Is dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation

Roger Arditi, Claude Lobry, Tewfik Sari

▶ **To cite this version:**

Roger Arditi, Claude Lobry, Tewfik Sari. Is dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation. 2015. hal-01153368v1

HAL Id: hal-01153368

https://hal.science/hal-01153368v1

Preprint submitted on 19 May 2015 (v1), last revised 18 Sep 2015 (v2)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Is dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation

Roger Arditi
Department of Biology, University of Fribourg,
Chemin du Musée 10, 1700 Fribourg, Switzerland
e-mail: roger.arditi@unifr.ch

Claude Lobry
EPI INRA-INRIA MODEMIC, 2004 route des Lucioles,
06902 Sophia-Antipolis cedex, France
and Université de Nice-Sophia-Antipolis, France
e-mail: claude.lobry@inria.fr

Tewfik Sari
IRSTEA, UMR ITAP, 361 rue Jean-François Breton,
34196 Montpellier cedex, France
and Université de Haute Alsace, Mulhouse, France
e-mail: tewfik.sari@irstea.fr

May 19, 2015

Abstract. The standard model for the dynamics of a fragmented density-dependent population is built from several local logistic models coupled by migrations. First introduced in the 1970s and used in innumerable articles, this standard model applied to a two-patch situation has never been completely analyzed. Here, we complete this analysis and we delineate the conditions under which fragmentation is either beneficial or detrimental to total population abundance. Therefore, this is a contribution to the SLOSS question. Importantly, we also show that, depending on the underlying mechanism, there is no unique way to generalize the logistic model to a patchy situation. In many cases, the standard model is not the correct generalization. We analyze several alternative models and compare their predictions. Finally, we emphasize the shortcomings of the logistic model when written in the *r*-*K* parameterization and we explain why Verhulst's original polynomial expression is to be preferred.
Keywords. Intraspecific competition, fragmentation, SLOSS, slow-fast systems

1 Introduction

The theoretical literature on spatially-distributed population dynamics is huge. However, we have found that even the simplest and most ancient model still contained unresolved aspects and that unsupported generalizations were common.

In this paper, we explore the details of various ways to generalize the standard logistic model to a two-patch situation, i.e., the simplest way to describe the dynamics of a spatially-distributed, density-dependent population. The standard model commonly used in this situation has never been completely analyzed. We will complete this analysis and we will delineate the conditions under which fragmentation can either be beneficial or detrimental to total population abundance. More importantly, we will show that this standard two-patch logistic model is, in many cases, an incorrect description of the dynamics of a fragmented density-dependent population.

Assume that some population N follows the standard logistic model when growing in a uniform environment:

$$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right). \tag{1}$$

This model assumes perfect mixing of the population. For modelling the dynamics of the same species in a patchy environment, it is widely accepted to assume that each subpopulation in each patch follows a local logistic law and that the various patches are coupled by migrations. Taking the case of two patches as a simple example, the following model describes logistic growth in two patches linked symmetrically by migration:

$$\begin{cases} \dfrac{dN_1}{dt} &= r_1N_1\left(1-\frac{N_1}{K_1}\right)+\beta(N_2-N_1), \\ \dfrac{dN_2}{dt} &= r_2N_2\left(1-\frac{N_2}{K_2}\right)+\beta(N_1-N_2), \end{cases} \tag{2}$$

where N_i is the abundance of the species in patch i and βN_i is the emigration flow from patch i to the other patch ($\beta \geq 0$). The parameters r_i and K_i are respectively the intrinsic growth rate and the carrying capacity in patch i. This model was first studied by Freedman and Waltman (1977), later by DeAngelis et al. (1979) and Holt (1985), and a graphical presentation was given by Hanski (1999, pp. 43–46) in his reference book about metapopulations. More recently, DeAngelis and Zhang (2014) have brought new developments.

We denote by N_1^* and N_2^* the population abundances at equilibrium. With no loss of generality, we assume that patch 1 has the lower carrying capacity (i.e., $K_1 \leq K_2$). In isolation ($\beta = 0$), each population equilibrates at its local carrying capacity: $N_i^* = K_i$. A well-known result is that, in the presence of dispersal ($\beta > 0$), the total equilibrium population $N_T^* = N_1^* + N_2^*$ is generally different from the sum of the carrying capacities $K_1 + K_2$. Freedman and Waltman (1977) have shown that, in the case of perfect mixing ($\beta \to \infty$), both patch populations tend to equal values and that the total equilibrium population tends to:

$$N_T^* = K_1 + K_2 + (K_1 - K_2)\frac{r_1K_2 - r_2K_1}{r_1K_2 + r_2K_1}, \quad \text{in the limit } \beta \to \infty. \tag{3}$$

[Note that this expression contained typos in Freedman and Waltman (1977, their equation 3.3) that were only partially corrected by Holt (1985).] Depending on the sign of the numerator present in equation (3), dispersal can either be beneficial or detrimental

with respect to the total carrying capacity. Thus, if $r_1K_2 < r_2K_1$ (with $K_1 < K_2$), we will have

$$N_T^* > K_1 + K_2 \quad \text{if } \beta \text{ is sufficiently large.} \tag{4}$$

This spectacular result, somewhat paradoxical, has been widely discussed and has led to speculations about the general virtues of patchiness and dispersal, for example in the context of conservation ecology and the SLOSS question (e.g., Hanski 1999).

Freedman and Waltman (1977) only contrasted the situations of perfect isolation and perfect mixing; they did not study the effect of intermediate values of the dispersal parameter β. This effect was studied in the recent paper of DeAngelis and Zhang (2014), but only in the special case $r_1/K_1 = r_2/K_2$.

In the present paper, we will bring two contributions. Firstly, we will present the analysis of model (2) in the full parameter space and we will determine the exact conditions under which $N_T^* > K_1 + K_2$.

Secondly, we will question the legitimacy of modelling a patchy logistic population as in the standard system (2), using several very simple examples. The logistic model is often justified on phenomenological grounds. However, it can also be derived from mechanistic considerations. Depending on the mechanism being considered, we will show that the correct generalization to a patchy situation is not necessarily represented by model (2) and that the equilibrium total population can be different from that predicted by this model.

2 Theoretical analysis of the standard two-patch logistic model

In this section, we summarize some of the properties of the standard model (2). Formal proofs are given in the Mathematical Appendices.

As already mentioned in the Introduction, with no dispersal ($\beta = 0$), each patch equilibrates at its own carrying capacity and the total equilibrium number of individuals is just the sum of the carrying capacities: $N_T^* = K_1 + K_2$. This remains true with dispersal ($\beta > 0$) if the two carrying capacities are identical: $K_1 = K_2$. However, if the carrying capacities are not identical ($K_1 < K_2$), the equilibrium densities are such that

$$K_1 < N_1^* < N_2^* < K_2, \tag{5}$$

meaning that, in general, $N_T^* \neq K_1 + K_2$ (see Proposition A.1 and Section B.2 in the Mathematical Appendices).

In particular, the total equilibrium population N_T^* can be *greater* than the sum of the carrying capacities. In the Introduction, we mentioned Freedman and Waltman's result in the case of perfect mixing ($\beta \to \infty$) (eqs. 3–4). This can also occur with imperfect mixing, for example, if $r_1/K_1 < r_2/K_2$ (with $K_1 < K_2$), in which case, as shown in the Mathematical Appendices,

$$N_T^* > K_1 + K_2 \text{ as soon as } \beta > 0. \tag{6}$$

The Appendix A.1 gives the full mathematical analysis of the equilibrium properties of the coupled logistic model (2). The main qualitative results are summarized by Figure 1. Depending on the inequalities between r_1 and r_2, and between r_1/K_1 and r_2/K_2, three different domains must be considered in the parameter space $r_1 \times r_2$. We

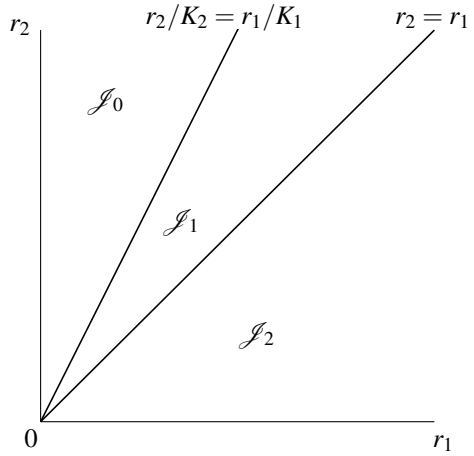


Figure 1: In $\mathscr{J}_0$, patchiness has a beneficial effect on total carrying capacity. This effect is detrimental in $\mathscr{J}_2$. In $\mathscr{J}_1$, it depends on the value of the migration coefficient β. Note that, because of the assumption $K_1 \leq K_2$, the two oblique lines cannot be reversed. See text for additional explanations.

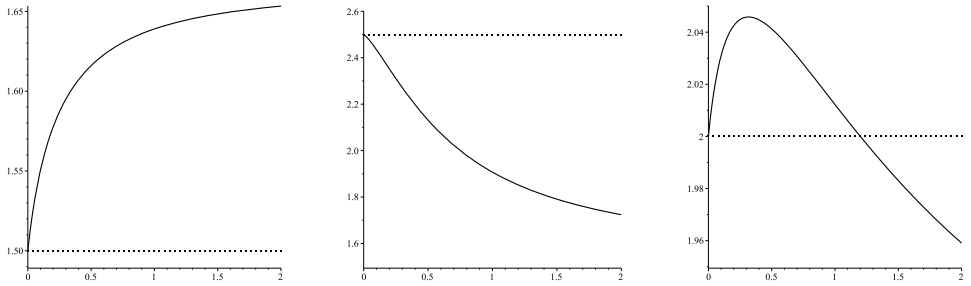
define $\mathscr{J}_0$ by the condition $r_2/K_2 \geq r_1/K_1$, $\mathscr{J}_2$ by the condition $r_2 \leq r_1$, and $\mathscr{J}_1$ by the condition $r_2/K_2 < r_1/K_1$ and $r_2 > r_1$.

The effect of patchiness and migration is different in the three domains. In $\mathscr{J}_0$, this effect is beneficial: N_T^* is always greater than $K_1 + K_2$. In $\mathscr{J}_2$, the opposite is true: patchiness is detrimental since N_T^* is always smaller than $K_1 + K_2$. In $\mathscr{J}_1$, the effect of patchiness depends on the migration rate: it is beneficial at lower values of the migration coefficient β while this effect becomes detrimental at high values. This is illustrated by Figure 2, in which the total equilibrium abundance N_T^* is plotted as a function of the migration rate β. Depending on the choice of parameter values (given in Table 1), this figure shows three different example patterns, belonging respectively to $\mathscr{J}_0$, $\mathscr{J}_2$, and $\mathscr{J}_1$.

Table 1: Parameter values of the three cases of Figure 2. The derivative $\frac{d}{d\beta}N_T^*(0)$ is calculated with the expression given in Proposition A.3 and the perfect mixing abundance $N_T^*(+\infty)$ with equation (20).

	r_1	K_1	r_2	K_2	$\frac{d}{d\beta}N_T^*(0)$	$N_T^*(+\infty)$
Figure 2a	0.5	0.5	2	1	0.75>0	$1.67 > K_1 + K_2$
Figure 2b	1	0.5	0.8	2	$-0.375 < 0$	$1.5 < K_1 + K_2$
Figure 2c	1	0.5	2	1.5	$0.5 > 0$	$1.8 < K_1 + K_2$

Figure 2a is an example response in $\mathscr{J}_0$: as soon as there is some migration ($\beta > 0$), the global carrying capacity N_T^* is greater than $K_1 + K_2$. In Figure 2b, we show an example response in $\mathscr{J}_2$: the total equilibrium population N_T^* is always lower than $K_1 + K_2$. Finally, Figure 2c shows a response in the intermediate domain $\mathscr{J}_1$, in which the lower values of the migration rate have a beneficial effect while this effect becomes detrimental at high values.



(a) (b) (c)

Figure 2: Total equilibrium population as a function of migration: $N_T^*(\beta)$. The horizontal dotted line is $K_1 + K_2$. Depending on the parameter values (given in Table 1), three different patterns can be obtained, corresponding to the three domains of Figure 1. (a) Example in $\mathscr{J}_0$. (b) Example in $\mathscr{J}_2$. (c) Example in $\mathscr{J}_1$. See text for more comments.

3 Mechanism 1: Logistic growth induced by resource consumption

Consider a population of bacteria consuming a substrate in a batch culture. This process occurs on a fast time scale, on which bacterial mortality can be ignored. Assuming perfect mixing of both the substrate and the population, this situation is modelled by:

$$\left\{ \begin{array}{rcl} \dfrac{dR}{dt} & = & -\rho RN, \\ \dfrac{dN}{dt} & = & \varepsilon \rho RN, \end{array} \right. \tag{7}$$

where R is the substrate concentration and N is the bacterial density. We have:

$$\frac{d(\varepsilon R + N)}{dt} = 0$$

and thus $\varepsilon R(t) + N(t) = \varepsilon R(0) + N(0) = M$. Substituting $(M - N)$ to εR in the second equation of (7), one gets:

$$\frac{dN}{dt} = \rho N(M - N), \tag{8}$$

which is equivalent to the logistic equation (1) with $K = M$ and $r = \rho M$. This equation, derived from (7), has been shown to describe perfectly the dynamics of a batch culture of bacteria.

Consider now two coupled batch reactors, with the same bacteria and substrate, and differing only in the initial conditions. Denote by R_1, N_1, R_2 and N_2 the population sizes of substrate and bacteria in reactors 1 and 2 respectively. Let $M_1 = \varepsilon R_1(0) + N_1(0)$ and $M_2 = \varepsilon R_2(0) + N_2(0)$. If we assume linear migration (i.e., diffusion) between the two patches and if we ignore the consumption mechanism leading to the equation (8), it is tempting to model the coupled reactors by coupling the corresponding reduced equations (8) with the addition of migrations:

$$\left\{\begin{array}{rcl} \dfrac{dN_1}{dt} & = & \rho N_1(M_1-N_1)+\beta(N_2-N_1), \\ \dfrac{dN_2}{dt} & = & \rho N_2(M_2-N_2)+\beta(N_1-N_2). \end{array}\right. \tag{9}$$

We said in the previous section (and proved in the Mathematical Appendix A.1) that, if we denote by (N_1^*, N_2^*) the equilibrium of (9), then

$$N_1^* + N_2^* > M_1 + M_2 \tag{10}$$

as soon as $\beta > 0$ and $M_1 \neq M_2$.

Despite its perfect mathematical derivation, this result *is false* for the coupling of the two reactors. The correct description in this case must be done by modelling the consumption mechanism (7) in the two patches with possibly different diffusion rates for the substrate (α) and for the bacteria (β):

$$\left\{\begin{array}{rcl} \dfrac{dR_1}{dt} & = & -\rho\, R_1 N_1 + \alpha(S_2 - S_1), \\ \dfrac{dN_1}{dt} & = & \varepsilon\, \rho\, R_1 N_1 + \beta(N_2 - N_1), \\ \dfrac{dR_2}{dt} & = & -\rho\, R_2 N_2 + \alpha(S_1 - S_2), \\ \dfrac{dN_2}{dt} & = & \varepsilon\, \rho\, R_2 N_2 + \beta(N_1 - N_2). \end{array}\right. \tag{11}$$

Adding the four equations, one gets:

$$\frac{d(\varepsilon R_1 + \varepsilon R_2 + N_1 + N_2)}{dt} = 0,$$

which means:

$$\varepsilon R_1(t) + \varepsilon R_2(t) + N_1(t) + N_2(t) = \varepsilon R_1(0) + \varepsilon R_2(0) + N_1(0) + N_2(0) = M_1 + M_2.$$

Note that we always have, including at equilibrium:

$$N_1(t) + N_2(t) \leq M_1 + M_2$$

because the quantity $R_1(t) + R_2(t)$ must be positive!

Since at equilibrium $R_1^* = R_2^* = 0$, we conclude that

$$N_1^* + N_2^* = M_1 + M_2,$$

in contradiction with the result (10) obtained when coupling the reduced logistic models (8). This is completely independent of the value of α, the substrate diffusion rate.

The flaw in obtaining the wrong inequality (10) was that it was derived on the basis of the reduced model (9), itself derived from the first integral $\varepsilon R(t) + N(t) = \varepsilon R(0) + N(0)$ of (7), which is no longer a first integral of the full system (11).

4 Mechanism 2: Logistic growth induced by MacArthur's reduction

Consider the following model for a resource-consumer interaction (see MacArthur 1969, 1970):

$$\begin{cases} \dfrac{dR}{dt} &= \left[r\left(1-\dfrac{R}{K}\right) - aN \right] R, \\ \dfrac{dN}{dt} &= \varepsilon(awR-q)N, \end{cases} \tag{12}$$

where R is the population density of the resource (prey) and N is the population density of the consumer (predator). Here a is the probability that a consumer encounters and eats a resource unit in a unit of time, w is the weight (caloric value) of the resource, q is the metabolic rate for maintenance of the consumer and ε is a proportionality constant governing the biochemical conversion of resource R into consumer N. For the sake of simplicity, we denote $b = aw$.

This model is more appropriate than the previous one in situations in which the resource can reproduce with its own dynamics and in which the consumer has some loss term (e.g., due to basal metabolism or mortality). Here, the conversion coefficient ε is assumed to be small.

MacArthur's reduction (MacArthur 1969, 1970) consists, taking advantage of the separation of time scales, in considering the "quasi-steady state" defined by the (fast) first equation in (12) and replacing R by it in the second equation. The quasi-steady state R, that is, the solution of the algebraic equation $r\left(1-\frac{R}{K}\right) - aN = 0$ is given by

$$R = K - \frac{a}{r}KN$$

and substituting it into the second equation in (12) gives:

$$\frac{dN}{dt} = \varepsilon\left(bK - q - \frac{ab}{r}KN\right)N, \tag{13}$$

which is once more a logistic equation that can be written as:

$$\frac{dN}{dt} = \sigma N\left(1-\frac{N}{M}\right),$$

with intrinsic growth rate σ and carrying capacity M:

$$\sigma = \varepsilon(bK-q), \quad M = \frac{r}{a}\frac{bK-q}{bK}.$$

Let us now consider two patches and assume some migration between the two. If we model this situation directly with MacArthur's reduced logistic form (13), we have:

$$\begin{cases} \dfrac{dN_1}{dt} &= \varepsilon_1\left(b_1K_1 - q_1 - \frac{a_1b_1}{r_1}K_1N_1\right)N_1 + \beta(N_2-N_1), \\ \dfrac{dN_2}{dt} &= \varepsilon_2\left(b_2K_2 - q_2 - \frac{a_2b_2}{r_2}K_2N_2\right)N_2 + \beta(N_1-N_2). \end{cases} \tag{14}$$

With no migration ($\beta = 0$), each patch equilibrates at its respective carrying capacity,

$$M_1 = \frac{r_1}{a_1}\frac{b_1K_1-q_1}{b_1K_1}, \quad M_2 = \frac{r_2}{a_2}\frac{b_2K_2-q_2}{b_2K_2}, \tag{15}$$

and the total number of individuals present at equilibrium is just the sum of the carrying capacities, $N_T^* = M_1 + M_2$.

Let us denote by (N_1^*, N_2^*) the positive (and globally stable) equilibrium of (14). We will compare the total population $N_T^* = N_1^* + N_2^*$ with the total population obtained for the complete two-patch extension of (12), which is:

$$\begin{cases} \dfrac{dR_1}{dt} &= \left[r_1 \left(1 - \dfrac{R_1}{K_1} \right) - a_1 N_1 \right] R_1 + \alpha(R_2 - R_1), \\ \dfrac{dR_2}{dt} &= \left[r_2 \left(1 - \dfrac{R_2}{K_2} \right) - a_2 N_2 \right] R_2 + \alpha(R_1 - R_2), \\ \dfrac{dN_1}{dt} &= \varepsilon_1 (b_1 R_1 - q_1) N_1 + \beta(N_2 - N_1), \\ \dfrac{dN_2}{dt} &= \varepsilon_2 (b_2 R_2 - q_2) N_2 + \beta(N_1 - N_2). \end{cases} \tag{16}$$

The term $\alpha(R_2 - R_1)$ represents some possible migration of the resource, which is not present in the reduced system (14) since the variable R does not appear in the equations.

Computer simulations show that system (16) has an equilibrium, which is globally stable[1], and we denote it by

$$E^{**} = (R_1^{**}, R_2^{**}, N_1^{**}, N_2^{**}). \tag{17}$$

We must now compare the effect of migrations expressed in the complete model (16) and in the reduced model (14). We simulate for a long time (namely 100 units of time) until the equilibrium is almost reached and then compute the total consumer population for both models (14) and (16):

$$N_T^* = N_1^* + N_2^*, \qquad N_T^{**} = N_1^{**} + N_2^{**}.$$

We can redefine the resource migration parameter α as $\alpha = k\beta$. Although the general case can be studied with no special difficulty, we will consider in this paper two special cases in order to simplify the presentation:

$$k = 1, \text{ i.e., } \alpha = \beta \text{ and } \beta \geq 0, \text{ in Section 4.1,}$$

and

$$k = 0, \text{ i.e., } \alpha = 0 \text{ and } \beta \geq 0, \text{ in Section 4.2.}$$

In order to single out the role of migration strength, we will compare the graphs of $N_T^*(\beta)$ and $N_T^{**}(\beta)$ as functions of β with $\beta \geq 0$, all other parameters being fixed.

4.1 Migration of both the resource and the consumer

In this section, the migration between the two patches is $\alpha = \beta$ and $0 \leq \beta \leq 1$. The simulations will be done with the values given in Tables 2 and 3. We first set the parameter values as in line 1 of Table 2.

On Figure 3a, the value of $M_1 + M_2$ is represented by the horizontal dotted line. As soon as β is strictly positive, there is a departure from this value and the picture shows a great difference between the two models. The value predicted by the reduced model is quite different from the one predicted by the complete model. This is not

Table 2: Numerical values of the parameters in Figures 3, 4 and 5.

	r_1	K_1	q_1	r_2	K_2	q_2	a_1	a_2	b_1	b_2	ε_1	ε_2
Figure 3a	1	1	0.5	3	3	2	1	1	1	1	1	1
Figure 3b	1	2.8	1.5	3	3.2	0.5	1	1	1	1	1	1
Figure 4a	1	2	0.5	3	2	2	1	0.8	1	2	0.2	0.1
Figure 4b	1	1.5	1	1	3	2	1	0.5	1	1.5	0.5	0.5
Figure 5	1	1	0.1	1	2.5	1	4	0.1	1	1	0.6	0.4

Table 3: Numerical values of σ_1, σ_2, M_1, M_2, $\frac{d}{d\beta}N_T^*(0)$, $\frac{d}{d\beta}N_T^{**}(0)$, $N_T^*(\infty)$, $N_T^{**}(\infty)$ and M_1+M_2. The derivatives $\frac{d}{d\beta}N_T^*(0)$ and $\frac{d}{d\beta}N_T^{**}(0)$ and the perfect mixing abundances $N_T^*(\infty)$ and $N_T^{**}(\infty)$ are calculated with the expressions given in Propositions A.4 and A.6 and in equation (23).

	σ_1	σ_2	M_1	M_2	$\frac{d}{d\beta}N_T^*(0)$	$\frac{d}{d\beta}N_T^{**}(0)$	$N_T^*(\infty)$	$N_T^{**}(\infty)$	M_1+M_2
Figure 3a	0.5	1	0.5	1	0.5	2.75	1.5	1.5	1.5
Figure 3b	1.3	2.7	0.464	2.531	0.824	2.158	2.069	2.705	2.995
Figure 4a	1.5	0.2	0.75	1.875	-4.875	-4.5	1.614	3.148	2.625
Figure 4b	0.25	1.25	0.333	1.111	2.489	2.322	1.6	1.067	1.444
Figure 5	0.54	0.6	0.225	6	1.07	-5.68	0.91	0.66	6.225

surprising since the reduced model does not take into account the migration of the resource modelled by $\alpha = \beta > 0$.

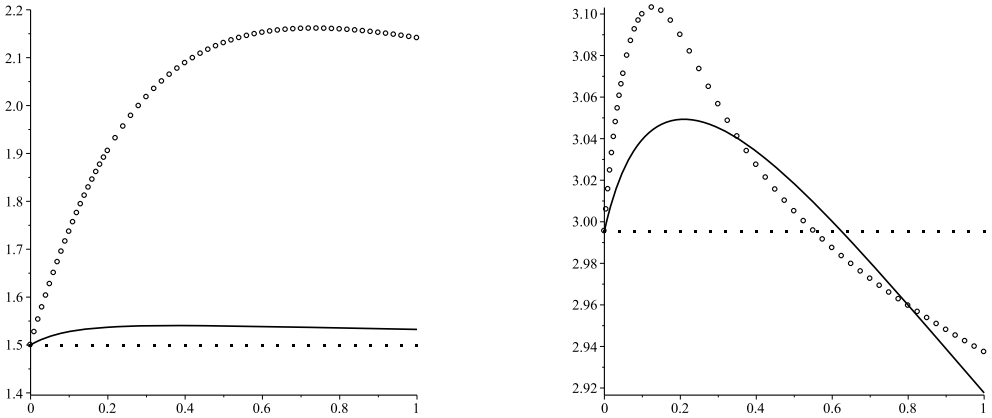
In the previous example, the total population with migrations for the complete model is always greater than the total population with migrations for the reduced model, which is itself always greater than the sum of the populations without migration. This is not true in general, as shown by Figure 3b, obtained with the parameter values in line 2 of Table 2. In this example, $M_1+M_2 \approx 2,995$ (see line 2 of Table 3). We see that small values of migration improve the total population but large values deteriorate it. Therefore the total population is not always greater than the sum of the two carrying capacities, nor the total population for the complete model is always greater than the total population of the reduced model. More precisely, all the possible inequalities between N_T^*, N_T^{**}, and M_1+M_2 can actually be obtained, depending on the value of the migration intensity β, as shown by Figure 3b, in which we have successively: $N_T^{**} > N_T^* > M_1+M_2$, $N_T^* > N_T^{**} > M_1+M_2$, $N_T^* > M_1+M_2 > N_T^*$, $M_1+M_2 > N_T^* > N_T^{**}$ or $M_1+M_2 > N_T^{**} > N_T^*$.

Figure 4a is obtained with the parameter values in line 3 of Table 2. Since $\sigma_2 < \sigma_1$, $N_T^*(\beta) < M_1+M_2$ and $(N_T^*)'(\beta) < 0$ for any $\beta > 0$. We see that $N_T^{**}(\beta)$ decreases first and then increases.

Figure 4b is obtained with the parameter values in line 4 of Table 2. Since $\sigma_2/M_2 > \sigma_1/M_1$, we have $N_T^*(\beta) > M_1+M_2$ for any $\beta > 0$. However, we see that $N_T^{**}(\beta) > M_1+M_2$ for small β and the opposite holds for large β.

Figure 5 is obtained with the parameter values in line 5 of Table 2. Since $\sigma_2 > \sigma_1$ and $\frac{\sigma_2}{M_1} < \frac{\sigma_1}{M_1}$, we have that $N_T^*(\beta) > M_1+M_2$ for β small enough and $N_T^*(\beta) < M_1+$

[1]The mathematical proof of this statement is beyond the scope of this paper.



(a) (b)

Figure 3: Total consumer population as a function of migration: N_T^* (solid curve) for the reduced model ; N_T^{**} (curve with circles) for the complete model. See Table 2 for the parameter values and text in Section 4.1 for explanations.

M_2 for β large enough. We see that $N_T^{**}(\beta)$ has a completely different behaviour. It should be noticed (see Table 3) that $\frac{d}{d\beta}N_T^{**}(0) < 0$ and $\frac{d}{d\beta}N_T^{*}(0) > 0$, as shown also in the zoom in Figure 5b. Hence, $N_T^{**}(\beta)$ is first decreasing, then increasing, then decreasing again, while $N_T^{*}(\beta)$ is first increasing and then decreasing.

4.2 Migration of the consumer alone

Since MacArthur's reduction does not contain the resource as an explicit variable, it certainly cannot, as shown above, account for the resource migration. However, if we assume that *there is no resource migration*, one may wonder whether it doesn't become accurate. The complete model is system (16) with $\alpha = 0$. It can be analyzed mathematically to a large extent (see the Mathematical Appendices). Here, we present illustrations obtained by numerical simulation.

We set the parameter values as in line 1 of Table 4. The migration rates are $\alpha = 0$ and $0 \leq \beta \leq 1$. On Figure 6a, the value $M_1 + M_2$ is represented by the horizontal dotted line. As soon as β is strictly positive, there is a departure from this value. The value predicted by the reduced model is the same as the one predicted by the complete model. Indeed, for this set of parameters, the reduced model gives a correct picture of the complete model. However, this is not the general case, as will be shown in the following example.

Table 4: Numerical values of the parameters of Figure 6. The values of the other parameters in (16) are $\varepsilon_i = 0.1$, $a_i = b_i = 1$.

	r_1	K_1	q_1	r_2	K_2	q_2
Figure 6a	2.5	2.5	0.2	3	3	2.5
Figure 6b	1	1	0.4	3	3	1

We now set the parameters as in line 2 of Table 4, with the same migration rates as in the previous example. On Figure 6b, the value $M_1 + M_2$ is represented by the horizontal dotted line. As soon as β is strictly positive, there is a departure from this

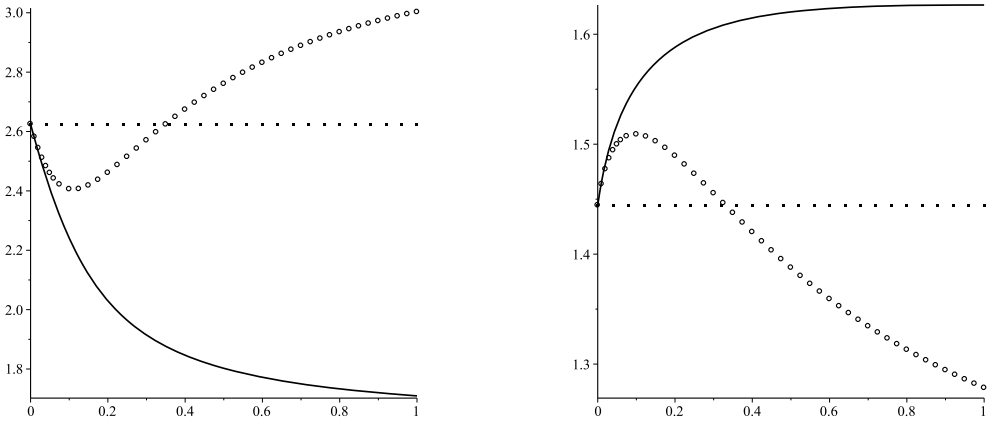


Figure 4: Total consumer population as a function of migration: N_T^* (solid curve) for the reduced model ; N_T^{**} (curve with circles) for the complete model. See Table 2 for the parameter values and text in Section 4.1 for explanations.

value. The value predicted by the reduced model is the same as the one predicted by the complete model when β is small enough. After a certain value ($\beta \approx 0.5$), the prediction of the reduced model (solid curve) is quite smaller than the prediction of the complete model (curve with circles).

5 Discussion

When we say that the logistic equation (1) is a model for the growth of some population N, what do we mean exactly? Usually, we say nothing about the actual mechanisms that explain this kind of growth. What we mean is roughly the following argument:

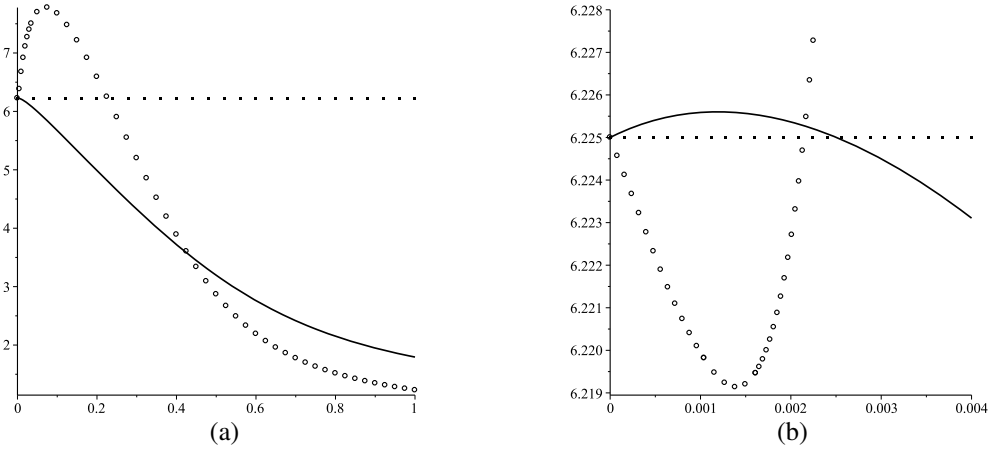
1. Let $\mu(N)$ be the specific growth rate of a population. If we want the population to be bounded, $\mu(N)$ must decrease to 0.
2. The simplest function of N that decreases to 0 is $\mu(N) = r\left(1 - \frac{N}{K}\right)$.
3. Equation (1) is a good approximation of some more complicated model.
4. The fit of the logistic model (1) to actual populations is often fairly good.

From the above considerations, it seems natural to model migrations between two patches directly as in system (2). However, the correct generalization depends on the mechanisms that underly the logistic growth and that are not specified in the items 1 to 4 above. In the examples we have studied, we have shown that the patch version (2) could be incorrect.

Nevertheless, it can be correct under specific assumptions. For instance, the logistic model can be derived from the following mechanism, different from those of Sections 3 and 4. Assume that the population basically follows exponential growth:

$$\frac{dN}{dt} = rN$$

and that some proportion of the encounters between two individuals lead to mortality. In this case, if we also assume perfect mixing, the number of individuals dying during



(a) (b)

Figure 5: Total consumer population as a function of the migration coefficient β: N_T^* (solid curve) for the reduced model ; N_T^{**} (curve with circles) for the complete model. See Table 2 for the parameter values and text in Section 4.1 for explanations. Panel (b) is a zoom of (a) in a narrow range of very small values of β.

a small time interval dt is simply proportional to the product $N^2\,dt$. Subtracting this mortality rate, we obtain the equation:

$$\frac{dN}{dt} = rN - \lambda N^2 = rN\left(1 - \frac{\lambda}{r}N\right), \tag{18}$$

which is a logistic. This is a mechanistic derivation of the logistic equation that assumes direct intraspecific interference. Now, if we consider two patches with linear diffusion between them, we can assume the same mechanism and build the two-patch model (2) directly as a whole. In this case, we can be confident about the predictions of model (2), which is the traditional two-patch generalization of the logistic model.

Our complete mathematical analysis of this model, summarized by Figures 1 and 2, has determined the exact conditions under which fragmentation increases the total carrying capacity. This occurs in $\mathscr{J}_0$ for all migration rates (Fig. 2a) and in $\mathscr{J}_1$ for the lower migration rates (Fig. 2c). Thus, a necessary condition is $r_2 > r_1$ (which is not always sufficient). Recalling that $K_2 > K_1$, this means that, when the "good" patch 2 is the better one both in terms of carrying capacity and in terms of intrinsic growth rate, fragmentation can indeed have a beneficial effect. Fragmentation is always detrimental if carrying capacity and growth rate are negatively correlated, i.e., if $K_2 > K_1$ and $r_2 < r_1$. One may reasonably assume that this condition occurs much less frequently than positive correlation (i.e., $K_2 > K_1$ and $r_2 > r_1$). Therefore, our analysis confirms the earlier partial results of other authors (e.g., Freedman and Waltman 1977, Holt 1985, DeAngelis and Zhang 2014) who suggested that, in general, fragmentation was beneficial.

While this first message of our paper generally confirms previous results, our second message is more critical. We have shown that, if the logistic model is viewed as a mechanistic model (e.g., the two different mechanisms presented in Sections 3 and 4), then the correct two-patch generalization is different from the traditional reduced model (2). Moreover, the effect of fragmentation can be quite different from that predicted by the latter model. Figures 3, 4, 5, 6 have shown that this effect can be either detrimental or beneficial, sometimes in a direction opposite to that predicted by the

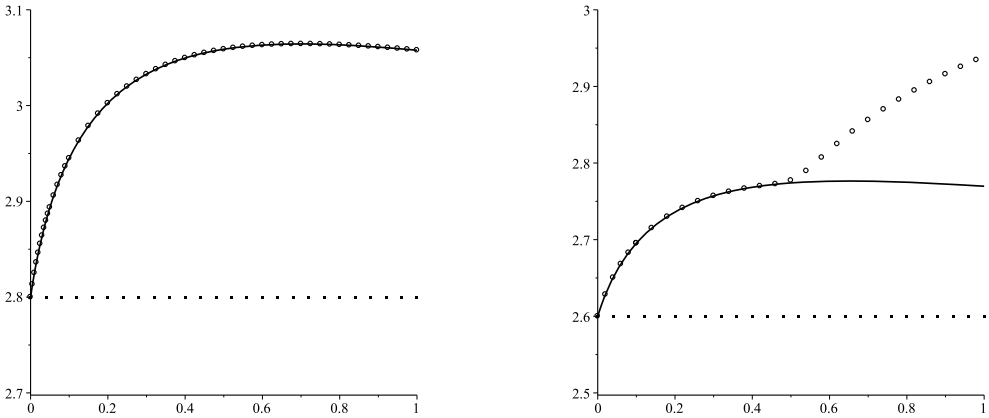


Figure 6: Total consumer population as a function of migration: N_T^* (solid curve) for the reduced model ; N_T^{**} (curve with circles) for the complete model. See Table 2 for the parameter values and text in Section 4.2 for explanations.

traditional model (2).

This second message of our paper brings some new light to earlier criticisms of the logistic equation, especially in the parameterization of equation (1) (e.g., Kuno 1991, Ginzburg 1992). Particularly, the expression "carrying capacity" for K is very unfortunate because it suggests that it is an intrinsic property of the environment. With this view, our results would lead to say that the total carrying capacity of a patchy environment is different from the sum of the patches' carrying capacities. Instead, K must be better viewed as the asymptotic, maximal value of the population abundance. This question was notably discussed by Gabriel et al. (2005) and by Mallet (2012), who pointed out that it makes much more sense to write the logistic equation as in equation (18) because it makes clear that the asymptotic limit of population abundance is due to intraspecific competition. Moreover, historically, this was the original way in which Pierre-François Verhulst first wrote the logistic equation (Verhulst, 1838).

A Mathematical Appendices

A.1 Appendix to Section 2

In this section, we explain why, in general, the total equilibrium population in the system of coupled logistic growths (2) is different from the sum of the carrying capacities. More precisely, we give the exact conditions under which $N_T^* > K_1 + K_2$. Recall that if $K_1 = K_2$, then $N_1^* = K_1$ and $N_2^* = K_2$ for any $\beta \geq 0$. Therefore $N_T^* = K_1 + K_2$ for any $\beta \geq 0$. When K_1 is not equal to K_2, we have the following result, where $N_T^*(\beta)$ is studied as a function of the migration rate β.

Proposition A.1 *We recall the assumption that $K_1 < K_2$.*

1. *If $\frac{r_2}{K_2} \geq \frac{r_1}{K_1}$, then $N_T^*(\beta) > K_1 + K_2$ for any $\beta > 0$.*
2. *If $\frac{r_2}{K_2} < \frac{r_1}{K_1}$ and $r_2 > r_1$, then $N_T^*(\beta) > K_1 + K_2$ for $0 < \beta < \beta_0$ and*

$N_T^*(\beta) < K_1 + K_2$ *for* $\beta > \beta_0$, *where* $\beta_0 > 0$ *is defined by*

$$\beta_0 = \frac{r_2 - r_1}{\frac{K_2}{r_2} - \frac{K_1}{r_1}} \frac{1}{\frac{r_2}{K_2} + \frac{r_1}{K_1}}.$$

3. *If* $r_2 \leq r_1$, *then* $N_T^*(\beta) < K_1 + K_2$ *for any* $\beta > 0$.

The proof is given in Section B.2.

The behaviour of the system for perfect mixing ($\beta \to \infty$) is given by the following result.

Proposition A.2 *Let* $(N_1(t,\beta), N_2(t,\beta))$ *be a solution of (2) with initial condition* (N_{10}, N_{20}). *When* $\beta \to \infty$ *then, with the exception of a small initial interval,* $N_1(t,\beta)$ *and* $N_2(t,\beta)$ *are both approximated by the solution* $N(t)$ *of the logistic equation*

$$\frac{dN}{dt} = \frac{r_1 + r_2}{2} N \left(1 - N \frac{r_1/K_1 + r_2/K_2}{r_1 + r_2} \right) \tag{19}$$

with initial condition $N_0 = \frac{N_{10}+N_{20}}{2}$.

The proof is given in Section B.3.

The equation (19) is simply a logistic equation whose positive equilibrium is given by

$$N^* = \frac{r_1 + r_2}{r_1/K_1 + r_2/K_2}.$$

Hence, in the limit $\beta \to \infty$, we get $N_1^*(+\infty) = N_2^*(+\infty) = N^*$, so that $N_T^*(+\infty) = N_1^*(+\infty) + N_2^*(+\infty)$ is given by

$$N_T^*(+\infty) = 2 \frac{r_1 + r_2}{r_1/K_1 + r_2/K_2}. \tag{20}$$

Remark. The property $N_1^*(+\infty) = N_2^*(+\infty) = \frac{r_1+r_2}{r_1/K_1+r_2/K_2}$ had already been obtained by Freedman and Waltman (1977) (their Theorem 3.1) by a direct computation on the equations (30). See also Holt (1985) (his Section 2.3). We have obtained here this formula from the model (19) to which the model (2) reduces in the limit $\beta \to \infty$. This approach is more general than the direct computations used by Freedman and Waltman (1977) and will be useful for other models considered in this paper.

A more complete understanding of the effect of migration is provided by the following proposition, which gives additional information on the derivative of $N_T^*(\beta)$ with respect to β.

Proposition A.3 1. $\frac{d}{d\beta} N_T^*(0) = (K_1 - K_2) \left(\frac{1}{r_2} - \frac{1}{r_1} \right) = (K_1 - K_2) \frac{r_1 - r_2}{r_1 r_2}$.

2. *If* $N_T^*(\beta) < K_1 + K_2$ *then* $\frac{d}{d\beta} N_T^*(\beta) < 0$.

The proof is given in Section B.4.

Using (20) and Proposition A.3 we can notice that

- $\mathscr{J}_0$ is characterized by the condition $N_T^*(+\infty) \geq K_1 + K_2$,
- $\mathscr{J}_1$ is characterized by the conditions $N_T^*(+\infty) < K_1 + K_2$ and $\frac{d}{d\beta} N_T^*(0) > 0$,
- $\mathscr{J}_2$ is characterized by the condition $\frac{d}{d\beta} N_T^*(0) \leq 0$.

A.2 Appendix to Section 4.1

We assume in this section that the dispersion rates of the consumer and the resource are equal. The mathematical model is system (16) with $\alpha = \beta$, that is:

$$\left\{\begin{array}{rcl} \dfrac{dR_1}{dt} &=& \left[r_1\left(1-\dfrac{R_1}{K_1}\right)-a_1N_1\right]R_1+\beta(R_2-R_1),\\ \dfrac{dR_2}{dt} &=& \left[r_2\left(1-\dfrac{R_2}{K_2}\right)-a_2N_2\right]R_2+\beta(R_1-R_2),\\ \dfrac{dN_1}{dt} &=& \varepsilon_1(b_1R_1-q_1)N_1+\beta(N_2-N_1),\\ \dfrac{dN_2}{dt} &=& \varepsilon_2(b_2R_2-q_2)N_2+\beta(N_1-N_2). \end{array}\right. \tag{21}$$

This system can have many equilibria, whose analytical study is difficult (if not impossible). This study is beyond the scope of this paper. As already mentioned in Section 4, computer simulations show that (21) has a globally stable equilibrium. Assuming that this equilibrium exists for each value of β and is positive, we can consider, as in the previous section, its dependence with respect to β. Let $(R_1^{**}(\beta),R_2^{**}(\beta),N_1^{**}(\beta),N_2^{**}(\beta))$ be the positive and stable equilibrium of (21). Let $(N_1^*(\beta),N_2^*(\beta))$ be the globally stable equilibrium of the corresponding reduced model (14). We consider here some properties of $N_T^*(\beta)$ and $N_T^{**}(\beta)$ as functions of the migration rate β.

As a consequence of (20) and Proposition A.3 we have the following result.

Proposition A.4 *We have*

$$\frac{d}{d\beta}N_T^*(0)=(M_1-M_2)\left(\frac{1}{\sigma_2}-\frac{1}{\sigma_1}\right),\quad N_T^*(+\infty)=2\frac{\sigma_1+\sigma_2}{\sigma_1/M_1+\sigma_2/M_2},$$

where $\sigma_i=\varepsilon_i(b_iK_i-q_i)$ *and* $M_i=\frac{r_i}{a_i}\frac{b_iK_i-T_i}{b_iK_i}$.

The behaviour of (21) for perfect mixing ($\beta\to\infty$) is given by the following result.

Proposition A.5 *Let* $(R_1(t,\beta),R_2(t,\beta),N_1(t,\beta),N_2(t,\beta))$ *be a solution of (21) with initial condition* $(R_{10},R_{20},N_{10},N_{20})$. *When* $\beta\to\infty$ *then, with the exception of a small initial interval,* $R_1(t,\beta)$ *and* $R_2(t,\beta)$ *are both approximated by* $R(t)$ *and* $N_1(t,\beta)$ *and* $N_2(t,\beta)$ *are both approximated by* $N(t)$, *where* $(R(t),N(t))$ *is the solution of MacArthur's single-patch model*

$$\left\{\begin{array}{rcl} \dfrac{dR}{dt} &=& \left[\frac{r_1+r_2}{2}\left(1-R\frac{\frac{r_1}{K_1}+\frac{r_2}{K_2}}{r_1+r_2}\right)-\frac{a_1+a_2}{2}N\right]R,\\ \dfrac{dN}{dt} &=& \frac{1}{2}\left[(\varepsilon_1b_1+\varepsilon_2b_2)R-(\varepsilon_1q_1+\varepsilon_2q_2)\right]N. \end{array}\right. \tag{22}$$

with initial condition $R_0=\frac{R_{10}+R_{20}}{2}$ *and* $N_0=\frac{N_{10}+N_{20}}{2}$.

The proof is given in Section B.6.

The positive equilibrium of (22) is given by

$$R^*=\frac{\varepsilon_1q_1+\varepsilon_2q_2}{\varepsilon_1b_1+\varepsilon_2b_2},\quad N^*=\frac{r_1+r_2}{a_1+a_2}\left(1-R^*\frac{\frac{r_1}{K_1}+\frac{r_2}{K_2}}{r_1+r_2}\right).$$

This equilibrium is positive if and only if

$$\frac{\varepsilon_1 q_1 + \varepsilon_2 q_2}{\varepsilon_1 b_1 + \varepsilon_2 b_2} < \frac{r_1 + r_2}{\frac{r_1}{K_1} + \frac{r_2}{K_2}}.$$

Hence, in the limit $\beta \to \infty$, we get $N_1^{**}(+\infty) = N_2^{**}(+\infty) = N^*$, so that $N_T^{**}(+\infty) = N_1^{**}(+\infty) + N_2^{**}(+\infty)$ is given by

$$N_T^{**}(+\infty) = 2\frac{r_1 + r_2}{a_1 + a_2}\left(1 - \frac{\varepsilon_1 q_1 + \varepsilon_2 q_2}{\varepsilon_1 b_1 + \varepsilon_2 b_2}\frac{\frac{r_1}{K_1} + \frac{r_2}{K_2}}{r_1 + r_2}\right). \tag{23}$$

A more complete understanding of the effect of migration is provided by the following proposition, which gives the derivative of $\frac{d}{d\beta}N_T^{**}(0)$.

Proposition A.6 *We have*

$$\frac{d}{d\beta}N_T^{**}(0) = \left(\frac{b_2}{a_2 q_2} - \frac{b_1}{a_1 q_1}\right)\left(\frac{q_1}{b_1} - \frac{q_2}{b_2}\right) + \frac{d}{d\beta}N_T^*(0).$$

The proof is given in Section B.5.

A.3 Appendix to Section 4.2

Here, we give the mathematical analysis of the complete resource-consumer model in the case in which the consumer alone can disperse. The mathematical model is system (16) with α set to 0, that is:

$$\begin{cases} \dfrac{dR_1}{dt} &= \left[r_1\left(1 - \dfrac{R_1}{K_1}\right) - a_1 N_1\right] R_1, \\ \dfrac{dR_2}{dt} &= \left[r_2\left(1 - \dfrac{R_2}{K_2}\right) - a_2 N_2\right] R_2, \\ \dfrac{dN_1}{dt} &= \varepsilon_1(b_1 R_1 - q_1)N_1 + \beta(N_2 - N_1), \\ \dfrac{dN_2}{dt} &= \varepsilon_2(b_2 R_2 - q_2)N_2 + \beta(N_1 - N_2). \end{cases} \tag{24}$$

We start with the following observation.

Proposition A.7 *Let $E^* = (R_1^*, R_2^*, N_1^*, N_2^*)$ be a positive equilibrium of (24). Then (N_1^*, N_2^*) is a positive equilibrium of the reduced model (14). Conversely, let (N_1^*, N_2^*) be a positive equilibrium of the reduced model (14). Then $E^* = (R_1^*, R_2^*, N_1^*, N_2^*)$, where R_1^*, R_2^* are defined by*

$$R_1^* = K_1\left(1 - \frac{a_1}{r_1}N_1^*\right), \quad R_2^* = K_2\left(1 - \frac{a_2}{r_2}N_2^*\right),$$

is a positive equilibrium of (24) if and only if $N_1^* < \frac{r_1}{a_1}$ and $N_2^* < \frac{r_2}{a_2}$.

The proof is given in Section B.7.

The model (24) was already considered by Holt (1984) (his equations 6–7). In the case of resource exponential growth instead of logistic growth, he gave the condition on β for resource persistence in both patches at equilibrium. He did not consider, however,

the links between (24) and the reduced two-patch logistic equation (14), as we did in our study. We will now consider this question of equilibrium resource persistence in both patches with logistic growth. More precisely, we investigate the links between the equilibrium of (24) and the equilibrium of the reduced model (14). Let $(N_1^*(\beta), N_2^*(\beta))$ be a positive equilibrium of the reduced system (14). The resource abundances are positive if and only if

$$N_1^*(\beta) < \frac{r_1}{a_1}, \quad N_2^*(\beta) < \frac{r_2}{a_2}.$$

Recall that

$$N_1^*(0) = M_1 < \frac{r_1}{a_1}, \quad N_2^*(0) = M_2 < \frac{r_2}{a_2},$$

where M_1 and M_2 are the carrying capacities defined by (15). Using (5) we get

$$M_1 < N_1^*(\beta) < N_2^*(\beta) < M_2 < \frac{r_2}{a_2}.$$

Hence, the condition $N_2^*(\beta) < \frac{r_2}{a_2}$ is satisfied for every $\beta > 0$ and the condition $N_1^*(\beta) < \frac{r_1}{a_1}$ is also satisfied when β is small enough. This means that, for β small enough, the positive equilibrium E^{**} of (24) defined by (17) is the same as the equilibrium E^* considered in Proposition A.7 and corresponding to the positive equilibrium (N_1^*, N_2^*) of the reduced model (14). Thus, for β small enough we have $N_T^{**}(\beta) = N_T^*(\beta)$, as illustrated in Figure 6.

However, when β increases, it can happen that, for some critical value β_c, we have $N_1^*(\beta_c) = \frac{r_1}{a_1}$ and $N_1^*(\beta) > \frac{r_1}{a_1}$ for $\beta > \beta_c$. Hence when $\beta > \beta_c$, the equilibrium $(N_1^*(\beta), N_2^*(\beta))$ no longer corresponds to a positive equilibrium of (24). Actually, the corresponding equilibrium E^* of (24) described by Proposition A.7, becomes negative when $\beta > \beta_c$, since $R_1^*(\beta) < 0$.

Besides the equilibrium $E^*(\beta) = (R_1^*(\beta), R_2^*(\beta), N_1^*(\beta), N_2^*(\beta))$ described by Proposition A.7, (24) can have the boundary equilibrium

$$E^\star(\beta) = (0, R_2^\star(\beta), N_1^\star(\beta), N_2^\star(\beta))$$

where $R_2^\star(\beta)$, $N_1^\star(\beta)$, $N_2^\star(\beta)$ are positive solutions of the set of equations

$$\left\{ \begin{array}{rcl} 0 & = & r_2 \left(1 - \frac{R_2^\star}{K_2}\right) - a_2 N_2^\star, \\ 0 & = & -q_1 N_1^\star + \beta (N_2^\star - N_1^\star), \\ 0 & = & (b_2 R_2^\star - q_2) N_2^\star + \beta (N_1^\star - N_2^\star). \end{array} \right. \tag{25}$$

Solving the first equation for $R_2^\star$ yields

$$R_2^\star = K_2 \left(1 - \frac{a_2}{r_2} N_2^\star\right).$$

Replacing $R_2^\star$ by this expression in the second and third equations of (25) yields a set of two equations that can be solved for $N_1^\star$ and $N_2^\star$.

For $\beta = \beta_c$, there is a bifurcation of $E^*(\beta)$ with $E^\star(\beta)$. When $\beta > \beta_c$, we observed numerically that $E^\star(\beta)$ becomes stable and attracts all solutions. Therefore, for $\beta > \beta_c$, the stable equilibrium (17) of (24) is non longer equal to $E^*(\beta)$, which has become

negative, but is equal to the boundary equilibrium $E^\star(\beta)$. Therefore, there is a critical value β_c such that (see Figure 6b)

$$N_T^{**}(\beta) = \begin{cases} N_1^*(\beta) + N_2^*(\beta) = N_T^*(\beta) & \text{for} \quad 0 \leq \beta \leq \beta_c \\ N_1^\star(\beta) + N_2^\star(\beta) \neq N_T^*(\beta) & \text{for} \quad \beta > \beta_c. \end{cases}$$

The behaviour of (24) for perfect mixing ($\beta \to \infty$) is given by the following result.

Proposition A.8 *Let $(R_1(t,\beta), R_2(t,\beta), N_1(t,\beta), N_2(t,\beta))$ be a solution of (24) with initial condition $(R_{10}, R_{20}, N_{10}, N_{20})$. When $\beta \to \infty$ then, with the exception of a small initial interval, $R_1(t,\beta)$ and $R_2(t,\beta)$ are approximated by $R_1(t)$ and $R_2(t)$, and $N_1(t,\beta)$ and $N_2(t,\beta)$ are both approximated by $N(t)$, where $(R_1(t), R_2(t), N(t))$ is the solution of MacArthur's single-patch model*

$$\begin{cases} \dfrac{dR_1}{dt} &= \left[r_1 \left(1 - \dfrac{R_1}{K_1} \right) - a_1 N \right] R_1, \\ \dfrac{dR_2}{dt} &= \left[r_2 \left(1 - \dfrac{R_2}{K_2} \right) - a_2 N \right] R_2, \\ \dfrac{dN}{dt} &= \frac{1}{2} \left(\varepsilon_1 b_1 R_1 + \varepsilon_2 b_2 R_2 - \varepsilon_1 q_1 - \varepsilon_2 q_2 \right) N. \end{cases} \tag{26}$$

with initial condition R_{10}, R_{20} and $N_0 = \frac{N_{10}+N_{20}}{2}$.

The proof is given in Section B.8.

In this MacArthur model for one consumer and two resources, all resources are not necessarily present at equilibrium. For instance, assuming that the resources are labelled such that $\frac{r_1}{a_1} > \frac{r_2}{a_2}$, we have the following results, which are particular cases of the results in Holt (1977) obtained for the model of a consumer and $n \geq 2$ resources.

1. If $\varepsilon_1 b_1 K_1 + \varepsilon_2 b_2 K_2 > \varepsilon_1 q_1 + \varepsilon_2 q_2$ then no resource is present at equilibrium
2. If $\varepsilon_1 b_1 K_1 + \varepsilon_2 b_2 K_2 \leq \varepsilon_1 q_1 + \varepsilon_2 q_2$ then resource R_1 is always present at equilibrium and resource R_2 is present if and only if the following condition holds

$$\frac{\varepsilon_1 q_1 + \varepsilon_2 q_2}{\varepsilon_1 b_1 K_1} > 1 - \frac{a_1}{r_1} \frac{r_2}{a_2} \tag{27}$$

Notice that the condition (27) of existence of the species R_2 at equilibrium is independent of its own carrying capacity K_2 yet may critically depend on K_1. This behaviour of resources sharing a common consumer is known as apparent competition.

This behaviour of the limiting model (26) when $\beta \to \infty$, explains why there is a critical value β_c such that, for $\beta > \beta_c$ the resource R_1 is not present at equilibrium, see Figure 6b. It should be noticed that for the numerical simulation shown in this figure one has $\frac{r_1}{a_1} = 2.5 < 3 = \frac{r_2}{a_2}$. This explains why it is the resource R_1 (and not R_2) that is eliminated from the equilibrium by apparent competition. In the presentation of the results of Holt (1977), following him, we have used the conventional inequality $r_1/a_1 > r_2/a_2$.

B Proofs

B.1 Some formulas

Let us first prove the following preliminary result.

Proposition B.1 *Let $(N_1^*(\beta),N_2^*(\beta))$ be an equilibium of (2).*

- *If $K_1 < K_2$ and $\beta > 0$, then $K_1 < N_1^*(\beta) < N_2^*(\beta) < K_2$ (i.e. (5) holds).*
- *Let $N_T^*(\beta) = N_1^*(\beta) + N_2^*(\beta)$. Then*

$$N_T^* = K_1 + K_2 + \beta \frac{N_2^* - N_1^*}{\frac{r_1}{K_1}\frac{r_2}{K_2}N_1^*N_2^*}\left(\frac{r_2}{K_2}N_2^* - \frac{r_1}{K_1}N_1^*\right) \tag{28}$$

and

$$\frac{d}{d\beta}N_T^*(\beta) = \frac{N_2^* - N_1^*}{\det A}\left[\beta\left(\frac{N_1^*}{N_2^*} - \frac{N_2^*}{N_1^*}\right) + \frac{r_2}{K_2}N_2^* - \frac{r_1}{K_1}N_1^*\right]. \tag{29}$$

Let us prove that (5) holds. The equilibria are the solutions of the set of equations

$$\left\{\begin{array}{rcl} 0 & = & r_1N_1\left(1-\frac{N_1}{K_1}\right) + \beta(N_2 - N_1), \\ 0 & = & r_2N_2\left(1-\frac{N_2}{K_2}\right) + \beta(N_1 - N_2). \end{array}\right. \tag{30}$$

Solving the first equation for N_2 and the second for N_1 yields that the equilibria are the nonnegative intersections of the two parabolas $\mathscr{P}_1$ and $\mathscr{P}_2$ of equations $N_2 = P_1(N_1)$ and $N_1 = P_2(N_2)$, where the functions P_1 and P_2 are defined by

$$P_1(N_1) = N_1 - \frac{r_1}{\beta}N_1\left(1-\frac{N_1}{K_1}\right), \quad P_2(N_2) = N_2 - \frac{r_2}{\beta}N_2\left(1-\frac{N_2}{K_2}\right).$$

These parabolas are simply the isoclines $\dot{N}_1 = 0$ and $\dot{N}_2 = 0$. The isoclines intersect at $(0,0)$ and at $E = (N_1^*,N_2^*)$. Since $P_1(K_1) = K_1$, the point $A = (K_1,K_1)$ belongs to $\mathscr{P}_1$. Since $P_2(K_2) = K_2$, the point $B = (K_2,K_2)$ belongs to $\mathscr{P}_2$. Hence, the equilibrium E belongs to the triangle ABC, where $C = (K_1,K_2)$ (see Figure 7). Thus $K_1 < N_1^* < N_2^* < K_2$, which is (5).

Remark. The stability study of $E = (N_1^*,N_2^*)$ comes from the analysis of the variational matrix. See Freedman and Waltman (1977), DeAngelis et al. (1979), where it is proved that E is stable. Actually E is globally asymptotically stable (Holt 1985).

Let us prove that (28) holds. At the equilibrium (N_1^*,N_2^*), one has:

$$\left\{\begin{array}{rcl} 0 & = & \frac{r_1}{K_1}N_1^*(K_1 - N_1^*) + \beta(N_2^* - N_1^*), \\ 0 & = & \frac{r_2}{K_2}N_2^*(K_2 - N_2^*) + \beta(N_1^* - N_2^*). \end{array}\right. \tag{31}$$

Dividing the first equation by $\frac{r_1}{K_1}N_1^*$, the second by $\frac{r_2}{K_2}N_2^*$, and adding the two, one gets:

$$K_1 + K_2 - (N_1^* + N_2^*) + \beta\frac{N_2^* - N_1^*}{\frac{r_1}{K_1}N_1^*} + \beta\frac{N_1^* - N_2^*}{\frac{r_2}{K_2}N_2^*} = 0.$$

Hence

$$N_1^* + N_2^* = K_1 + K_2 + \beta\frac{N_2^* - N_1^*}{\frac{r_1}{K_1}\frac{r_2}{K_2}N_1^*N_2^*}\left(\frac{r_2}{K_2}N_2^* - \frac{r_1}{K_1}N_1^*\right),$$

which is (28).

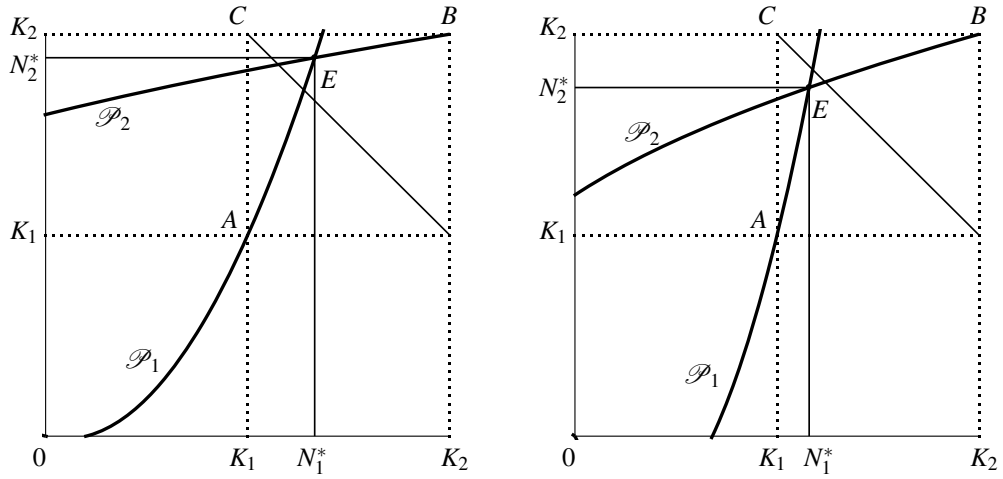


Figure 7: Phase-plane diagram for (2). $E = (N_1^*, N_2^*)$, the positive intersection of $\mathscr{P}_1$ and $\mathscr{P}_2$, is a stable equilibrium and 0 is an unstable one. On the left, the case $N_T^* > K_1 + K_2$. On the right, the case $N_T^* < K_1 + K_2$.

Let us prove that (29) holds. The computation of the derivative of $N_T^*(\beta)$ with respect of β requires the implicit function theorem. Let us calculate the derivatives $\frac{d}{d\beta}N_1^*(\beta)$ and $\frac{d}{d\beta}N_2^*(\beta)$. We have

$$\begin{bmatrix} \frac{d}{d\beta}N_1^*(\beta) \\ \frac{d}{d\beta}N_2^*(\beta) \end{bmatrix} = -A^{-1} \begin{bmatrix} N_2^*(\beta) - N_1^*(\beta) \\ N_1^*(\beta) - N_2^*(\beta) \end{bmatrix}, \tag{32}$$

where

$$A = \begin{bmatrix} r_1\left(1 - \frac{N_1^*(\beta)}{K_1}\right) - \beta - \frac{r_1}{K_1}N_1^*(\beta) & \beta \\ \beta & r_2\left(1 - \frac{N_2^*(\beta)}{K_2}\right) - \beta - \frac{r_2}{K_2}N_2^*(\beta) \end{bmatrix}$$

is the matrix of partial derivatives of equations (30) with respect to N_1 and N_2 evaluated at $N_1^*(\beta)$ and $N_2^*(\beta)$, and the last vector is the vector of derivatives of equations (30) with respect to β evaluated at $N_1^*(\beta)$ and $N_2^*(\beta)$. Using the formulas

$$r_1\left(1 - \frac{N_1^*}{K_1}\right) - \beta = -\beta\frac{N_2^*}{N_1^*}, \quad r_2\left(1 - \frac{N_2^*}{K_2}\right) - \beta = -\beta\frac{N_1^*}{N_2^*},$$

and after some algebraic manipulation, equation (32) reduces to

$$\begin{bmatrix} \frac{d}{d\beta}N_1^* \\ \frac{d}{d\beta}N_2^* \end{bmatrix} = \frac{1}{\det A} \begin{bmatrix} \beta\frac{N_1^*}{N_2^*} + \frac{r_2}{K_2}N_2^* & \beta \\ \beta & \beta\frac{N_2^*}{N_1^*} + \frac{r_1}{K_1}N_1^* \end{bmatrix} \begin{bmatrix} N_2^* - N_1^* \\ N_1^* - N_2^* \end{bmatrix}$$

where

$$\det A = \left(\beta\frac{N_2^*}{N_1^*} + \frac{r_1}{K_1}N_1^*\right)\left(\beta\frac{N_1^*}{N_2^*} + \frac{r_2}{K_2}N_2^*\right) - \beta^2 > 0.$$

Therefore

$$\frac{d}{d\beta}N_1^* = \frac{1}{\det A}\left[\left(\beta\frac{N_1^*}{N_2^*} + \frac{r_2}{K_2}N_2^*\right)(N_2^* - N_1^*) + \beta\,(N_1^* - N_2^*)\right],$$

$$\frac{d}{d\beta}N_2^* = \frac{1}{\det A}\left[\left(\beta\frac{N_2^*}{N_1^*}+\frac{r_1}{K_1}N_1^*\right)(N_1^*-N_2^*)+\beta\,(N_2^*-N_1^*)\right].$$

Adding the two equations, one obtains (29).

B.2 Proof of Proposition A.1

From (28), we can study the cases 1 and 3 of Proposition A.1.

- If $\frac{r_2}{K_2} \geq \frac{r_1}{K_1}$ then, using (5), we have

$$\frac{r_2}{K_2}N_2^* - \frac{r_1}{K_1}N_1^* \geq \frac{r_1}{K_1}N_2^* - \frac{r_1}{K_1}N_1^* = \frac{r_1}{K_1}\,(N_2^*-N_1^*)\,.$$

  Therefore, using $N_2^* > N_1^*$ and (28), we have $N_T^* > K_1 + K_2$.

- If $r_2 \leq r_1$ then, using (5), we have $\frac{N_2^*}{K_2} < 1$ and $\frac{N_1^*}{K_1} > 1$, so that

$$\frac{r_2}{K_2}N_2^* - \frac{r_1}{K_1}N_1^* = r_2\frac{N_2^*}{K_2} - r_1\frac{N_1^*}{K_1} < r_2 - r_1 \leq 0.$$

  Therefore, using $N_2^* > N_1^*$ and (28), we have $N_T^* < K_1 + K_2$.

The study of the case 2 of Proposition A.1 requires both (28) and (29). From (28) we deduce that $N_T^*(\beta) = K_1 + K_2$ for $\beta > 0$, if and only if

$$\frac{r_2}{K_2}N_2^* - \frac{r_1}{K_1}N_1^* = 0. \tag{33}$$

Using (29) we see that (33) necessarily implies that $\frac{d}{d\beta}N_T^*(\beta) < 0$. Hence, we can have $N_T^*(\beta) = K_1 + K_2$ for at most one value of $\beta > 0$. For such value of β, (N_1^*, N_2^*) is a solution of the set of linear equations formed by (33) and the condition

$$N_1^* + N_2^* = K_1 + K_2. \tag{34}$$

Solving (33–34) we obtain

$$N_1^* = \frac{K_1}{r_1}\frac{K_1+K_2}{\frac{K_1}{r_1}+\frac{K_2}{r_2}}, \quad N_2^* = \frac{K_2}{r_2}\frac{K_1+K_2}{\frac{K_1}{r_1}+\frac{K_2}{r_2}}.$$

Using (31) we obtain that

$$\beta = \frac{r_2 - r_1}{\frac{K_2}{r_2}-\frac{K_1}{r_1}}\frac{1}{\frac{r_2}{K_2}+\frac{r_1}{K_1}}.$$

We conclude that $N_T^*(\beta) = K_1 + K_2$ if and only if β is equal to this value, and that $N_T^*(\beta) < K_1 + K_2$ if and only if β is greater than this value.

B.3 Proof of Proposition A.2

Let $N = \frac{N_1+N_2}{2}$. We can rewrite (2) using the variables N_1 and N (notice that $N_2 = 2N - N_1$):

$$\left\{\begin{array}{rcl} \dfrac{dN_1}{dt} & = & r_1N_1\left(1-\frac{N_1}{K_1}\right)+2\beta(N-N_1), \\ \dfrac{dN}{dt} & = & \frac{1}{2}\left[r_1N_1\left(1-\frac{N_1}{K_1}\right)+r_2(2N-N_1)\left(1-\frac{2N-N_1}{K_2}\right)\right]. \end{array}\right. \tag{35}$$

The system (35) is a slow and fast system whose slow variable is N and fast variable is N_1. In the limit $\beta \to \infty$, we can replace the fast variable N_1 is the second equation by its quasi-steady state approximation $N_1 = N$ obtained from the first equation, and we get

$$\frac{dN}{dt} = \frac{1}{2}\left[r_1 N\left(1-\frac{N}{K_1}\right) + r_2 N\left(1-\frac{N}{K_2}\right)\right] = \frac{r_1+r_2}{2} N\left(1 - N\frac{r_1/K_1 + r_2/K_2}{r_1+r_2}\right),$$

which is the logistic equation (19).

B.4 Proof of Proposition A.3

Using $N_1^*(0) = K_1$, $N_2^*(0) = K_2$ in (29), we get

$$\frac{d}{d\beta} N_T^*(0) = \left(\frac{1}{r_2} - \frac{1}{r_1}\right)(K_1 - K_2).$$

This is item 1 of Proposition A.3.

From (28) we deduce that $N_T^*(\beta) < K_1 + K_2$ if and only if

$$\frac{r_2}{K_2} N_2^* - \frac{r_1}{K_1} N_1^* < 0.$$

Using (29) we see that this condition necessarily implies that $\frac{d}{d\beta} N_T^*(\beta) < 0$. This is item 2 of Proposition A.3

B.5 Proof of Proposition A.6

Let $(R_1^{**}(\beta), R_2^{**}(\beta), N_1^{**}(\beta), N_2^{**}(\beta))$ be a positive equilibrium of (21). Thus, it is a solution of the set of equations

$$\left\{\begin{array}{rcl} 0 &=& \left[r_1\left(1-\dfrac{R_1^{**}}{K_1}\right) - a_1 N_1^{**}\right] R_1^{**} + \beta(R_2^{**} - R_1^{**}) \\ 0 &=& \left[r_2\left(1-\dfrac{R_2^{**}}{K_2}\right) - a_2 N_2^{**}\right] R_2^{**} + \eta(R_1^{**} - R_2^{**}) \\ 0 &=& \varepsilon_1(b_1 R_1^{**} - q_1) N_1^{**} + \beta(N_2^{**} - N_1^{**}) \\ 0 &=& \varepsilon_2(b_2 R_2^{**} - q_2) N_2^{**} + \beta(N_1^{**} - N_2^{**}). \end{array}\right. \tag{36}$$

As in Section B.1, we use the implicit function theorem and calculate the derivatives $\frac{d}{d\beta} R_i^{**}(\beta)$ and $\frac{d}{d\beta} N_i^{**}(\beta)$. We have

$$\left[\begin{array}{c} \frac{d}{d\beta} R_1^{**}(\beta) \\ \frac{d}{d\beta} R_2^{**}(\beta) \\ \frac{d}{d\beta} N_1^{**}(\beta) \\ \frac{d}{d\beta} N_2^{**}(\beta) \end{array}\right] = -A^{-1} \left[\begin{array}{c} R_2^{**}(\beta) - R_1^{**}(\beta) \\ R_1^{**}(\beta) - R_2^{**}(\beta) \\ N_2^{**}(\beta) - N_1^{**}(\beta) \\ N_1^{**}(\beta) - N_2^{**}(\beta) \end{array}\right], \tag{37}$$

where A is the matrix of partial derivatives of equations (36) with respect to (R_1, R_2, N_1, N_2) evaluated at $R_i^{**}(\beta)$ and $N_i^{**}(\beta)$, and the last vector is the vector of derivatives of equations (36) with respect to β evaluated at $R_i^{**}(\beta)$ and $N_i^{**}(\beta)$.

Using $R_i^{**}(0) = \frac{q_i}{b_i}$ and $N_i^{**}(0) = M_i$, we get

$$A = \begin{bmatrix} -\frac{r_1 q_1}{K_1 b_1} & 0 & -\frac{a_1 q_1}{b_1} & 0 \\ 0 & -\frac{r_2 q_2}{K_2 b_2} & 0 & -\frac{a_2 q_2}{b_2} \\ \varepsilon_1 b_1 M_1 & 0 & 0 & 0 \\ 0 & \varepsilon_2 b_2 M_2 & 0 & 0 \end{bmatrix}.$$

After some algebraic manipulation, for $\beta = 0$, equation (37) reduces to

$$\begin{bmatrix} \frac{d}{d\beta} R_1^{**}(0) \\ \frac{d}{d\beta} R_2^{**}(0) \\ \frac{d}{d\beta} N_1^{**}(0) \\ \frac{d}{d\beta} N_2^{**}(0) \end{bmatrix} = \begin{bmatrix} 0 & 0 & -\frac{1}{\varepsilon_1 b_1 M_1} & 0 \\ 0 & 0 & 0 & -\frac{1}{\varepsilon_2 b_2 M_2} \\ \frac{b_1}{a_1 q_1} & 0 & \frac{1}{\sigma_1} & 0 \\ 0 & \frac{b_2}{a_2 q_2} & 0 & \frac{1}{\sigma_2} \end{bmatrix} \begin{bmatrix} \frac{q_2}{b_2} - \frac{q_1}{b_1} \\ \frac{q_1}{b_1} - \frac{q_2}{b_2} \\ M_2 - M_1 \\ M_1 - M_2 \end{bmatrix}.$$

Therefore

$$\frac{d}{d\beta} N_1^{**}(0) = \frac{b_1}{a_1 q_1} + \left(\frac{q_2}{b_2} - \frac{q_1}{b_1} \right) + \frac{1}{\sigma_1} (M_2 - M_1),$$
$$\frac{d}{d\beta} N_1^{**}(0) = \frac{b_2}{a_2 q_2} + \left(\frac{q_1}{b_1} - \frac{q_2}{b_2} \right) + \frac{1}{\sigma_2} (M_1 - M_2).$$

Adding these equations one obtains

$$\frac{d}{d\beta} N_T^{**}(0) = \left(\frac{b_2}{a_2 q_2} - \frac{b_1}{a_1 q_1} \right) \left(\frac{q_1}{b_1} - \frac{q_2}{b_2} \right) + (M_1 - M_2) \left(\frac{1}{\sigma_2} - \frac{1}{\sigma_1} \right).$$

B.6 Proof of Proposition A.5

We use here the singular perturbation analysis outlined in Section B.3 to obtain the behaviour of the system as $\beta \to \infty$. Let

$$R = \frac{R_1 + R_2}{2}, \quad N = \frac{N_1 + N_2}{2}.$$

We can rewrite (16) using the variables R_1, N_1 and R, N (using $R_2 = 2R - R_1$ and $N_2 = 2N - N_1$):

$$\begin{cases} \frac{dR_1}{dt} &= \left[r_1 \left(1 - \frac{R_1}{K_1} \right) - a_1 N_1 \right] R_1 + 2\beta (R - R_1) \\ \frac{dN_1}{dt} &= \varepsilon_1 (b_1 R_1 - q_1) N_1 + 2\beta (N - N_1) \\ \frac{dR}{dt} &= \frac{1}{2} \left[\left[r_1 \left(1 - \frac{R_1}{K_1} \right) - a_1 N_1 \right] R_1 + \left[r_2 \left(1 - \frac{2R - R_1}{K_2} \right) - a_2 (2N - N_1) \right] (2R - R_1) \right] \\ \frac{dN}{dt} &= \frac{1}{2} \left[\varepsilon_1 (b_1 R_1 - q_1) N_1 + \varepsilon_2 (b_2 (2R - R_2) - q_2)(2N - N_2) \right]. \end{cases} \tag{38}$$

System (38) is a slow and fast system whose slow variables are R and N and fast variables are R_1 and N_1. In the limit $\beta \to \infty$, we can replace the fast variables R_1 and N_1 in the third and fourth equations by their quasi-steady state approximations $R_1 = R$ and $N_1 = N$ obtained from the first and second equations. We obtain

$$\begin{cases} \frac{dR}{dt} &= \frac{1}{2} \left[\left[r_1 \left(1 - \frac{R}{K_1} \right) - a_1 N \right] R + \left[r_2 \left(1 - \frac{R}{K_2} \right) - a_2 N \right] R \right] \\ \frac{dN}{dt} &= \frac{1}{2} \left[\varepsilon_1 (b_1 R - q_1) N + \varepsilon_2 (b_2 R - q_2) N \right]. \end{cases}$$

This is simply the MacArthur resource-consumer model (22).

$$\left\{\begin{array}{rcl} \dfrac{dR}{dt} & = & \left[\frac{r_1+r_2}{2}\left(1-R\frac{\frac{r_1}{K_1}+\frac{r_2}{K_2}}{r_1+r_2}\right)-\frac{a_1+a_2}{2}N\right]R \\ \dfrac{dN}{dt} & = & \frac{\varepsilon_1+\varepsilon_2}{2}\left(\frac{\varepsilon_1 b_1+\varepsilon_2 b_2}{\varepsilon_1+\varepsilon_2}R-\frac{\varepsilon_1 q_1+\varepsilon_2 q_2}{\varepsilon_1+\varepsilon_2}\right)N. \end{array}\right.$$

B.7 Proof of Proposition A.7

An equilibrium point $(R_1^*, R_2^*, N_1^*, N_2^*)$ of (24) is a solution of the set of equations

$$\left\{\begin{array}{rcl} 0 & = & \left[r_1\left(1-\frac{R_1^*}{K_1}\right)-a_1 N_1^*\right]R_1^*, \\ 0 & = & \left[r_2\left(1-\frac{R_2^*}{K_2}\right)-a_2 N_2^*\right]R_2^*, \\ 0 & = & \varepsilon_1(b_1R_1^*-q_1)N_1^*+\beta(N_2^*-N_1^*), \\ 0 & = & \varepsilon_2(b_2R_2^*-q_2)N_2^*+\beta(N_1^*-N_2^*). \end{array}\right. \tag{39}$$

If this equilibrium is positive, then we must have

$$r_1\left(1-\frac{R_1^*}{K_1}\right)-a_1N_1^*=0, \quad r_2\left(1-\frac{R_2^*}{K_2}\right)-a_2N_2^*=0.$$

Therefore

$$R_1^*=K_1\left(1-\frac{a_1}{r_1}N_1^*\right)>0, \quad R_2^*=K_2\left(1-\frac{a_2}{r_2}N_2^*\right)>0. \tag{40}$$

Replacing these values in the third and fourth equations in (39), we get

$$\left\{\begin{array}{rcl} 0 & = & \varepsilon_1\left(b_1K_1-q_1-\frac{a_1b_1}{r_1}K_1N_1^*\right)N_1^*+\beta(N_2^*-N_1^*), \\ 0 & = & \varepsilon_2\left(b_2K_2-q_2-\frac{a_2b_2}{r_2}K_2N_2^*\right)N_2^*+\beta(N_1^*-N_2^*). \end{array}\right. \tag{41}$$

Hence (N_1^*, N_2^*) is a positive equilibrium of the reduced model (14). The converse holds as long as the inequalities (40) are satisfied.

B.8 Proof of Proposition A.8

We use here the singular perturbation analysis outlined in Section B.3 to obtain the behaviour of the system as $\beta \to \infty$. Let $N=\frac{N_1+N_2}{2}$. We can rewrite (24) using the variables R_1, R_2, N and N_1 (using $N_2=2N-N_1$):

$$\left\{\begin{array}{rcl} \dfrac{dR_1}{dt} & = & \left[r_1\left(1-\dfrac{R_1}{K_1}\right)-a_1N_1\right]R_1 \\ \dfrac{dR_2}{dt} & = & \left[r_2\left(1-\dfrac{R_2}{K_2}\right)-a_2N_2\right]R_2 \\ \dfrac{dN}{dt} & = & \frac{1}{2}\left[\varepsilon_1(b_1R_1-q_1)N_1+\varepsilon_2(b_2R_2-q_2)(2N-N_2)\right] \\ \dfrac{dN_1}{dt} & = & \varepsilon_1(b_1R_1-q_1)N_1+2\beta(N-N_1) \end{array}\right. \tag{42}$$

System (42) is a slow and fast system whose slow variables are R_1, R_2 and N and fast variables are N_1. In the limit $\beta \to \infty$, we can replace the fast variable N_1 in the first three equations of (42) by its quasi-steady state approximations $N_1 = N$ obtained from the fourth equation. We obtain

$$\left\{ \begin{array}{rcl} \dfrac{dR_1}{dt} & = & \left[r_1 \left(1 - \dfrac{R_1}{K_1} \right) - a_1 N \right] R_1 \\ \dfrac{dR_2}{dt} & = & \left[r_2 \left(1 - \dfrac{R_2}{K_2} \right) - a_2 N \right] R_2 \\ \dfrac{dN}{dt} & = & \frac{1}{2} \left[\varepsilon_1 (b_1 R_1 - q_1) N + \varepsilon_2 (b_2 R_2 - q_2) N \right] \end{array} \right.$$

This is simply the MacArthur two resource–one consumer model (26).

Acknowledgments

Our ideas germinated during a stimulating workshop organized in August 2014 at the Centre Interfacultaire Bernoulli (CIB) of the Ecole Polytechnique Fédérale de Lausanne (EPFL) in Switzerland, with funding of the Swiss National Science Foundation.

References

[1] DeAngelis, D.L., C.C. Travis, and W.M. Post. (1979) Persistence and stability of seed-dispersed species in a patchy environment. Theoretical Population Biology, 16, 107–125.

[2] DeAngelis, D.L., and B. Zhang. (2014) Effects of dispersal in a non-uniform environment on population dynamics and competition: a patch model approach. Discrete and Continuous Dynamical Systems Series B, 19, 3087–3104.

[3] Freedman, H.I., and D. Waltman. (1977) Mathematical models of population interactions with dispersal. I. Stability of two habitats with and without a predator. SIAM Journal of Applied Mathematics, 32, 631–648.

[4] Gabriel, J.P., F. Saucy, and L.F. Bersier. (2005) Paradoxes in the logistic equation? Ecological Modelling, 185, 147–151.

[5] Ginzburg, L.R. (1992) Evolutionary consequences of basic growth equations. Trends in Ecology and Evolution, 7, 133–133.

[6] Hanski, I. (1999) Metapopulation Ecology. Oxford University Press.

[7] Holt, R.D. (1977) Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology, 12, 197–229.

[8] Holt, R.D. (1984) Spatial heterogeneity, indirect interactions, and the coexistence of prey species. The American Naturalist, 124, 377–406.

[9] Holt, R.D. (1985) Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology, 28, 181–208.

[10] Kuno, E. (1991) Some strange properties of the logistic equation defined with r and K: inherent defects or artifacts? Researches in Population Ecology, 33, 33–39.

[11] MacArthur, R.H. (1969) Species packing and what interspecies competition minimizes. Proceedings of the National Academy of Sciences, 64, 1369–1371.

[12] MacArthur, R.H. (1970) Species packing and competitive equilibrium for many species. Theoretical Population Biology, 1, 1–11.

[13] Mallet, J. (2012) The struggle for existence: how the notion of carrying capacity, K, obscures the links between demography, Darwinian evolution, and speciation. Evolutionary Ecology Research, 14, 627–665.

[14] Verhulst, P.F. (1838) Notice sur la loi que la population suit dans son accroissement. Correspondances mathématiques et physiques, 10, 113–121.