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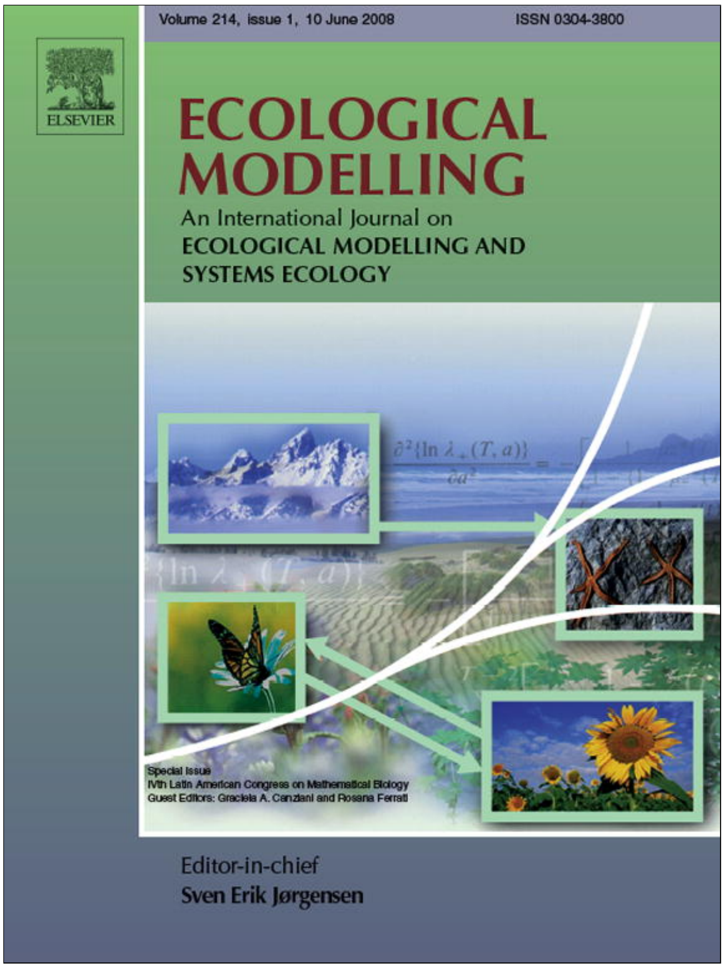
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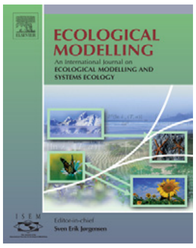

Spatiotemporal dynamics in variable population interactions with density-dependent interaction coefficients

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ABSTRACT

In this article, I present a two-patch metapopulation model with locally explicit dynamics to study the effect of spatial heterogeneity and dispersal upon population interactions with variable or conditional outcomes. These are interactions that may be either detrimental or beneficial for each species depending on the balance of the density-dependent costs and benefits involved. The local dynamics respond to density-dependent α-interaction functions that may change sign, thus yielding a diversity of possible local outcomes for the association in terms of type of interaction and in the number of stable solutions. The spatiotemporal model predicts that the fragmentation of space and dispersal between patches may cause further variation in these outcomes. First, the demographic performance of a species in the association is enhanced if migrations cause a proportional increase of individuals of its own species; being so, a victim may become a mutualist or an exploiter, an excluded species may invade, and a good competitor may overcome its own carrying capacity: the '*enhancement effect of dispersal*'; a sort of rescue effect in source-sink dynamics. The underlying mechanisms involve an interplay between density-dependent effects of dispersal per se and the relative local and global average α-interaction functions, which involve costs and benefits at both the local and regional level that may either counteract or reinforce each other; thus, localities and/or populations may change dynamically their sink or source role in the spatial dynamics. A significant insight arises herewith: in the context of variable or conditional interactions the concept of the *role of a species* does not make strict sense; it becomes a *spatiotemporal dynamic quality*. Second, regardless of which species disperses, bifurcation of equilibria may occur in those patches that receive the migrating individuals, and annihilation of equilibria in those from where migration leaves; thus, the number of equilibria increases or decreases accordingly.

1. Introduction

The study of population interactions provides a basis to understand community structure. The dynamics of all types of population interactions – competition, mutualism, predation, etc. – have been studied from both the empirical and theoretical points of view. A diversity of models have been developed to analyse the spatiotemporal dynamics of interacting populations, that is, the performance at both the local and the regional level (e.g. reviews in Gilpin and Hanski, 1991; Renshaw, 1991; Hanski and Gilpin, 1997; Rhodes et al., 1996). The approaches to these studies range from the classical patch-occupancy model (Levins, 1969, 1970), with or without structure, spatially explicit or not, to more complex models as

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those including locally explicit dynamics. However, the role of spatial heterogeneity and dispersion on populations with *variable or conditional outcomes* has not been studied from a theoretical approach.

Many authors acknowledge that variable or conditional population interactions exist and that these are not easily categorized within the standard forms of interactions (Abrams, 1987; Thompson, 1988; Bronstein, 1994; Cushman, 1991; Cushman and Addicott, 1991); also, some theoretical approaches have been attempted to characterize and understand their (temporal) dynamics (Wolin and Lawlor, 1984; Hernandez, 1998; Hernandez and Barradas, 2003; Zhang, 2003; Neuhasser and Fargione, 2004). Variable or conditional population interactions refer to those associations that can yield different outcomes depending on a diversity of factors, e.g. environmental conditions, population abundances, size, age, or stage of development of individuals, and so forth. One approach to the study of these interactions considers that the ultimate outcome depends on the net balance of density-dependent costs and benefits associated to the presence of the partner species (Bronstein, 1994; Holland et al., 2002; Hernandez and Barradas, 2003). This might be the case of the interaction between some species of ants and homopteran herbivores, in which the homopterans obtain the benefit of protection from the ants in exchange for food (honeydew in excretions or secretions), but when the ants have another source of food in the environment, e.g. flowers, and under appropriate relative ant-homopteran abundances, they may predate on the homopterans; thus, a mutualistic association turns into a predator–prey interaction (Addicott, 1979; Cushman, 1991; Cushman and Addicott, 1991; Stadler and Dixon, 1998; Del-Claro and Oliveira, 2000; Offenberg, 2001). The switching of roles is particularly interesting in the case reported by Barkai and McQuaid (1988) in Malgas and Marcus Islands in South Africa. At Malgas, rock lobsters predate on whelks (among other preys), but in Marcus, only 4 km apart, an abundant population of whelks exist, which were able to consume within a week, a thousand lobsters introduced in an attempt to recolonize that region. Density-dependent costs and benefits provide also a framework of study for the outcome of the interaction between Mullerian mimics, which facilitate the training of predators in recognizing unpalatable preys, but at high densities compete for resources (Gilbert, 1983); and, in the outcome of epibiotic interactions in aquatic environments, in which hosts receive the benefits of camouflage from epibionts attached to their surfaces in exchange for mobility for the epibionts, but when epibionts are abundant the association may provide high costs to the hosts in terms of damage to the surface or mobility impairment (Vance, 1978; Duffy, 1990; Threlkeld et al., 1993), or even by attracting other predators (Wahl and Hay, 1995).

In this article, I present a theoretical study of the *spatiotemporal dynamics* of population interactions with *variable outcomes*. Considering the nature of these interactions, I use a metapopulation model with locally explicit dynamics, since the main concern is whether or not spatial heterogeneity and dispersal can influence the outcome of the interaction, as it would be determined by the local dynamics (with no dispersal). I use the model developed by Hernandez (1998) and Hernandez and Barradas (2003) as the base model to predict the local outcomes, and I examine and discuss the spatiotemporal dynamics under the light of source-sink dynamics models. This theoretical approach highlights the density-dependent nature of both the local and regional dynamical processes.

Sink populations are localities where the species have a negative growth rate; *source* populations have positive growth rate. In a metacommunity mutualism model (Armstrong, 1987; Amarasekare, 2004a) sink localities are those in which the pollinator and/or plant densities are below the critical threshold that would permit pollination, and therefore persistence of the populations (*Allee effect*), so they go extinct. Dispersal of pollinators from source localities (those with densities above threshold, thus, in stable coexistence) into sink populations prevents local extinction (*rescue effect*). In a metapopulation competition model (Amarasekare and Nisbet, 2001) patches occupied by superior competitors are sink for inferior competitors, so the latter become locally excluded. However, patches occupied by inferior competitors only, or by both competitors at stable coexistence, are sources of emigrating inferior competitors that under certain conditions, rescue those at sink populations allowing local coexistence of the two species. The key result is that dispersal of individuals per se involves density-dependent effects, which can act positively or negatively on population growth rates, and therefore on stability conditions and the outcomes of population interactions.

2. The model

I use a two patch locally explicit dynamics model to assess the effect of spatial heterogeneity and dispersal on the outcome of variable interactions between two species.

2.1. *Local dynamics (within a patch)*

The basic model for the dynamics of interacting populations is a system of ODEs, one for the dynamics of each species (*sp1* and *sp2*),

$$\frac{dN_i}{dt} = r_i N_i \left[1 - \frac{N_i}{K_i} + \alpha_{ij}\frac{N_j}{K_i}\right], \qquad i, j = 1, 2 \tag{1}$$

where N_i, r_i, K_i, and α_{ij} are population densities, intrinsic rates of increase, carrying capacities, and interaction coefficients, respectively, for each population. This model corresponds to facultative interactions for both species, i.e. each population may persist alone and reach its carrying capacity.

To model *variable population interactions*, I consider that the α_{ij} are density-dependent functions (sensu Hernandez, 1998). Such an α-interaction function is a result of the balance of costs and benefits associated to the presence of the partner species, which are density-dependent. For this work, I chose a linear α-interaction function, that is, $\alpha_{ij} = b_i - c_i N_j$, where b_i and c_i are parameters (>0) related to the intrinsic properties of the interaction. This is the simplest functional form of an α-interaction function that keeps the main characteristic required to represent the dynamics of a variable interaction, this is, that the magnitude of α_{ij} changes sign with the partner's density. In this case, the α_{ij}'s take positive values at low

N_j densities, and negative values at higher N_j densities. This means that at low densities benefits are greater than costs whereas at higher densities the association may become detrimental as costs become greater than benefits.

The local model for the dynamics of the two populations with variable interaction thus becomes

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1\left[1-\frac{N_1}{K_1}+(b_1-c_1N_2)\frac{N_2}{K_1}\right]\\ \frac{dN_2}{dt} &= r_2 N_2\left[1-\frac{N_2}{K_2}+(b_2-c_2N_1)\frac{N_1}{K_2}\right]\end{aligned} \tag{2}$$

The detailed dynamics of this and equivalent versions of this model are given in Hernandez (1998) and Hernandez and Barradas (2003). The relevant features for the purpose of the spatiotemporal analysis to be presented in this paper can be summarized as

(i) Numerical and graphical analyses of model (2) shows that the system may present either a *single* global stable solution or *multiple* locally stable solutions (two for the linear α-function) depending on the set of parameter values.

(ii) The two populations may *coexist* stably as: mutualists (+ +), as victim–exploiters, both (+ −) and (− +) situations, but not as competitors (− −); or there can be *exclusion* of one species from the association, that is, stable solutions at (K_1, 0) or (0, K_2). The (0, 0) solution is always unstable (saddle point).

(iii) The model predicts the possibility of *variation in the outcome or type of interaction*, i.e. populations may have alternative stable interaction regimes with different types of interaction associated, either for the same or for different environmental conditions (determined by the set of parameter values). These are called *homo-environmental* and *allo-environmental variations*, respectively. Variation in parameter values may induce bifurcations and/or annihilation of equilibria, and subsequently catastrophic phenomena (hysteresis) can occur between stable equilibria (of different, or the same, type of interaction).

(iv) The type of interaction is characterized by comparing the *ultimate* performances of each population in association with the performances alone, that is, the effect of *spi* on *spj* is positive if *spj* reaches a stable density higher than its own carrying capacity when associated with *spi*.

Fig. 1 summarizes these results in the form of some of the different nullcline patterns possible for the local dynamics of a variable population interaction.

2.2. Regional dynamics (between patches)

Consider now a two patch model with locally explicit dynamics as defined by the local model above and migration of individuals occurring between patches (Fig. 2 illustrates the metapopulation dynamics). The model becomes

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1\left[1-\frac{N_1}{K_1}+(b_1-c_1N_2)\frac{N_2}{K_1}\right]-\gamma_1N_1+\delta_1M_1\\ \frac{dN_2}{dt} &= r_2 N_2\left[1-\frac{N_2}{K_2}+(b_2-c_2N_1)\frac{N_1}{K_2}\right]-\gamma_2N_2+\delta_2M_2\\ \frac{dM_1}{dt} &= s_1 M_1\left[1-\frac{M_1}{L_1}+(g_1-h_1M_2)\frac{M_2}{L_1}\right]-\delta_1M_1+\gamma_1N_1\\ \frac{dM_2}{dt} &= s_2 M_2\left[1-\frac{M_2}{L_2}+(g_2-h_2M_1)\frac{M_1}{L_2}\right]-\delta_2M_2+\gamma_2N_2\end{aligned} \tag{3}$$

with variables and parameters as defined in Table 1. Density-dependent interaction functions in patch 2 are also linear, defined as $\beta_{ij}=g_i-h_iM_j$.

Other model assumptions are: (i) dispersion is density independent, (ii) patches are of equal size, (iii) the number of migrants is conserved between patches, i.e. the number of individuals from one species that leave one

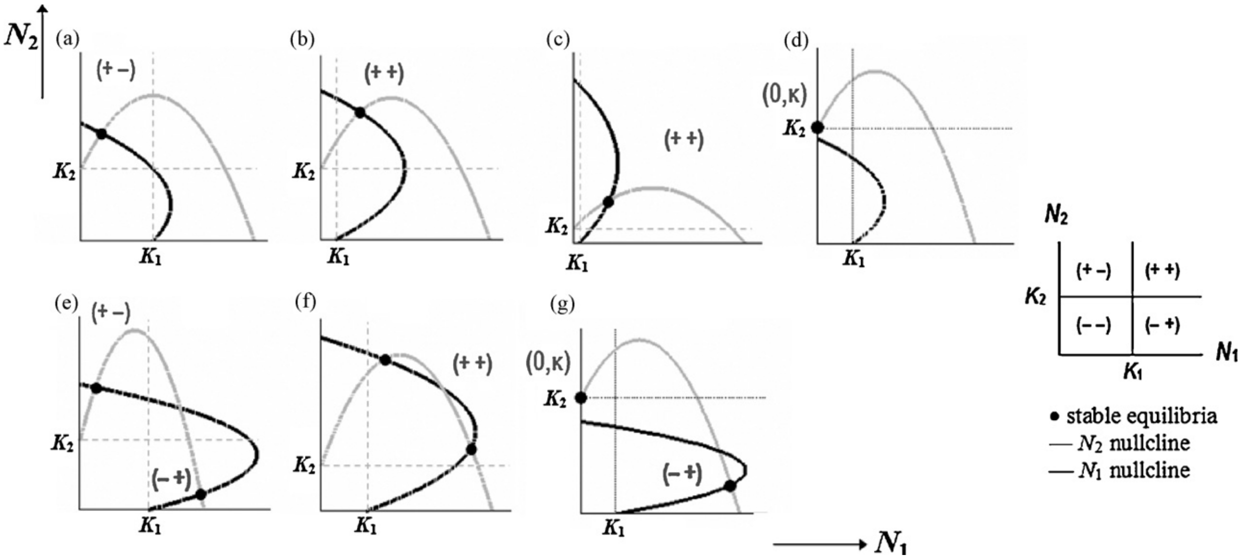

Fig. 1 – Main features of the local dynamics of variable population interactions with density-dependent linear α-interaction functions. The graphs show some of the possible nullcline patterns: *one* (a–d) or *two* (e–g) stable solutions; in which species may *coexist* (a–c, e–g) or one may be *excluded* (d and g); and with the possibility of *variation* in the type of interaction: (+ −) in (a and e), (+ +) in (b, c and f), (− +) in (e and g). The legend in the figure shows graphically the definition of type of interaction used in this approach.

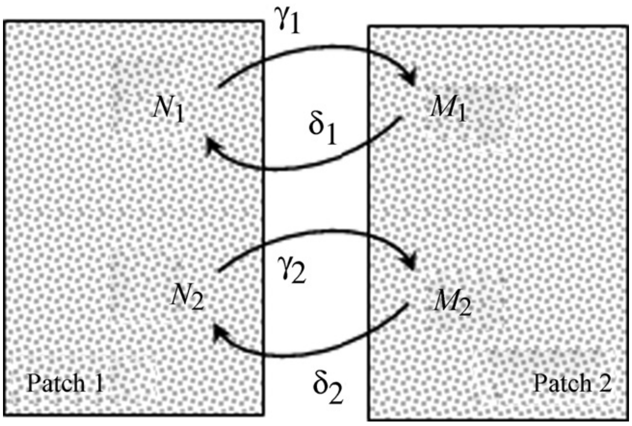

Fig. 2 – Sketch of the two-patch metapopulation model with locally explicit dynamics. See Eq. (3) and Table 1.

patch is the same as the number that arrives at the other patch.

2.2.1. *Spatial heterogeneity and environmental parameters*

Parameters K_i, b_i, c_i, and L_i, g_i, h_i are the expressions of the environment in patch 1 (P1) and patch 2 (P2), respectively. These environments can be either the same for the two patches ($K_i = L_i$, $b_i = g_i$, $c_i = h_i$), or different (some $K_i \neq L_i$, $b_i \neq g_i$, $c_i \neq h_i$). When the patches have equal environments (P1 = P2), spatial heterogeneity occurs if they are not contiguous, that is, they are islands of suitable habitats for both species within a wider non-suitable regional space. In this case, the *local* (i.e. with no migration) outcomes of the interactions – number of equilibria, stability and type of interaction – are the same for both patches. When the environments are different (P1 ≠ P2), they can be either contiguous or not; and the results for equilibria and stability should be different for the isolated patches, whereas the outcome of the type of interaction might be different or not (see Fig. 1).

Table 1 – Variables and parameters in the spatiotemporal two-patch model for the dynamics of variable interaction (Eq. (3))

Patch 1	Patch 2	
N_1, N_2	M_1, M_2	*sp1* and *sp2* population densities, respectively
K_1, K_2	L_1, L_2	*sp1* and *sp2* carrying capacities, respectively
α_{12}, α_{21}	β_{12}, β_{21}	density-dependent interaction-functions $\alpha_{ij} = b_i - c_i N_j$, $\beta_{ij} = g_i - h_i M_j$
b_1, c_1	g_1, h_1	Parameters for linear α_{12} and β_{12} for *sp1*
b_2, c_2	g_2, h_2	Parameters for linear α_{21} and β_{21} for *sp2*
γ_1	Migration fraction of *sp1* individuals from Patch 1 to Patch 2	
γ_2	Migration fraction of *sp2* individuals from Patch 1 to Patch 2	
δ_1	Migration fraction of *sp1* individuals from Patch 2 to Patch 1	
δ_2	Migration fraction of *sp2* individuals from Patch 2 to Patch 1	

See also Fig. 2.

2.2.2. *Migration modes and parameters*

Migrations between patches may be *specifically*, or *geographically* driven. In the first case, only one of the two species migrates due to intrinsic biological characteristics of the species; thus, when *spi* migrates, and *spj* does not, migration parameters take values $\gamma_i > 0$, $\delta_i > 0$, $\gamma_j = 0$, $\delta_j = 0$. In the second case, migrations occur in only one direction due to spatial or geographic characteristics of the environment; for instance, air drafts or water currents, climatic gradients, physical barriers, etc. Thus, when movement goes from P1 to P2 migration parameters are both $\gamma_i > 0$ and both $\delta_i = 0$, and vice versa when movement goes from P2 to P1.

Obviously, intermediate migration and spatial modes can occur, with all parameters taking values accordingly.

3. Numerical analysis and results for selected situations

The main interest in this work is to study the effects of spatial heterogeneity on interactions with variable outcomes using the density-dependent coefficients model. Thus, I analysed different migration patterns comparing results with those of isolated patches (i.e. with no migration), but varying the migration parameters γ_i and δ_i only, so that whatever effects observed would be due to species movements and not to local environmental variations.

Due to the high non-linearity of the model it was studied numerically, inspecting through wide parameter ranges in order to cover all possible situations of both spatial and migration modes. In each case I looked at:

(i) Variations in the *stable outcomes of the local interactions*, distinguishing:
  - *coexistence* in mutualism (+ +), competition (− −), or victim–exploiter (+ −), (− +), interactions;
  - *exclusion* of species 1: (0, κ), or of species 2: (κ, 0), where κ may stand for either K_i or L_i.

(ii) Variations in the *number of local stable solutions*: from single to multiple solutions, or vice versa, via bifurcations and annihilations.

I chose to present here four particular situations that jointly provide a scope of the general performance of the model, that is, combinations of: patches of different or equal environments, with single or multiple stable solutions when isolated, in which populations can coexist or be excluded. These are cases 1–4, described in detail below. Although all solutions were obtained numerically and recorded in figures, for the sake of clarity only the graphical solutions are presented here. Figs. 3–6 show the results in graphic form correspondingly. The phase plane graphs in these figures show stable (black dot) and unstable (white dot) equilibrium solutions for each patch (P1, P2), when they are (a) isolated, or (b and c) when migration

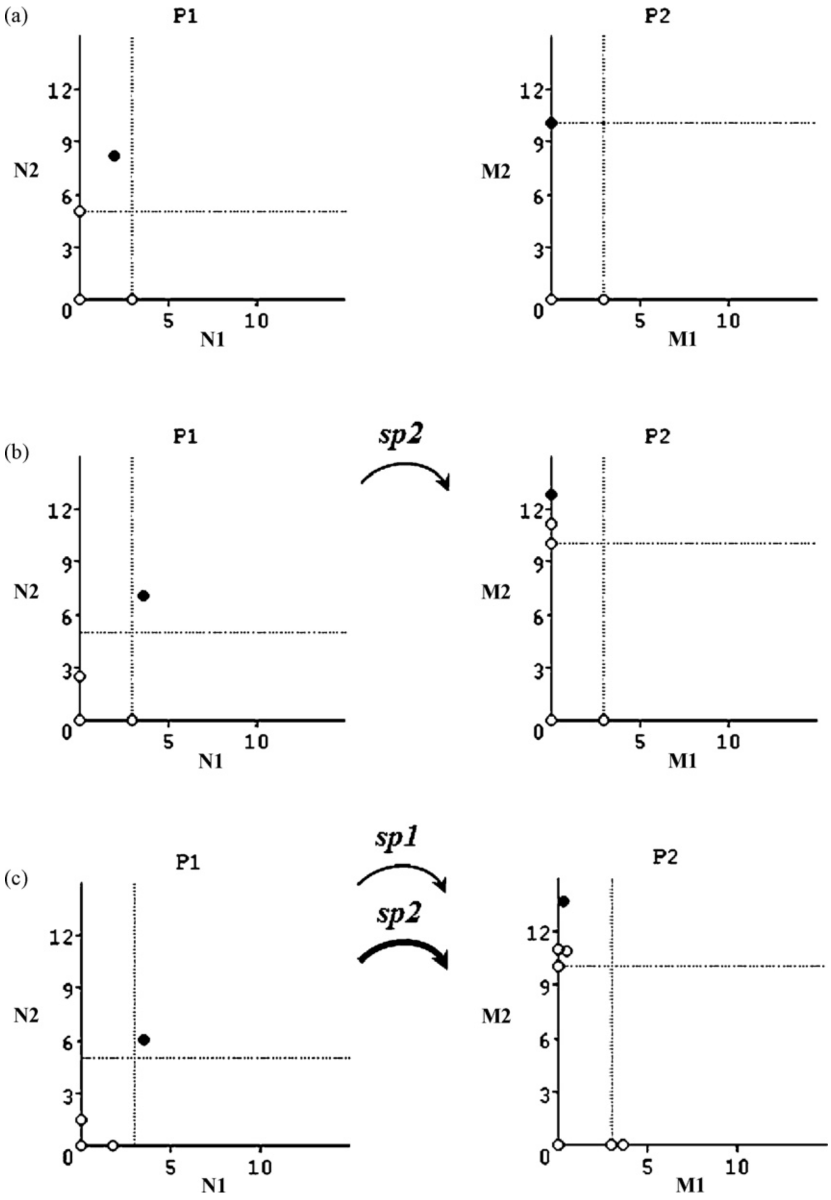

Fig. 3 – Case 1: patches with different environments; single stable solutions in each isolated patch: victim–exploiter and exclusion of one species. Stable (black dot) and unstable (white) solutions (a) without migration, (b and c) with migration rates as displayed in Table 2. See text for details.

of individuals between patches occur. The particular migration patterns for each case are shown in Table 2. The position within the quadrants allows the characterization of the type of interaction as always (see graphic legend in Fig. 1).

3.1. *Case 1—patches with different environments; single stable solutions in each isolated patch: victim–exploiter, and exclusion of one species*

Consider that in patch 1 (P1) there is a single stable solution where species coexist in a victim–exploiter interaction (+ −), where *sp1* is the victim and *sp2* the exploiter. In patch 2 (P2) there is a single stable solution where *sp1* is excluded and *sp2* is at its carrying capacity, that is, $(0, \kappa) \equiv (0, L_2)$. Note that these correspond to the situations depicted in Fig. 1(a) and (d), respectively, and Fig. 3(a) depicts graphically the corresponding equilibrium solutions for the isolated patches.

Fig. 3(b) and (c) show comparatively the results with two different migration patterns (see Table 2). In (b), a fraction of *sp2* population (N_2) migrates from P1 to P2 ($\gamma_2 = 0.5$). In P1 the single stable solution switches to a mutualism (+ +), that is, *sp1*, which played the victim role in the isolated patch goes to a positive balance in the interaction; *sp2* remains in a beneficial relationship but note that reaches a slightly lower equilibrium density. In P2 the single stable solution is still the exclusion of *sp1*, but observe that *sp2* reaches a stable density greater than its carrying capacity ($M_2^* > L_2$), which is denoted in Table 2 as $(0, \kappa+)$.

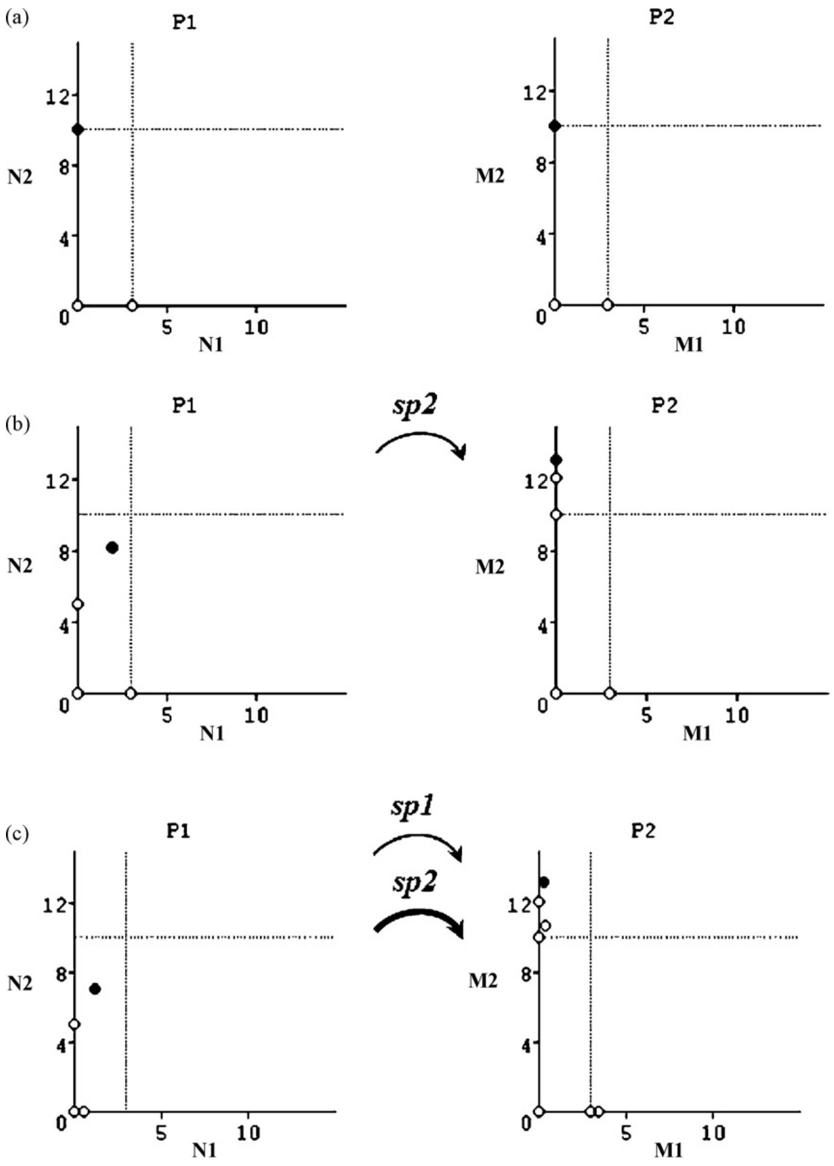

Fig. 4 – Case 2: patches with equal environments; single stable solutions in each isolated patch: exclusion of one species. Stable (black dot) and unstable (white) solutions (a) without migration, (b and c) with migration rates as displayed in Table 2. See text for details.

In (c), fractions of both species (N_1 and N_2) migrate from P1 to P2 ($\gamma_1 = 0.4$, $\gamma_2 = 0.7$). In P1, the single stable solution switches to a mutualism (+ +) as in the previous situation. In P2 the single stable solution is now coexistence in a victim–exploiter interaction (+ −), i.e. *sp1* invades and coexists as a victim with *sp2* as an exploiter; note that this means that the stable equilibrium density for *sp2* is again higher than its carrying capacity.

Other results (shown in Table 2, not in graphics) state that when only *sp1* (N_1) migrates from P1 to P2 (i.e. only $\gamma_1 > 0$) the result is (+ −) in both patches; that is, the excluded species invades P2, but stays as victim in P1. On the other hand, when only *sp2* (M_2) migrates from P2 to P1 ($\delta_2 > 0$), the situation in P1 remains as (+ −) but *sp1* invades in P2 and coexist as a competitor (− −) when migration rate is low ($\delta_2 = 0.2$), or as an exploiter (− +) when migration is higher ($\delta_2 = 0.8$); in both cases *sp2* goes from carrying capacity to a (−) role in the interaction. Note that the (− −) interaction is not a feasible stable solution in isolated patches for this model.

3.2. *Case 2—patches with equal environments; single stable solutions in each isolated patch: exclusion of one species*

In this case, environments are the same for both patches; in isolation there is a single stable solution where *sp1* is excluded and *sp2* is at its carrying capacity, that is, in P1: $(0, \kappa) \equiv (0, K_2)$, and in P2: $(0, \kappa) \equiv (0, L_2)$. This situation corresponds again to nullclines in Fig. 1(d); and Fig. 4(a) shows all equilibria with no migration.

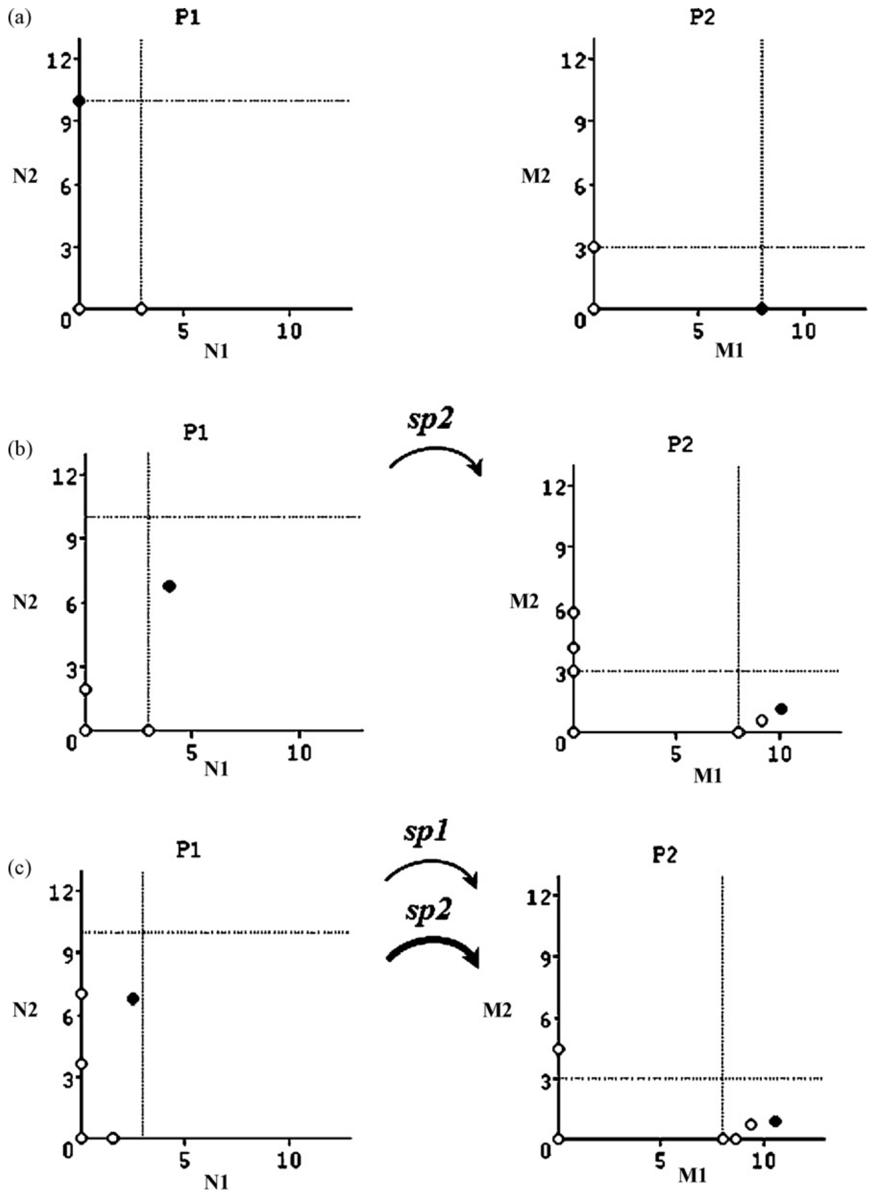

Fig. 5 – Case 3: patches with different environments; single stable solutions in each isolated patch: exclusion of one species in both but roles reversed. Stable (black dot) and unstable (white) solutions (a) without migration, (b and c) with migration rates as displayed in Table 2. See text for details.

Now consider movement of individuals between patches (see Table 2 for migration rates). Fig. 4(b) shows the result for a fraction of *sp2* population (N_2) migrating from P1 to P2 ($\gamma_2 = 0.5$). In P1 *sp1* invades and coexists with *sp2* in a (− −) association; it is a single stable solution. That is, the excluded species invades and persists in the patch even if it is under a negative interaction (below carrying capacity). In P2, the single stable solution is still the exclusion of *sp1*, but *sp2* reaches a stable density greater than its carrying capacity ($M_2{}^* > L_2$), in Table 2 as (0, κ+). Note that the situation in P1 requires an initial external source of individuals of the excluded species since none exists originally at the isolated patches, but once the invasion occurs the source is no longer needed for the association to persist as long as the emigration of *sp2* continues.

In (c), both species (N_1 and N_2) disperse from P1 to P2 ($\gamma_1 = 0.5$, $\gamma_2 = 0.8$). Now, in both patches *sp1* invades and coexists with *sp2*, in P1 in a (− −) interaction as above, but in P2 in a (+ −) i.e. *sp1* as a victim in both patches (although allowed to invade) but *sp2* is in a (−) interaction in one patch and in a (+) interaction (above carrying capacity) in the other. Both are single stable solutions. Again, an initial source of individuals of *sp1* is needed but the system is subsequently self-maintained by dispersal.

When only *sp1* migrates from P1 to P2 (i.e. only $\gamma_1 > 0$, see Table 2, not shown in graphics) there is no invasion of *sp1* possible in either patch, not even at high migration rates. That is, the excluded species invades a patch only when *sp2* emigrates or when both species immigrate.

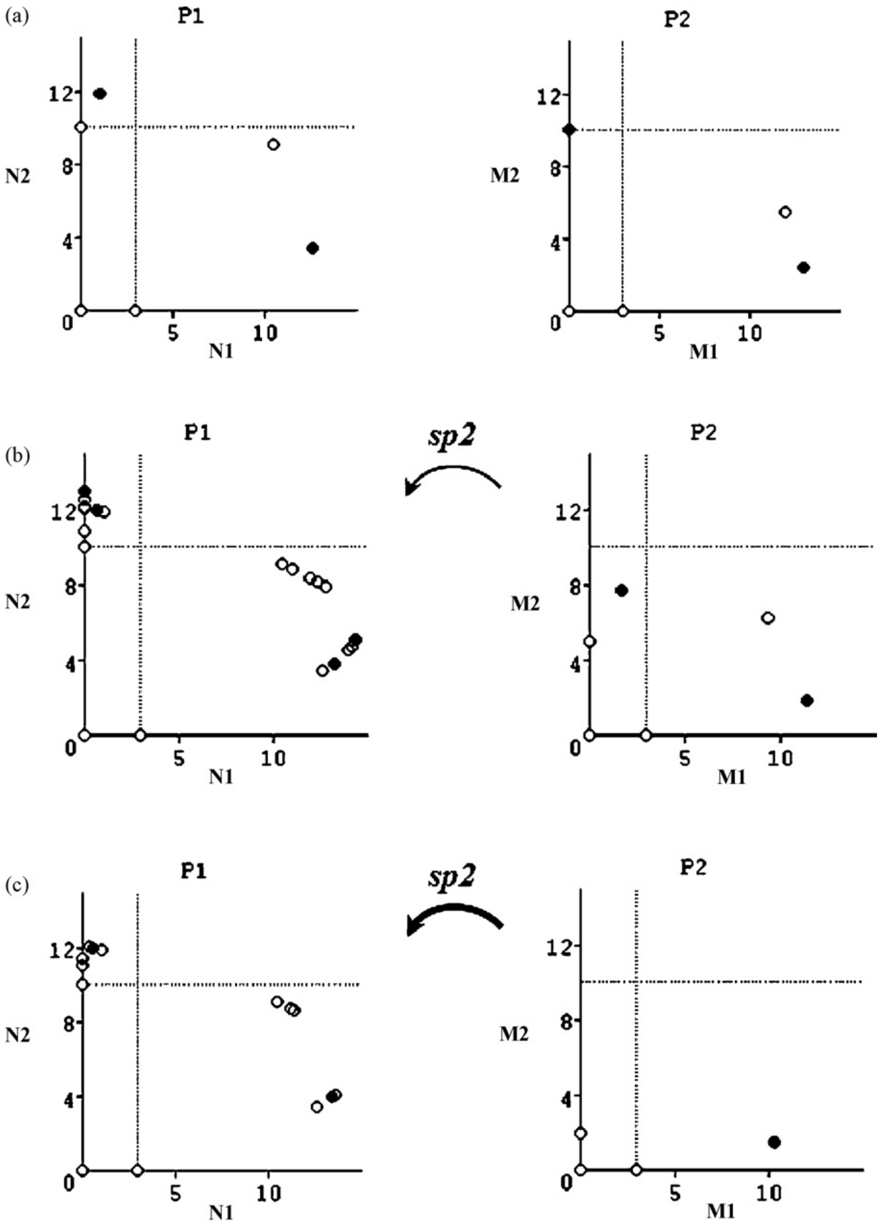

Fig. 6 – Case 4: patches with different environments; multiple stable solutions in each isolated patch: victim–exploiter with role reversal; and victim–exploiter and exclusion of one species. Stable (black dot) and unstable (white) solutions (a) without migration, (b and c) with migration rates as displayed in Table 2. See text for details.

3.3. Case 3—patches with different environments; single stable solutions in each isolated patch: exclusion of one species in both but roles reversed

In this case, the environments are such that each species exclude the other in one isolated patch; i.e. the interaction is asymmetric. In P1 *sp2* excludes *sp1* and reaches its carrying capacity $(0, \kappa) \equiv (0, K_2)$, and in P2 *sp1* excludes *sp2* and the system goes to stable $(\kappa, 0) \equiv (L_1, 0)$. That is, both correspond to the situation in Fig. 1(d) but in a reversed form for P2; all equilibrium points are depicted in Fig. 5(a).

Fig. 5(b) and (c) show the results for different migration patterns as indicated in Table 2. In (b), a fraction of *sp2* population (N_2) migrates from P1 to P2 ($\gamma_2 = 0.8$). Note that this is the resident species emigrating from the patch where it is dominant, moving to the patch where it is locally excluded. In both patches invasion of the excluded species occurs resulting in stable (− +) interactions. That is, in P1 *sp1* not only invades but reaches density higher than its carrying capacity and *sp2* (originally dominant) becomes the victim; in P2 the same relationship results although the former local dominant species (*sp1*) stays in the dominant role as exploiter. Although not shown here, for smaller γ_2 the result can be a stable (− −) interaction in P1, that is, invasion of the excluded *sp1* but with stable density lower than its carrying capacity.

In (c), both species (N_1 and N_2) disperse ($\gamma_1 = 0.5$, $\gamma_2 = 0.8$) and invade, in P1 in a (− −) association and in P2 as victim–exploiter (− +); that is, they reach stable coexistence

Table 2 – Parameter values and outcome of interaction

K_1, K_2	b_1, b_2	c_1, c_2	L_1, L_2	g_1, g_2	h_1, h_2
Case 1					
3, 5	1.5, 2	0.2, 0.2	3, 10	1.5, 2	0.2, 0.2
Case 2					
3, 10	1.5, 2	0.2, 0.2	3, 10	1.5, 2	0.2, 0.2
Case 3					
3, 10	1.5, 2	0.2, 0.2	8, 3	2, 2.5	0.2, 0.4
Case 4					
3, 10	4, 2	0.35, 0.2	3, 10	6, 2	0.8, 0.2

	γ_1	γ_2	δ_1	δ_2	P1	P2
Case 1						
a	–	–	–	–	(+ −)	$(0, \kappa)$
b	–	0.5	–	–	(+ +)	$(0, \kappa^+)$
c	0.4	0.7	–	–	(+ +)	(+ −)
d	0.4	–	–	–	(+ −)	(+ −)
e	–	–	–	0.2	(+ −)	(− −)
f	–	–	–	0.8	(+ −)	(− +)
Case 2						
a	–	–	–	–	$(0, \kappa)$	$(0, \kappa)$
b	–	0.5			(− −)	$(0, \kappa^+)$
c	0.5	0.8	–	–	(− −)	(+ −)
d	0.9	–	–	–	$(0,\kappa)$	$(0, \kappa)$
Case 3						
a	–	–	–	–	$(0, \kappa)$	$(\kappa, 0)$
b	–	0.8			(− +)	(− +)
c	0.5	0.8	–	–	(− −)	(− +)
d	–	–	–	0.8	$(0, \kappa)$	$(\kappa, 0)$
Case 4						
a	–	–	–	–	(+ −) (− +)	$(0, \kappa)$ (− +)
b	–	–	–	0.5	$(0, \kappa)_1$ $(+\,-)_2$ $(-\,+)_3$ $(-\,+)_4$	$(-\,-)_{1,3}(-\,+)_{2,4}$
c	–	–	–	0.8	(+ −) (− +)	annih (− +)

Upper part of the table: local environmental and interaction parameters. Lower part: migration parameters and corresponding outcome of type of interaction in patches P1 and P2, for (a) no dispersal, (b and c) two different migration patterns with graphic representations in Figs. 3–6, (d–f) other migration patterns not shown graphically. See text for more details.

in both patches as in the previous situation, but in this case *sp1* stays at stable densities below carrying capacity in P1. As in the previous case, since both migrations occur from P1 to P2, an initial source of individuals of *sp1* is needed.

When only the excluded species emigrates (either *sp1* from P1 or *sp2* from P2), there is no stable invasion in either patch ($\delta_2 = 0.8$ in Table 2, not shown in graphics). As above, the excluded species invades a patch only when either the resident dominant species emigrates or when both species immigrate.

3.4. *Case 4—patches with different environments; multiple stable solutions in each isolated patch: victim–exploiter with role reversal; and victim–exploiter and exclusion of one species*

Now consider different environments with alternative stable solutions (two) in each isolated patch. In P1, species coexist either in a victim–exploiter fashion (+ −), i.e. *sp1* is the victim and *sp2* the exploiter; or with roles reversed between species (− +), i.e. where *sp2* is the victim and *sp1* the exploiter. In P2, one stable solution is the exclusion of *sp1* with *sp2* at its carrying capacity, $(0, \kappa) \equiv (0, L_2)$; and the other is a victim–exploiter interaction (− +). These situations correspond to nullclines in Fig. 1(e) and (g), respectively; and Fig. 6(a) shows all equilibrium solutions for isolated patches.Table 2 shows the migration patterns considered for this case, and Fig. 6(b) and (c) the results. In (b), a fraction of *sp2* population (M_2) migrates from P2 to P1 ($\delta_2 = 0.5$). In P1 the number of equilibrium solutions increases (visualized in the figure as clouds of stable and unstable points). Both of the original stable equilibria bifurcate, thus there are four stable solutions now: the (− +) solution bifurcates into two (− +); and the (+ −) solution bifurcates into a (+ −) and a $(0, \kappa)$, so there is now a stable possibility of exclusion of *sp1* in P1 with N_2 at carrying capacity K_2. In P2, the exclusion of *sp1* is no longer a solution; instead *sp1* can invade and coexist with *sp2* in a (− −) interaction, and the possibility of a victim–exploiter coexistence (− +) stays. Note that not all possible combinations of these solutions between both patches are stable. The stable combinations are

$$\{P_1, P_2\} \equiv \{(0, \kappa),\ (-\,-)\},\quad \{(+\,-),\ (-\,+)\},\quad \{(-\,+),\ (-\,-)\},\quad \{(-\,+),\ (-\,+)\}$$

which are summarized in Table 2 using subindices. Also, in Table 2 bifurcations in P1 are positioned below each bifurcating point correspondingly.

In (c), a greater fraction ($\delta_2 = 0.8$) of *sp2* population (M_2) migrates from P2 to P1. In this case, although the migration rate is higher, there are no bifurcations in P1; the two alternative stable solutions are still at a (+ −) victim–exploiter. However, in P2 the annihilation of the stable solution $(0, \kappa)$ occurs; so, only one stable solution remains as a victim–exploiter (− +).

3.5. *General trends*

The results show that definitely spatial heterogeneity and dispersion may affect the local population dynamics, causing variations in the outcome of the interaction between associated species, both in the type of interaction, and in the condition of coexistence or exclusion. Numerical and graphical analyses have shown that the effects depend on the net balance of rates of migration via the four possible routes (each species, to and from each patch) and on the original configurations at the isolated patches. However, varied as they are, certain general trends can be established from the results presented above. These may be summarized as follows:

3.5.1. *In relation to the variation in the outcome of the interaction at stable equilibria*

(i) In a patch where the stable local solution without migration is the coexistence of the two species in a victim–exploiter association, a shift to *mutualism* is favoured by emigrations of individuals from the exploiter population and/or immigrations of individuals of the victim species. Thus, in this case the species in a (−) interaction goes to a (+).

(ii) In a patch where the stable local solution without migration is the *exclusion* of one species and the other (the resident or dominant) is at its carrying capacity, the *invasion* of the excluded (or weak) species is favoured by either the emigration of individuals of the resident population, or by immigrations of individuals of both the excluded and the resident species; that is, in this case there is a shift from *exclusion* to *coexistence*. This coexistence may occur under a *victim–exploiter* association, with the invader species either as the exploiter or as the victim; or, the populations may go to a *competition*, which was not a local (without migration) feasible stable option. Thus, in this case the *excluded* species invades to a (+) or a (−) interaction. On the other hand, if the patch receives immigration of individuals of the same resident (dominant) species, or of both species, either the condition of *exclusion* remains, or the species go to a stable *coexistence*, but in both cases the resident species reaches higher stable densities, i.e. above its own carrying capacity. Thus, the *resident* goes from κ to a $\kappa+$.

These results allow a significant general statement: the '*enhancement effect of dispersal*'. From the point of view of each species in the association, its general *demographic performance* is enhanced by spatial heterogeneity and dispersion if migrations are such that there is a *proportional increase of individuals of its own species*, either by emigration or by immigration of individuals. Being so, a victim may become a mutualist or an exploiter, an excluded species may invade, and a good competitor may overcome its own carrying capacity. And vice versa, dispersal is detrimental if it entails a proportional decrease in the species local density.

3.5.2. *In relation to the number of stable equilibria*

(i) Regardless of the species that migrates or the direction of dispersion, *bifurcation* of equilibria may occur in those patches that *receive* the migrating individuals, and *annihilation* of equilibria in those from where migration *leaves*. Thus, the number of stable equilibria increases or decreases accordingly. Obviously, when migrations occur in both directions, the result depends on the net balance of both effects. I must add that bifurcation and annihilation processes may also occur in cases of *local single* stable solutions (not shown here); however, these occur when parameter values are near those for *local multiple* stable solutions, that is to say, when local environmental conditions are close to those that favour alternative stable states.

(ii) There may be lower and upper critical *threshold migration rates* for the occurrence of bifurcation and annihilation of stable equilibria; that is, for either too low or too high migration rates these phenomena may not occur.

4. Discussion

A two-patch model coupled by migration is the simplest spatial model that allows stepping from the population to the metapopulation level; the locally explicit dynamics allow the study of possible connections between local and regional dynamics. Previous models of the (temporal) dynamics of *variable population interactions* have shown that when the outcome of the interaction is density-dependent, it may vary under different environmental regimes (expressed via parameters of the model) or may present alternative stable states for a given environment (Hernandez, 1998; Hernandez and Barradas, 2003). The spatiotemporal model presented here also predicts the variation in both the number and the type of population interactions but due to the dispersion of individuals between patches of the environment; that is to say, via the variation of different model parameters than above. Thus, it is important to distinguish between the two possible causes of variation in the outcome of the populations interaction, as they may be acting upon the system together, with either reinforcing or counteracting effects.

4.1. *Which species migrates? The specificity in mobility*

For the sake of the discussion I will be using here the terms '*victim*' and '*exploiter*' in a wide generalised form. *Victim* refers to that species in the interaction that would be either excluded by a superior competitor species, or play the (−) role in the interaction, that is, the prey, the host, or in general, the weak species. Likewise, *exploiter* is used for the superior or dominant competitor, the predator, the parasite, that one playing the (+) role in the interaction.

One general prediction of the model here states that the demographic performance of an interacting population is enhanced in a patch when dispersion is such that there is a proportional increase of individuals of this species with respect to the other species in the patch. This I have called the *enhancement effect* of dispersion. As a consequence, the outcome of an interaction in a spatially heterogeneous environment might depend on the role played by the species that migrates, especially in cases where migration is specifically driven, that is, when *only* the *victim* or *only* the *exploiter* disperses.

According to observations and empirical data the nature of the interacting species may determine differences in mobility. In some cases, it is observed that parasites or predators may be more mobile than hosts or preys; or in some mutualistic associations, such as pollinator and plant, only the pollinator is able to disperse. On the other hand, some metapopulation models in the literature dealing with population interactions – and well supported by empirical evidence – state that *regional* coexistence may be possible when the prey or the weak competitor is the migrating species since dispersion acts as a *refuge* for the species in the victim role (Armstrong, 1987; Hassell et al., 1991, 1994; Harrison and Taylor, 1997; Chesson, 2000a,b; Amarasekare and Nisbet, 2001; Amarasekare, 2003). This is particularly relevant when the victim–exploiter system is *locally* unstable, or, for inferior competitors, which can colonize empty patches and persist.

Sometimes, when only one of the species is mobile, it could be more appropriate to use a single species metapopulation model, particularly when dealing with patch occupancy models and extinction-colonization dynamics (Harrison and Taylor, 1997). However, spatial models of interacting populations with explicit local dynamics and density-dependent considerations may involve fairly more complex issues, so that both species dynamics play relevant roles in the model even when only one of the species is mobile. This is the case, for instance, of models with a source-sink dynamics approach; these allow the analysis of the effects of dispersion at a *local* level and not only at the *global* or *regional* level.

4.2. Source-sink dynamics and variable interactions: local versus global density-dependent effects

The dispersal of individuals per se involves density-dependent effects, which can act positively or negatively on population growth rates. The effect of dispersal is positive if it causes an increase in population growth rates when local population abundance is low, that is, it is beneficial for a sink population to receive individuals because it rescues it from extinction—*rescue effect*; but it is negative for the source population due to the costs associated to the loss of reproductive individuals, if this population is at low density it can become extinguished (Holt, 1985; Armstrong, 1987; Amarasekare and Nisbet, 2001; Gundersen et al., 2001; Amarasekare, 2004a,b).

In the *variable interaction model*, the extinction of both species is not a *local* stable solution. The two populations either coexist, or one of them is excluded and the resident reaches its carrying capacity. This is a result of both the facultative nature of the interactions in the model and the density-dependent feedback imposed by the α-interaction functions, which enhances growth rates at low densities and limits populations growth at high abundances. The notions of source and sink populations must be adapted to this context.

The results of the *spatiotemporal variable interaction model* presented here predict that given the right proportions of species migrating between patches, dispersal may enhance the performance of a given species, which alters the stable result predicted by the local dynamics. Conceptually, the global dynamics of this model follow the regular source-sink dynamics; where *sink* populations do not refer strictly to populations with negative growth rate or low abundances, but more generally to those that are *enhanced* by migrations from other patches, that would be, from *source* populations. That is, here the concept of *rescuing* refers to the effect that causes a population to go towards a type of interaction where it has a better performance: from a (−) to a (+) role in the interaction, or from κ (carrying capacity) to κ+ or a (+) role, or simply from being *excluded* to invade and *coexist*. A sink population, then, may refer to either that in a *victim* role or to the *exploiter*.

The mechanisms and issues underlying source-sink dynamics in the model here, concern aspects that work in an intermingled manner: density-dependent α-interaction functions, density-dependent effects of dispersal, and density-dependent costs and benefits associated to these.

The effect of dispersal on a given patch varies slightly depending on the local stable solution, that is, on whether there is coexistence or exclusion at the patch without migrations. When populations *coexist* the system is highly stable and persistent. The nature of the α-interaction function itself provides a sort of local rescuing effect at low population abundances (bear in mind that the α-interaction function for one species varies with the density of the other, and both α_{ij} are positive at low N_j), however, at high densities the α_{ij}'s take negative values and bound overgrowth; this works for each species, and results in coexistence in either a *victim–exploiter* or in a *mutualistic* interaction. On the other hand, above critical threshold parameters, the stable local solution is the *exclusion* of one species (either one species, or the other, or any depending on initial conditions as in a priority effect). That is, in this case the populations behave as competitors (although strictly the competition (− −) interaction is not a feasible local stable solution). This local interplay of density-dependent α-interaction functions has been explained in terms of density-dependent costs and benefits involved in the association (Hernandez and Barradas, 2003) and this balance may take values in the whole range of the positive to negative continuum, with the possibility of variations in the predicted local outcome of the interaction. Spatial heterogeneity plus migrations may induce changes on the local results by acting upon the critical parameter thresholds that determine these outcomes; this can be explained via two mechanisms:

(i) *Density-dependent effects of dispersal per se*: although dispersal between patches is density-independent, it induces a density-dependent effect that can either counteract or reinforce the local ones; that is, the local α-interaction functions, which are density-dependent but that may be either positive or negative due to its variable sign (just as dispersal mitigates local Allee effect in Amarasekare's, 2004a, model, but in this case it may work either way). Additionally, the migration of individuals may be detrimental for source populations due to the costs associated to the loss of reproductive individuals (Amarasekare, 2004b). Thus, there is another interplay at the *regional* level between the benefits to sink populations that are enhanced, and the costs to sources due to its losses; all this mediated by the magnitude and specificity of migrations. This can also either *reinforce* or *counteract* the local cost/benefit balance, with the possibility of causing a shift in the outcome of the interaction. One may say, for instance, in Case 1(b), or 1(c), in which dispersal causes a shift from (+ −) to (+ +) in P1, that the *local* cost/benefit relationship of the association had determined a *victim* role for *sp1*, but this balance shifts to a (+) due to dispersal; a sort of rescue effect (or enhancement) operating on the victim. The cost to the source is clear in the decrease observed in the stable density reached by *sp2* in P1. In this model, contrary to other spatial models with source-sink dynamics, high costs to source populations do not lead to the extinction of the species in a patch because it is not a feasible local solution; costs cause detrimental effects to a source population in its performance, so, an exploiter (+) may become a victim (−) in the interaction, or an extant species may become excluded from a locality.

(ii) *The relative values of local and regional average α-interaction functions*: in a spatial regime, in addition to local density-dependent α-interaction functions, we must acknowledge global or regional ones. These are α-interaction functions where α_{ij} strengths and signs are averaged across the metapopulation, for each species; obviously, they are also density-dependent and take values in the whole range from positive to negative, but respond to the global range of partner's density across the metapopulation. When dispersal causes an increase in a species density in a greater proportion relative to the other species, it means that the critical density threshold N_j between positive and negative α_{ij} values increase, therefore augmenting the range of partner's density to which positive α values correspond; consequently, its overall performance is enhanced. General mechanisms here may be visualized as in a metapopulation competition model (e.g. Amarasekare and Nisbet, 2001) transferring the conceptions of inferior and superior competitors to victims (or excluded) and exploiters (or residents). Local coexistence of the two competing species is favoured either when there is a trade-off between dispersal and competitive abilities (one species is superior in all patches but only the inferior disperses); or, when each species is superior in a different patch (spatial heterogeneity of competitive abilities) and there is concentration of global intraspecific competition in relation to the interspecific, measured by average global interaction coefficients. The first situation can be visualized in Cases 1 and 2 in this study: *sp1* plays the victim role and *sp2* the exploiter in both patches in both cases; some migration patterns allow the invasion by the victim species at patches where it is excluded. When only the victim disperses from P1 to P2 (only $\gamma_1 > 0$, see Table 2, not in graphics), it invades P2 in Case 1 but not in Case 2; that is, source localities where both species coexist are required for this invasion to happen. Thus, the relative interaction strengths between source and sink populations, both at local and global levels, impose conditions for local coexistence, or for, the focus in this study, the variation in the outcome of the interaction. However, local coexistence can also occur when *both* populations disperse or even when *only the exploiter* population migrates (c and b, respectively, for both Cases), thus, no actual trade-off between dispersal and competitive abilities is required. The requirement is on the proportion of victim/exploiter migration rates, as already stated, because the enhancement effect (not strictly a rescue effect) operates not only when victims immigrate but also when exploiters emigrate, or when both disperse with the same net effect. Additionally, in Case 2 an external initial source of individuals of the victim species must be implicitly assumed in the model here, but once invasion has occurred and as long as migration continues between the patches, the metapopulation system can persist on its own with both local and regional coexistence. On the other hand, Case 3 represents a corresponding situation to the spatial heterogeneity of competitive abilities (local and global asymmetry); that is, *sp1* is excluded and *sp2* is the resident in patch 1, but roles are reversed in patch 2; again, some migration patterns allow the invasion of the excluded species in the other patch, for both patches. This occurs when the resident species migrates to the other patch where it is excluded, or when both species migrate from one patch to the other (invasion does not occur when only the excluded species migrates to where it is resident). Under these dispersal patterns, local coexistence at both patches is a result that is easily understood in terms of sink-source dynamics; the movement of any of the resident species to the other patch in itself represents a double enhancement effect: emigration of the dominant species in one patch and immigration of its own species in the other patch. When both species disperse (as in Case 3c) the benefits for the excluded species in P1 are less than when only the dominant migrates (as in Case 3b), that is, in the former (3c) the weak species invades and coexists in a (−) role, while in the latter (3b) invades and coexists in a (+) role. That is, the effect when both disperse is enough to allow coexistence although weaker. This is explained in terms of the concentration of global intraspecific competition in relation to the interspecific, measured by average global interaction coefficients. These are quantities that are straightforwardly measured in a classical competition model from the constant, always negative and density-independent α interaction coefficients. However, although conceptually sensible, it is not as easily evaluated in the *spatial variable interaction model* because variable population interactions as considered in this study, although yielding stable solutions of exclusion of species, are not properly competition interactions. Thus, in this model it is also expected that the outcomes depend on the interplay between relative local and regional inter- and intra-specific interaction strengths; however, these are density-dependent quantities that can vary dynamically along the positive to negative continuum.

An interesting phenomenon arises from this interplay of dynamical local and global α-interaction functions, and local and global balance of costs and benefits: patches do behave as source or sink localities for each species, but additionally the *roles of source and sink may switch* dynamically for a patch, depending on the variations of the signs of the interaction coefficients with population abundances at both the local and global levels.

It is expected that those mechanisms studied by Chesson (2000a,b) for spatial heterogeneity regarding competition also hold for environments which are spatially heterogeneous with regard to the factors that determine local types of interaction; that is, storage effect, with differential responses of populations to environmental variation and damped population growth, and covariance between environment and interaction. Thus, if the environment (biotic and/or abiotic) is spatially heterogeneous and as a consequence there is variability in the outcome of the local interaction (differential local responses) then there might be a covariance between environment and the outcome of the interaction. This means that the relationship between the strength of intraspecific and interspecific interactions (not only those relative to competition but for any other type of interaction) concentrates in one or another of the localities in an aggregated manner in relation to favourable or unfavourable conditions for each species.

One important issue that can be inferred from the discussion so far is that in the context of variable or conditional interactions the concept of *the role* of a species does not make *strict* sense. A species may play different roles depending on the environment, or on the initial density conditions of the populations involved, or on migration patterns in fragmented landscapes. That is, the role of a species becomes a *spatiotemporal dynamic quality*.

4.3. *Where to and where from?*

Regarding the number of stable solutions in the metapopulation system, the results indicate that dispersal may be responsible for *bifurcations* and *annihilations* of stable equilibria. In particular, *immigrations* favour the generation of alternative stable equilibria (via bifurcations), whereas *emigrations* favour the reduction of possibilities (via annihilations), regardless of which species disperses.

The local (temporal) variable interaction dynamics model predicts the occurrence of catastrophic phenomena related to *environmental changes* (Hernandez, 1998; Hernandez and Barradas, 2003); in the spatiotemporal model these processes occur due to variations in the parameters relative to *migrations*. Again, the joint action at the two levels may either reinforce or counteract each other.

An important consequence of catastrophic phenomena on population dynamics is that it may involve drastic changes in equilibrium densities, and on the outcome of the population interactions. The magnitude of these changes depends on the initial state of the system. When there are alternative stable states, the system may be initially at one or the other, thus, when migration rates vary and stable points bifurcate, the system has the possibility to go to another stable solution, which can be of a very different nature. When cusp catastrophes are involved, the history of the dynamics becomes relevant. For instance, say a species exists on its own in a spatially homogeneous environment, at its carrying capacity, as *sp2* in Case 4(a) in P2 at the $M_2{}^* = L_2$ stable solution. Then, an environmental disturbance occurs, e.g. fragmentation of space or any other geographical phenomena, so that a fraction of individuals of the *sp2* population can migrate towards a nearby sub-environment where originally *sp2* coexists with a *sp1* population (say, as in P1). If dispersal is such that a high fraction of M_2 migrates to this newly connected environment (as in Case 4(c)) this may cause the annihilation of the $M_2{}^* = L_2$ stable solution in P2, and eventually the new demographic configuration in that patch will be a very depressed *sp2* population, coexisting with the *sp1* population, and with the role of victim in this association (the only stable solution in P2 in Case 4(c)). On the other hand, for *sp1* the change has been beneficial from the demographic point of view because it has invaded a new portion of space.

Cusp catastrophes, and its consequential bifurcations and annihilations of equilibria, occur when parameter variation have a joint but opposite effect on the variable under study (Zeeman, 1977; Hernandez and Barradas, 2003). As stated above, dispersal (via migration parameters) may have contrasting effects on population growth rates, which is to say, on the outcomes of both local and global interactions; all this mediated by density-dependent effects at all levels in the metapopulation system. Numerical and graphical analyses of the system lead to the conclusion that the immigration of individuals favours bifurcations whereas emigrations favour annihilations of equilibria. Additionally, it is important to observe that, for a given set of parameters, these bifurcation and annihilation phenomena occur within the limits of lower and upper threshold values for migration rates. For instance, in Case 4, bifurcation of stable solutions in P1 only occur for intermediate δ_2 values (in 4(b)) and not for lower, or for higher values (as in 4(c)). Clearly, these critical thresholds correspond to the turning points that characterize hysteresis curves.

Other metapopulation models, with spatial structure but not explicit local dynamics, typically yield multiple stable solutions as a result of bifurcation of equilibria, also caused by immigrations, and with turning points that determine lower and upper critical threshold values for migration rates (Gyllemberg and Hanski, 1992; Hanski and Zhang, 1993; Hanski et al., 1995). A strong rescue effect and the occurrence of alternative stable states explain the pattern of occupancy of either many, or just a few, of habitable spaces, in patches connected by migration. However, for spatial heterogeneity to be responsible for alternative stable states at a regional level, it must create the opportunity of *niche partitioning* between patches, for instance, spatial variation in resource availability for the species (Chesson, 2000b; Shurin et al., 2004).

Source-sink dynamics in systems with alternative stable equilibria add more complexity to the results of the spatial model studied here. As discussed before regarding the system with single solutions, the interplay of local and regional density-dependent effects (from different sources) may bring about changes in the source-sink roles of localities. When the set of parameters is such that alternative stable population configurations are possible within a patch, then, populations of the same species in the same patch may also play different roles in the different stable solutions, therefore, they can also switch dynamically between the roles of source and sink for another population whenever the interaction varies within the patch, due to changes in environmental conditions and/or dispersal regimes.

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