in 3(d). Transitions between two stable states may occur due to perturbations that make the system move from one domain of attraction to the other. After the perturbation, the environmental setting is the same but the system is in another stable state.

(ii) Allo-environmental variable outcomes. These refer to variations that occur for the same two species but under different environmental conditions; that is, variable stable states for a different set of parameters. Transitions between these states are induced by changes in environmental conditions, which is to say, in the parameters of the model. According to the nature of this parameter variation, two ways

are recognised: (1) Via the α-function parameters: b_i, c_i – e.g. figures 4(b) and 4(c). Variation in these parameters involves a modification in the way one species perceives the other, that is, in the responsiveness and sensitivity of the interaction. Thus, it is an effect that is *intrinsic to the association* between the two species. (2) Via the carrying capacities, K_i – e.g. figure 4(d). This parameter is *extrinsic to the association* itself; however, it evaluates the relative performances of *spi* alone and in association.

It is clear that both intrinsic and extrinsic sets of parameters act jointly, and are affected by all biotic and abiotic conditions that conform the general environment shared by the two populations. However, it is sensible to analyse partial effects to reach global conclusions.

6. Bifurcation diagrams and parameter charts

The processes of annihilation and bifurcation of equilibria are best represented and studied through bifurcation diagrams (see e.g. Seydel 1994, Kuznetsov 1998). Figure 5(a) shows the bifurcation diagram for the equilibrium density of *sp1*, N_1^*, with respect to its carrying capacity,K_1, for model (3). Three curves are shown corresponding to three different b_1 values; all other parameters are kept constant. The s-shape of the curves is typical of hysteresis phenomena. The upper and lower branches contain all stable solutions; the middle branch includes the unstable ones. At turning points P and R, small changes in parameter K_1 may cause catastrophic jumps between stable branches. Catastrophic phenomena have long been recognized in biological issues before (Noy-Meir 1975; Zeeman 1977).

Figure 5(b) shows the bifurcation diagram of N_1^* with respect to parameter b_1, for three different K_1 values. Constant parameters in figures 5(a) and 5(b) are the same; thus, the two graphs together show the effect of both *intrinsic* (b_1) and *extrinsic* (K_1) effects on equilibria concordantly. For completeness, figure 6 shows bifurcation diagrams for N_1^* vs. K_1 (for different c_1) and N_1^* vs. c_1 (for different K_1).

Observe that the hysteresis phenomenon occurs for all parameters in the model.

The general effect on *equilibrium population densities* can be globally appreciated. These figures show that magnitudes of N_1^* increase with both K_1 and b_1 values, but may either decrease or increase with c_1.

6.1. Coexistence and exclusion of species

In figures 5 and 6, values of $N_1^* = K_1$ obviously correspond to an *exclusion* of *sp2* (i.e. $N_2^* = 0$); for any other N_1^* on the curves there is *coexistence* of the populations (at a corresponding finite N_2^*). The critical value $N_1^* \equiv N_{2C}$ sets the limits between the two situations.

Two-dimensional surfaces represented in a (N_1^*,b_1,K_1) or a (N_1^*,c_1,K_1) three-dimensional space, would be s-shaped folded surfaces (cusp manifolds) containing all possible equilibrium solutions. Thus, a projection of the folded area on the two-parameter plane (parameter chart) corresponds to the region of multiple equilibria. Figure 7 depicts a parameter chart for c_1 and K_1. The shaded figure was numerically computed for the same parameter values as in figure 6(a); the light line behind

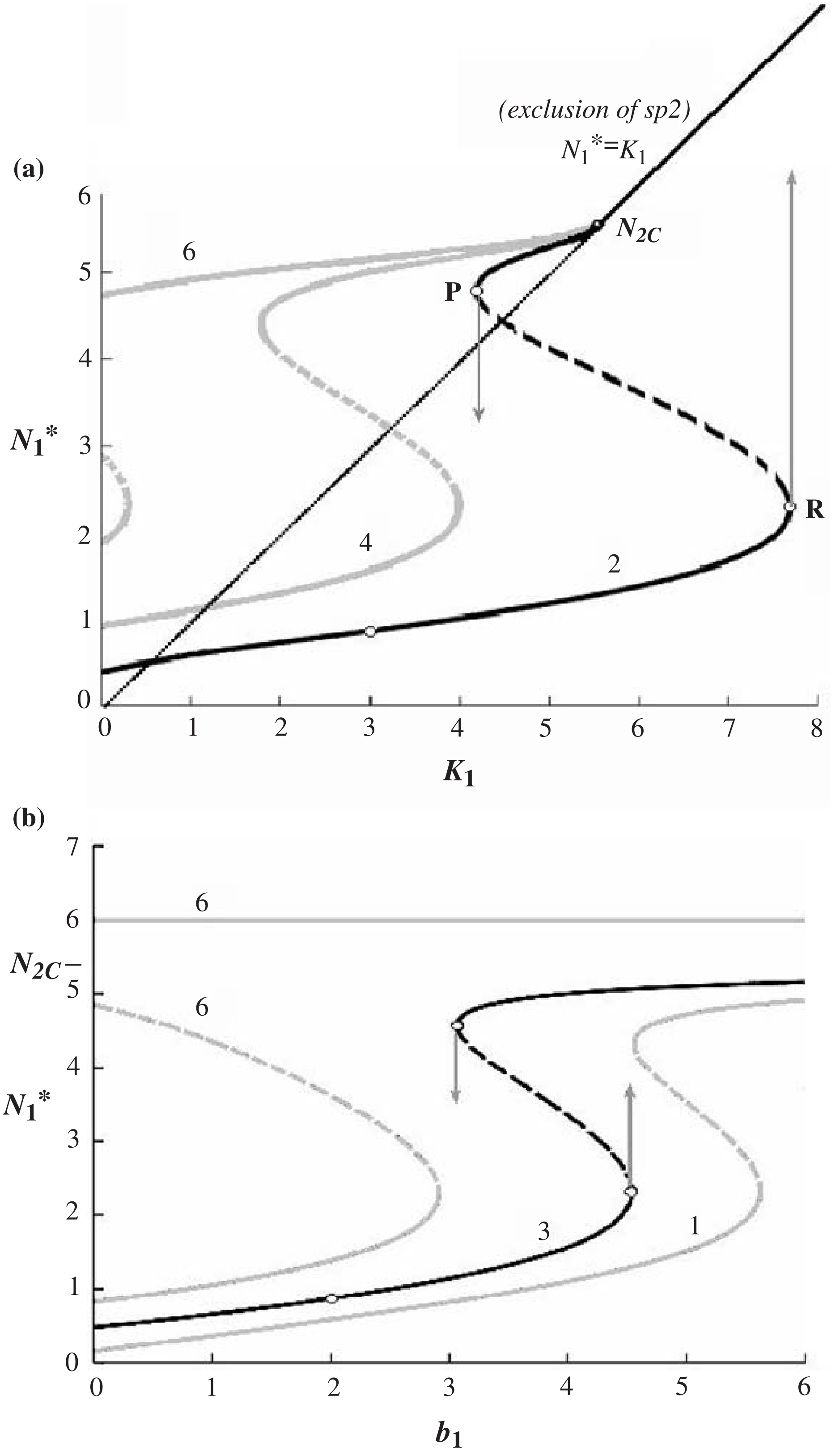

Fig. 5. Bifurcation diagrams for model (3). **(a)** Equilibrium density N_1^* versus parameter K_1 for three values of b_1 (=2, 4, 6; shown on the curves), **(b)** Equilibrium density N_1^* versus parameter b_1 for three values of K_1 (=1, 3, 6; shown on the curves). (——) Stable N_1^* and (- - - -) unstable N_1^* branches. Constant parameter values in both figures: $c_1 = c_2 = 0.5$, $K_2 = 1$, $b_2 = 5$. N_{2C} values were numerically calculated. These diagrams, and those in figures 6, 7, and 8, were computed using the program CONTENT (Kuznetsov & Levitin, 1998).

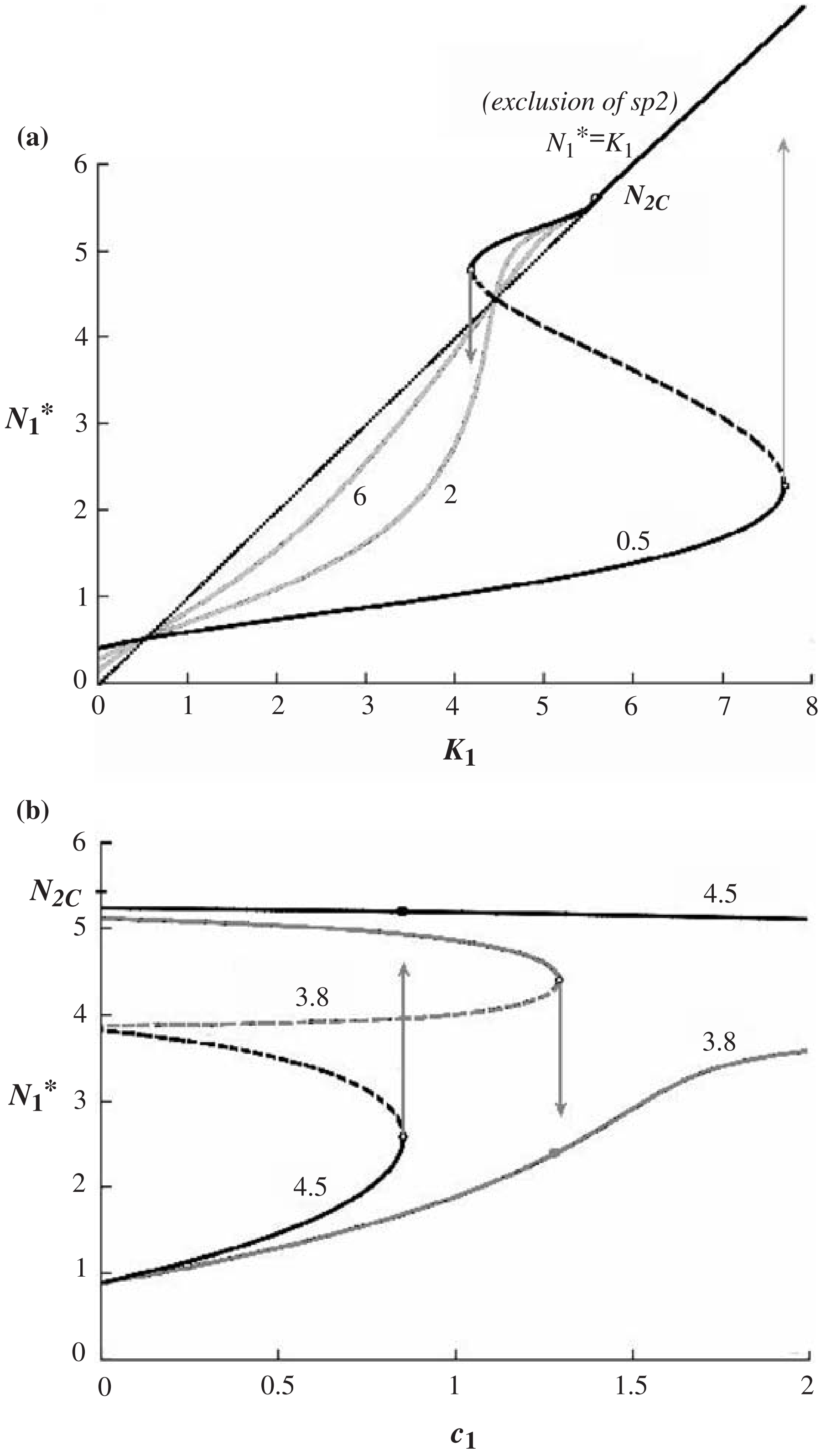

Fig. 6. Bifurcation diagrams for model (3). **(a)** Equilibrium density N_1^* versus parameter K_1 for three values of c_1 (=0.5, 2, 6; shown on the curves), **(b)** Equilibrium density N_1^* versus parameter c_1 for two values of K_1 (=3.8, 4.5; shown on the curves). (——) StableN_1^* and (- - - -) unstable N_1^* branches. Other parameter values used in the figures: $b_1 = 2$ in **(a)**, $b_1 = 3$ in **(b)**; and $K_2 = 1$, $b_2 = 5$, $c_2 = 0.5$ in both.

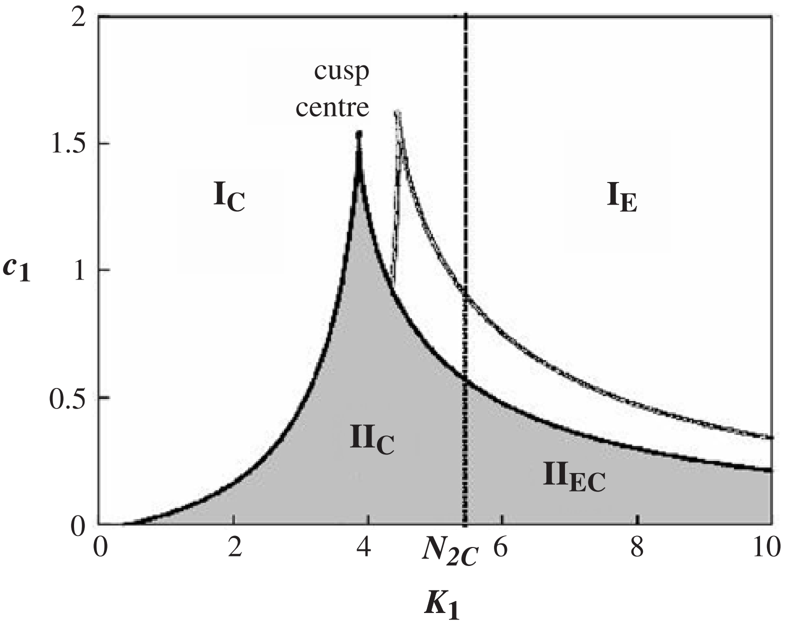

Fig. 7. Parameter chart for model (3): c_1 versus K_1. Non-shaded area corresponds to *single* stable equilibria **(I)**; inside shaded area – cusp – to *multiple* stable equilibria **(II)**; within these, $K_1 \equiv N_{2\mathrm{C}}$ delimits areas for *coexistence* **(C)** or *exclusion of sp2* **(E)**. Parameter values used in the figures: $b_1 = 3$ (shaded cusp), $b_1 = 2$ (behind), $K_2 = 1$, $b_2 = 5$, $c_2 = 0.5$. Curves in figure 6 are cross sections of this figure.

– displayed here to show a general trend among parameters – corresponds to a lower b_1 magnitude – the one used in figure 6(b); hence, diagrams in 6(a,b) are cross-sections of cusps in 7.

The boundary line of the cusp (catastrophe set) and the vertical line at the critical value $K_1 \equiv N_{2C}$ define four regions in the (K_1,c_1) parameter space for stable *coexistence* or *exclusion of one species*, and *multiple* or *unique* stable solutions. In the region where $K_1 < N_{2C}$, the shaded area corresponds to two possible stable *coexistence* solutions (II_C), and the clear area to one single *coexistence* (I_C). For $K_1 > N_{2C}$ the single solution is always an *exclusion of sp2* (I_E) whereas the multiple solutions within the shaded region include one stable *coexistence* and one *exclusion* (II_{EC}). Compare these results with the characterization of patterns in figure 3: there is a correspondence between 3(a) and the region for I_C; likewise for 3(b) and II_C; 3(d) and II_{EC}; and 3(e) and I_E.

6.2. Variable outcomes and dynamics of transitions

Bifurcation diagrams allow the visualization of different types of interactions and the dynamics of variable outcomes – *sensu* definitions in Section 2 and 5. Figure 8(a) depicts quadrants for (– +), (+ +), (+ –) and (– –) types of interaction. These are defined by two crossing straight lines: the bisector $N_1^* = K_1$ and the constant $N_1^* = b_2$. The former delimits positive and negative effects of the association on *sp1* (i.e. $N_1^* > K_1$ or $< K_1$); the latter on *sp2*. This is because b_2 is the threshold value for $N_2^* > K_2$ or $< K_2$ (check that $N_1^* = b_2$ is a solution for $N_2^* = K_2$), and thus for $\alpha_{21} > 0$ or < 0 – see figure 4(a).

As a general result, we see that as b_1 becomes higher, more equilibrium solutions lie on regions where the association is positive for *sp1* – c.f. figures 8(a) and

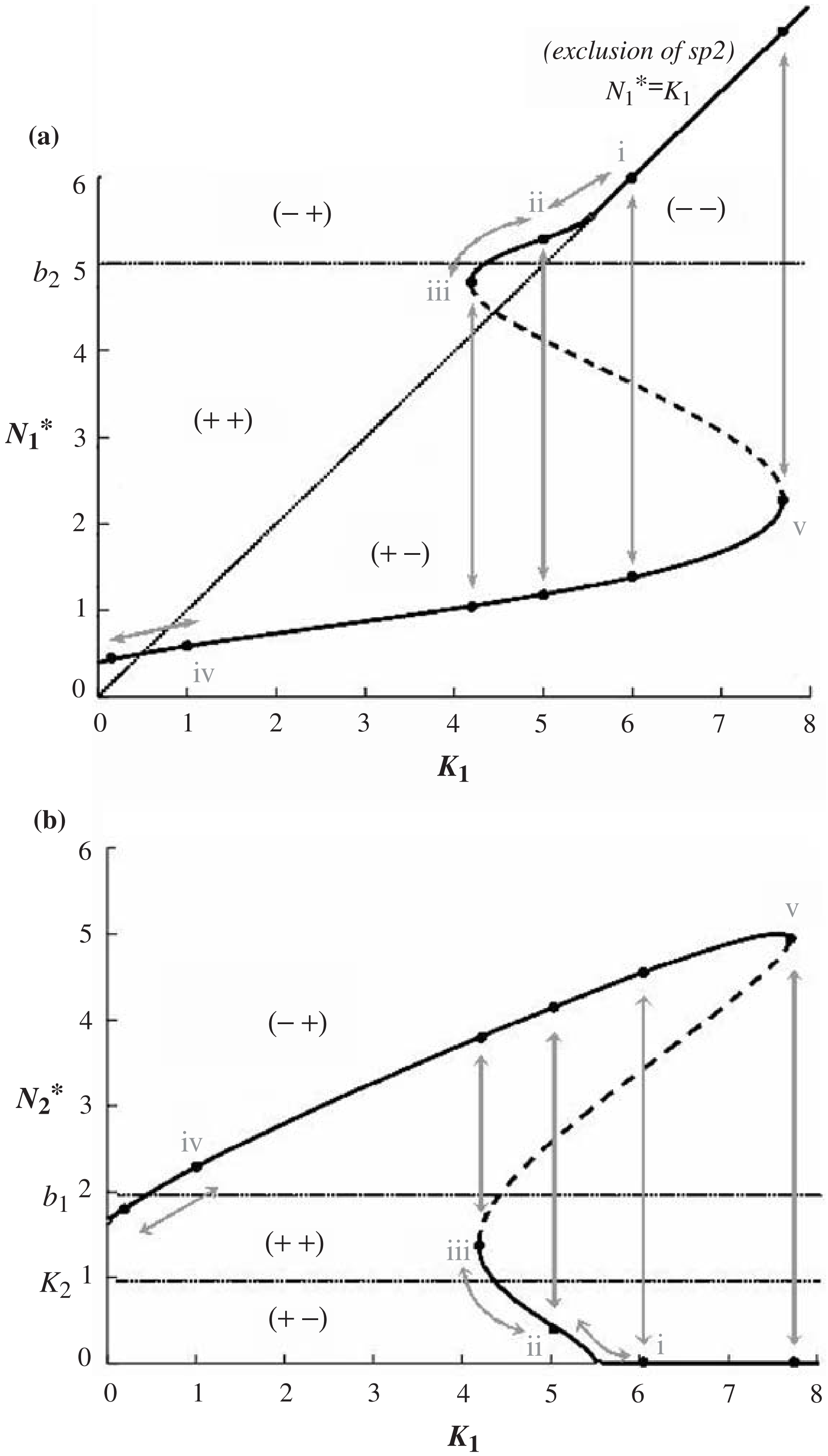

Fig. 8a, b.

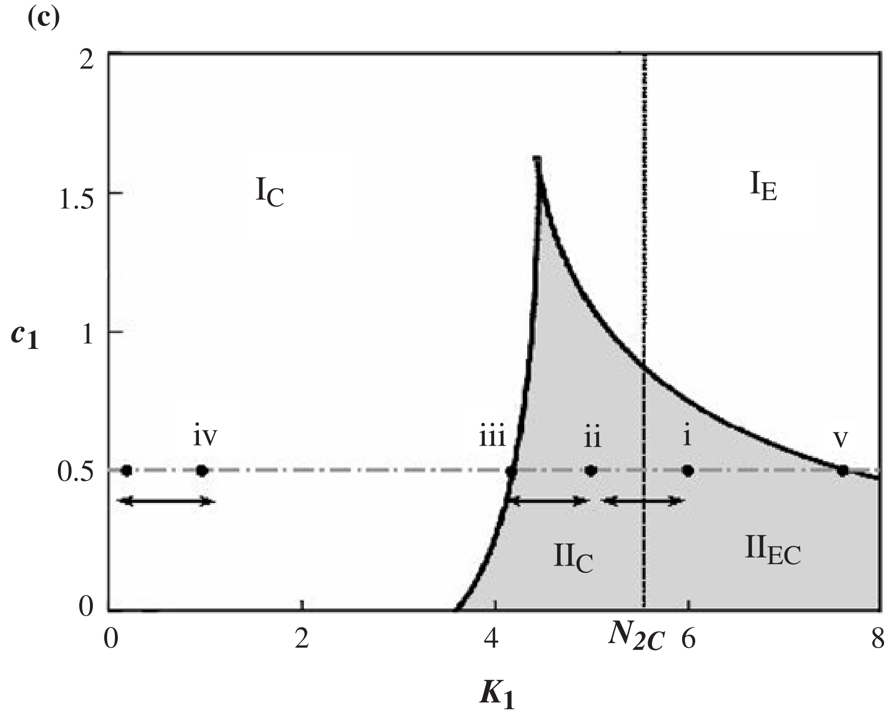

Fig. 8. (**a**) Bifurcation diagram N_1^* vs. K_1 and quadrants for different types of interactions: (+ −), (+ +), (− +), (− −), delimited by bisector $N_1^* = K_1$ and constant $N_1^* = b_2$, (**b**) Bifurcation diagram N_2^* vs. K_1 and stripes for types of interactions delimited by $N_2^* = K_2$ and $N_2^* = b_1$. (——) Stable and (- - - -) unstable equilibrium branches. (**c**) Parameter chart c_1 vs. K_1. Types of variable outcome, and transitions between them, are represented in all figures. *Homeo-environmental* variable outcomes occur between stable branches (i, ii, iii, v). A*llo-environmental* variable outcomes occur along the curve as parameter K_1 varies (i-ii-iii, and at iv) and at turning points in the form of catastrophic jumps. Parameter values used in all figures: $b_1 = 2$, $K_2 = 1$, $b_2 = 5$, $c_2 = 0.5$; and in (a) and (b): $c_1 = 0.5$.

5(a). On the other hand, as c_1 values grow, the curve tends to match the $N_1^* = K_1$ bisector – c.f. figures 8(a) and 6(a). These are expected results following the final global appreciation about the α-function parameters in Section 4.

Homeo-environmental variable outcomes may occur only if multiple equilibria exist. Arrow at **i** (downwards) illustrates the possibility of *sp2* invading *sp1* and making it its victim, even when $K_1 > N_{2C}$ (i.e. beyond the threshold invasion boundary). Arrow at **ii** illustrates the switching of roles in a victim-exploiter association. Bear in mind that these processes do not involve changes in the parameters of the model. Rather, the system is driven from one domain of attraction to another, eventually reaching the new equilibrium, but the environment where the populations interact remains the same.

Allo-environmental variable outcomes occur between stable points along the curve that lie on different quadrants. Points sequence **i**, **ii**, **iii** shows the possibility of *sp1* living alone, or associated with *sp2* as a victim, or as a mutualist, at different environmental conditions (K_1 values). At **iv** switching between mutualism and victim-exploiter associations occur again due to environmental variation.

At turning points **iii** and **v**, both *homeo-* or *allo-environmental* variations may occur, the latter in the form of catastrophic jumps due to changes in parameter K_1.

Figure 8(b) shows the bifurcation diagram of *sp2* equilibrium density, N_2^*, against parameter K_1 (observe that it is the equilibrium population density for one species with respect to the carrying capacity of the other); all other parameters are the same as those in figure 8(a). As already seen, the effects of increases in K_1 go from a stable coexistence of *sp1* and *sp2* – either at one, or two different configurations – to the exclusion of *sp2* as a unique possibility at high K_1. The figure shows clearly both routes of *sp2* to extinction as the carrying capacity of *sp1* improves. Constant lines at $N_2^* \equiv K_2$ and $N_2^* \equiv b_1$ confine stripes for the different types of interaction; hence, the possibilities of variation in the outcome, and the dynamics of transitions between them can also be displayed.

6.3. Dynamics associated to catastrophic regimes

Figure 8(c) is the parameter chart for K_1 and c_1 corresponding to 8(a) and 8(b). Observe that parameter values regarding *homeo-environmental* variable outcomes lie within the shaded area (multiple equilibria condition), whereas those for *allo-environmental* variations can be on either side. The turning points, where catastrophes may occur, delimit the borders.

The dynamics of populations with variable interactions are subject to the typical behaviour of systems with catastrophic regimes. That is, even small parameter oscillations, if they occur near the cusp centre, might make the system suffer circuitous catastrophic jumps between stable branches. In ecological terms: small environmental fluctuations – could be periodic or stochastic – say, in predator's abundance, or in resource availability, might be responsible for huge recurrent changes in the symbionts equilibrium densities and in the outcomes of the association. Conversely, if a catastrophic jump occurs where the cusp is wide, to revert the situation the parameter has to go back a very high order of magnitude – or it might be numerically impossible if it is truncated at zero. Large changes in an environmental condition might never occur due to natural constraints; or on the contrary, large environmental fluctuations might happen naturally due to a cyclic condition like, say, seasons where some environmental parameters take extreme opposite magnitudes along the year. This may give some insight into the mechanisms behind recurrent variations in the outcome of interactions, systematically following periodic environmental changes.

On the whole, in systems where bifurcations and catastrophes are involved, the particular *history* of the dynamics is determinant. That is, the ultimate outcome of the interaction between the two species depends upon initial density conditions and on the specific sequence of environmental variation thereafter.

7. Discussion

The results of the model reflect a two-sided issue in relation to the occurrence of conditional or variable interactions: (i) a somewhat *episodic* interpretation – two species may be found coexisting under one regime or another, and (ii) a *dynamical* view – transitions between different regimes. Behind both aspects lies the concept of density-dependent interaction coefficients that can change from beneficial to detrimental. This is a direct consequence of considering the interactions from a cost/benefit perspective, as has been recognised in several natural associations, but rarely included in the models. Previous theoretical studies have dealt with interactions that can be density-dependent (Addicott 1981; Wolin & Lawlor 1984), others do include the notion of costs and benefits involved in an association (Holland & De Angelis 2001); but, nonetheless, in all these models the outcomes remain bounded to being always beneficial or always detrimental. Some other theoretical and empirical literature have explored the gradient of outcomes in the mutualism/parasitism continuum aiming to explain evolutionary issues (Hochberg *et al.* 2000; and see Herre *et al.* 1999; Hoeksema & Bruna 2000, for reviews).

The model presented in this work explores formal expressions for the concept of variable outcomes as a result of the balance between benefits and costs for each partner species, in a way that may cover the whole range of natural possibilities. But particularly, the interaction α-function studied in this paper assumes that for a given species the association with another species promotes increases in its growth rate and equilibrium density, if the abundance of the latter is low (i.e. the benefits of the association outweigh any costs involved), but the effect is reversed as densities increase.

7.1. About catastrophes and conflicting factors

As expressed in the first ideas about catastrophic phenomena applied to biological issues, if two *conflicting* factors are influencing the state variable under study the result is a *cusp-catastrophe* (Zeeman 1977). Our results show environmental changes that cause conflicting effects on equilibrium population abundances of associated species, and on the outcome of the association. Specifically, large carrying capacities, K_i, bid for higher equilibrium densities; high b_i values promote positive outcomes in the association with the other species; and the effect of c_i magnitudes may be contrasting depending on relative population abundances. Hence, different combinations of parameter changes may act in conflicting ways. The main issue is that the influence of variations in the carrying capacities of the populations may be opposite to variations in the sensitivities of the interactions between the species; this is to say, factors that are *extrinsic* to the nature of the association and those that are *intrinsic* may act in conflicting ways upon the outcome and the dynamics of interacting populations.

The effects of these conflicting actions may balance out to some extent, as could be the case discussed in Section 5 about the simultaneous variation of predators abundance and environmental quality for a given species. This example deserves further comments. First, these environmental variations were represented by independent parameters (b_i and K_i); however, under some circumstances these are likely to be connected. For instance, an increase in predator's abundance carries along an implicit decrease in the carrying capacity since it also reflects quality of environment for the prey. Second, environmental changes are likely to cause alterations on the *sp2* nullcline also; particularly via variation in the parameters of the *sp2* interaction α-function; this is not represented in the figure. Nevertheless, the theoretical approach is appropriate to distinguish partial effects.

This example aims to shed light on the way environmental factors can operate in conflict in a natural situation, and how the model offers an interpretation. To faithfully represent a particular association with variable outcomes involves fitting α-functions for the two species taking into account their specific nature, and, if available, some data. Needless to say that the appropriate functional form is not necessarily the one analysed here. Additionally, it might occur that interaction coefficients are density dependent for only one of the species – so that only one of the nullclines show the humped shape, or, on the other hand, the interaction functions may depend on both populations' densities.

The results of the model allow for some global appreciations on the issue of the persistence of the association, that is, on conditions for *coexistence* in contrast to *exclusion of one species*. Low carrying capacity values promote coexistence, whereas higher magnitudes – above critical values – bid for the stable occurrence of one species alone with no possibility of invasion by the other. In terms of the model: for large K_1values we expect high N_1 magnitudes; but then, interaction coefficient α_{21}, goes into negative ranges. Consequently, *sp2* may be finally excluded from the association and prevented from invading. In ecological terms: in a facultative association, when environmental conditions are sufficiently good for a given species i, the cooperation that an associated species j has to offer might be a surplus item, regardless of how good it could get. Thus, the feasible outcome is the *exclusion* of the latter (this hints for self-regulatory mechanisms for mutualistic associations). On the other hand, the contribution from species j is much welcome when environmental conditions are tougher, and then stable *coexistence* is the most plausible situation.

It is interesting to comment here about the situation depicted in figure 3(c) where both K_1 and K_2 values are assumed very low; that is, extreme adverse conditions for both species. There are three possible stable solutions for coexistence, and all of them are mutualisms. It is important to notice that the density values in equilibrium are of the order of ten times the K_i values. This case is very close to an obligate mutualism.

7.2. A catastrophe for a predator

An interesting case reported in the literature allows venturing an interpretation of some of the ideas and conceptions proposed via the model in this work. This is the situation of a predator–prey reversal in a marine benthic ecosystem reported by Barkai & McQuaid (1988). After a perturbation that totally removed the key benthic predator (rock lobsters) in Marcus Island (South Africa), the community shifted to a wholly different configuration: extensive mussel beds and very high densities of whelks. In a closely located island (Malgas Island), with same abiotic conditions, the original configuration still exists: abundant rock lobsters, but most of its normal prey species (whelks) are nearly absent. In order to examine what prevents reinvasion of Marcus Island by the lobsters, a number of these were transferred there. These were overwhelmed and consumed by the whelks in a short period of time. The authors consider that this reversal in the predator-prey roles may provide an intrinsic mechanism for the continued exclusion of the predator.

This could be a case of a conditional outcome with two stable configurations, which may be interpreted, as a first approach, through the situation depicted in figure 3(d); *sp1* represents the whelks and *sp2* the lobsters. The situation in Malgas Island corresponds to coexistence at **X***, where the interaction is (+ –): lobsters predate on whelks although the association is not obligate since they consume other species present; the whelks are kept at a density below its carrying capacity by the predators. The situation in Marcus Island is the stable exclusion at (K_1,0): whelks are at their carrying capacity, which could be reached after the removal of the predators by the perturbation. Once at this state, re-invasion by lobsters starting from small densities would not be possible.

Now visualize it on the bifurcation diagram in figure 8(a), where N_1^* corresponds to the whelks equilibrium density. Assume that before the perturbation the situation in both Malgas and Marcus islands was at some point in the lower stable branch where the interaction is (+ –). A sudden and drastic removal of the predator species in Marcus Island can induce a *homeo-environmental* transition, for instance, at **i** upwards. Or, alternatively, the perturbation may translate into an increase in K_1 promoting an *allo-environmental* transition via catastrophic jump at **v** (the mere fact of the absence of the predator means an improvement in the environmental conditions for the whelks). In both cases, the new stable situation in Marcus Island is the *exclusion of the lobsters*, and the whelk population at its carrying capacity. Then, for the lobsters to re-invade Marcus Island as main predators again, the carrying capacity K_1 would have to go down to a value that leads the system to turning point at **iii**; where another catastrophic jump would allow the original condition again. Note that this K_1 value is lower than the one at which the first catastrophic transition occurred; thus, it is not necessarily a naturally feasible option for this environment.

As an additional comment, observe that for the transition at **v**, the carrying capacity K_1 has gone beyond the critical N_{2C} value – see figure 8(c) – even before reaching the turning point. This makes the interaction go from a (+ –) to an exclusion directly. However, if the transition occurs at a $K_1 < N_{2C}$, as in point **ii**, the system goes to a (– +) instead. It would be desirable to be able to assess this possibility. That is, if the quality of environment for the whelks deteriorates to a degree that sets the system in an stable point around **ii**, i.e. in the (– +) region; then, instead of the total exclusion of the lobsters, there should be a stable coexistence of whelks predating on lobsters. No doubt this would prove an ecologically interesting situation: alternative predator-prey roles only 4 km apart.

Although this is a speculative inference, it provides a clear insight into how the model analysed here interprets and represents the possible mechanisms involved in the dynamics of conditional or variable interactions.

8. Summary and general conclusions

The biological association between two species involves both costs and benefits for each partner population; the outcome of the interaction may be beneficial or detrimental depending on the net balance of these: *conditional or variable outcomes* – a phenomenon that is of common occurrence in nature. This article presents a study that aims to provide insight and mould a general concept on this phenomenon, and to fill the lack of theoretical analysis on associations that can switch between beneficial and detrimental. This is done by means of introducing density-dependent interaction coefficients that can take positive and negative values. The study casts the following general conclusions:

Ecological conditions determine the range of possible outcomes of a conditional interaction, and this is performed via two ways. One is *intrinsic to the nature of the association*: the sensitivity and responsiveness of each species to the presence of the other species – expressed in an *interaction α-function*. The other is *extrinsic to the association itself:* the quality of the environment related to each species when existing on its own – *carrying capacities*. These factors may act in conflict and consequently *catastrophic* events occur.

In facultative variable associations, poor extrinsic environmental conditions bid for a stable *coexistence* of the populations, that is, for the persistence of the association; otherwise, the *exclusion* of one species is a likely outcome.

Variation in the outcome of population interactions may occur for species under the same, or under different, ecological settings: *homeo-environmental* and *allo-environmental variable outcomes*, respectively. Transitions between them may involve catastrophic jumps. This catastrophic nature of the ecological process may lead the system to undergo large fluctuations in population abundances under minimal environmental variations; or to systems that come to states of no possible return.

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Appendix

In order to study the local stability of the different fixed points of the system (3), we take

$$r_1 N_1 \left[1 - \frac{N_1}{K_1} + \left(\frac{b_1 N_2 - N_2^2}{1 + c_1 N_2^2} \right) \frac{N_2}{K_1} \right] = 0 \tag{A.1}$$

and

$$r_2 N_2 \left[1 - \frac{N_2}{K_2} + \left(\frac{b_2 N_1 - N_1^2}{1 + c_2 N_1^2} \right) \frac{N_1}{K_2} \right] = 0 \tag{A.2}$$

If we look for non-trivial equilibria, the parameters satisfy the equations

$$1 - \frac{N_1}{K_1} + \left(\frac{b_1 N_2 - N_2^2}{1 + c_1 N_2^2} \right) \frac{N_2}{K_1} = 0 \tag{A.3}$$

and

$$1 - \frac{N_2}{K_2} + \left(\frac{b_2 N_1 - N_1^2}{1 + c_2 N_1^2} \right) \frac{N_1}{K_2} = 0 \tag{A.4}$$

The Jacobian matrix of equation (3) evaluated at any of the equilibria is then obtained by substituting (A.3) and (A.4)

$$\begin{bmatrix} -\frac{N_1 r_1}{K_1} & -\frac{N_1 r_1 \left[N_2^3 + 2(K_1 - N_1)\right]}{K_1 N_2 \left(c_1 N_2^2 + 1\right)} \\ -\frac{N_2 r_2 \left[N_1^3 + 2(K_2 - N_2)\right]}{K_2 N_1 \left(c_2 N_1^2 + 1\right)} & -\frac{N_2 r_2}{K_2} \end{bmatrix} \tag{A.5}$$

The characteristic polynomial has the form

$$(a + \lambda)(b + \lambda) - cd = 0 \tag{A.6}$$

with

$$a = \frac{N_1 r_1}{K_1}, \quad b = \frac{N_2 r_2}{K_2}, \quad c = \frac{N_2 r_2 \left[N_1^3 + 2(K_2 - N_2)\right]}{K_2 N_1 \left(c_2 N_1^2 + 1\right)},$$
$$d = \frac{N_1 r_1 \left[N_2^3 + 2(K_1 - N_1)\right]}{K_1 N_2 \left(c_1 N_2^2 + 1\right)} \tag{A.7}$$

Since solutions of equation (A.6) are of the form

$$\frac{-(a + b) \pm \sqrt{(a + b)^2 - 4(cd + ab)}}{2} \tag{A.8}$$

depending on the signs of both c and d, if the solutions are complex, then their real part is $-(a + b)/2$. If they are real, one is negative and the other one can be positive, in particular if the stationary solution is unstable, it is a saddle point.

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