Effects of Diffusion on Total Biomass in Simple Metacommunities

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Abstract

This paper analyzes the effects of diffusion on the overall population size of the different species of a metacommunity. Depending on precise thresholds, we determine whether increasing the dispersal rate of a species has a positive or negative effect on population abundance. These thresholds depend on the interaction type of the species and the quality of the patches. The motivation for researching this issue is that spatial structure is a source of new biological insights with management interest. For instance, in a metacommunity of two competitors, the movement of a competitor could lead to a decrease of the overall population size of both species. On the other hand, we discuss when some classic results of metapopulation theory are preserved in metacommunities. Our results complement some recent experimental work by Zhang and collaborators.

Keywords: Coexistence Mechanisms, Metapopulations vs Metacommunities, Dispersal Response, Paradoxical Effects

1 Introduction

The uncontrolled expansion and intensification of human land-use have increased the habitat fragmentation of many ecosystems worldwide. In fact, habitat fragmentation is now a serious threat for the viability of many endangered species [3,13]. To solve this problem, a possible conservation strategy is the construction of ecological corridors, (path-ways that facilitate the movement of individuals between two different patches [7,39]). The efficacy of corridors has been much debated in the ecological literature [12,15,21,22,38]. Among their many benefits, the extinction risk can be reduced by the colonization of new areas. At the same time, individuals may move from suitable to unsuitable regions in which they die or their reproductive output is decreased, threatening the viability of the population. For instance, Amstrom and Part [6] reported that the presence of corridors might have a detrimental impact on the population abundance in laboratory experiments with oribatid mites.

Understanding the precise implications of spatial fragmentation is of great importance for conservation and management, in particular, for the performance of ecological corridors [15–17,37]. In nature, most species occupy large habitats with a heterogeneous distribution of resources and other biological factors, with the interplay with other species as a typically relevant factor [10,19]. Actually, a population generally exists as a metapopulation, that is, a set of subpopulations confined in discrete patches among which an individual can move via dispersal routes [23]. Metapopulation

models are a valuable tool to guide population management [15–17, 37]. Nonetheless, drawing biological insights from classical models is not an easy task since they are remarkably resistant to analysis. It is worth noting that the dynamics of a single species that inhabits two different patches is already quite complex [4,11,20,24,26]. A striking result is that, in heterogeneous landscapes, total population size is a hump-shaped function when plotted on the dispersal rate [4,15,30,42]. In more mathematical terms, the overall population increases as dispersal increases with a relatively low dispersal rate, before reaching a maximum and then subsequently decreasing. The hump-shaped response has been detected in laboratory experiments with duckweed (*Lemmoideae*). Specifically, in a metapopulation with five patches, Zhang *et al.* [42] compared the total biomass with four different diffusion rates, namely $0\%, 6\%, 10\%, 20\%$. The non-zero values of the diffusion rate had a positive effect on the total population size and the maximum was attained at 6%.

This biological result, among many others, is derived from single-species models in which the biological parameters are fixed and independent of the densities of the interacting species [4, 12, 15, 25]. Nevertheless, any real population is limited by resources that are exploited and renewed; or is subject to competition from a different coexisting species [1, 43]. Therefore, supposing that the non-interaction of species is generally over-simplifying, approaches integrating predation or competition are critically needed. In fact, it is widely recognized that the interplay between dispersal and community structure plays an important role in the abundance and interaction of organisms at a local, as well as at a regional scale [8, 28, 32]. For instance, Gilbert *et al.* [18] have shown that the presence of ecological corridors increases the richness of species in a system of microarthropods inhabiting moss patches in stones. Furthermore, Livingston *et al.* [29] have demonstrated experimentally that the introduction of predators as a separate factor in prey communities could lead to an increment in species sorting. We emphasize that many results from metapopulation theory are not preserved in a metacommunity context. Recent experimental work in spatially diffusing laboratory populations of the heterotrophic budding yeast *Sacchraromyces cerevesiae* limited by an essential nutrient backs this claim. One of the main conclusions of Zhang *et al.* [43] was that the aforementioned hump-shaped response of dispersal is not generally preserved in metacommunities since the total population abundance was found to be higher in a homogeneous environment than in a heterogeneous environment with diffusion (with the same total resource level in both cases).

Despite significant progress in the understanding of the impact of spatial variables, most of this knowledge is still under development. In this paper, we analyze how the dispersal rate of a mobile species affects the population sizes of the species that inhabit a metacommunity. Specifically, our aim is to provide precise thresholds that determine when dispersal is detrimental or beneficial for the overall abundance of a specific species. Moreover, we will compare these quantities for the different interactions, e.g. competition and predation, and we will discuss the biological situations in which the results of single-species metapopulations are preserved. One of the motivations for investigating this issue is that spatial structure is a source of new biological insights with interest on management. Another goal is to complement the recent work of Zhang *et al.* [9, 42, 43].

The structure of the paper is as follows. Section 2 presents a classical model of the Lotka-Volterra type to analyze the dynamics of a metacommunity. Section 3 provides a theoretical investigation on the impact of the dispersal rate of a mobile species on the population abundance of the species. Our analysis covers both predator-prey and competition interactions. Furthermore, we will discuss how the introduction of a new source (a high quality region) in the landscape compensates any negative influence of predation and competition. Finally we will discuss the biological implications of our results in Section 4.

2 Description of the model

We are going to analyze the dynamics of two interacting species that inhabit a landscape of two patches. Species 1 can move between both patches and species 2 always remains in patch 2. A possible biological model is

$$
\begin{cases}
x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) + D(x_2 - x_1) \\
x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2} + \lambda y\right) + D(x_1 - x_2) \\
y' = sy \left(1 - \frac{y}{R} + \mu x_2\right)
\end{cases}
\tag{2.1}
$$

with $x_i(t)$ as the population abundance of species 1 in patch i and $y(t)$ as the population abundance of species 2. In system (2.1), Dx_i is the emigration flow from patch i to the other patch, $D \geq 0$. For simplicity, we suppose that an individual moves from patch 1 to patch 2 with the same probability as from 2 to 1. From this point of the paper, we suppose that the parameters with Latin letters are always positive. Here, r_i is the maximum growth rate of species 1 in patch i whereas k_i denotes the carrying capacity. Parameters s and R are associated with species 2 and have an analogous meaning. Depending on the signs of $\lambda, \mu \in \mathbb{R}$, system (2.1) can cover any possible interaction between the species. For instance, if $\lambda < 0 < \mu$, a consumer-resource (predator-prey) interaction exists in patch 2. Models like (2.1) have been widely used in theoretical ecology, see [4, 19, 26, 27, 36, 42] and the references therein.

The patches occupied by a concrete species are generally classified as sources or sinks [35]. Sources are areas in which reproduction is sufficient to compensate mortality and sinks are patches in which losses exceed births and growth. In the absence of interaction between the species ($\lambda = \mu = 0$), both patches in (2.1) are sources. In other words, the local populations persist in the absence of dispersal. In the next sections, we will see that the competition or predation between the species may alter this scenario. Another common notion in metapopulation theory is a pseudo-sink, *i.e.* a patch that could survive as a source even if isolated but appears as if it were a sink when connected with higher productivity patches due to net population influx, the patch's population above its natural carrying capacity (see [41]).

Most management and conservation plans aim to maximize the overall population size of a target species, see [15] and the references therein. However, the behaviour of the overall population size depending on the dispersal rate is quite subtle. As mentioned in the introduction, for single-species models, the total population size can be higher than the sum of the carrying capacities of the patches [4, 15, 30, 42]. In more mathematical terms, let us consider a metapopulation given by

$$
\begin{cases}
x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) + D(x_2 - x_1) \\
x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2}\right) + D(x_1 - x_2)
\end{cases}
\tag{2.2}
$$

and assume that $(p_1(D), p_2(D)) \in Int\mathbb{R}_+^2 = \{(x_1, x_2) : x_1 > 0, x_2 > 0\}$ is a global attractor for (2.2). Denote by

$$
TP(D) = p_1(D) + p_2(D)
$$

the total population size depending on D. If there is a positive $r - k$ relationship, that is, one of the following cases

- $r_1 > r_2$ and $k_1 > k_2$

- $r_2 > r_1$ and $k_2 > k_1$

holds, then

$$
TP(D) = p_1(D) + p_2(D) > k_1 + k_2
$$

for some range of small dispersal rates. The biological explanation of this fact is as follows (see [43] for more details): the number of emigrants from high-quality patches is greater than the loss to emigration in low-quality patches. Moreover, the migrants with a low quality natal habitat will have a higher reproduction rate than the individuals that do not move. See [31] for real situations in nature in which the positive $r - k$ relationship appears.

In Appendix 1, we show that

$$TP'(0) = \left(\frac{1}{r_2} - \frac{1}{r_1} \right) (k_1 - k_2).$$

Therefore, if $TP'(0) > 0$ (resp. $TP'(0) < 0$), a range of dispersal rates exists so that the total population increases (resp. decreases) as dispersal increases. Note that a big difference between the carrying capacities of the patches leads to a large benefit of the dispersal rate on population abundance. To avoid making misleading conclusions from the literature, we emphasize that Arditi *et al.* [4] and Zhang *et al.* [43] referred to a positive $r - k$ relationship if $k_1 > k_2$ and $r_1k_2 > r_2k_1$ or if $k_2 > k_1$ and $r_2k_1 > r_1k_2$. Note that our relationship is less restrictive than that considered in [4, 43]. One disadvantage of our correlation is that gives information only for small dispersal rates.

For the reader's convenience, we summarize the analysis carried out in [4]. Assume that $k_1 < k_2$. If $r_2/k_2 \geq r_1/k_1$,

$$\lim_{D \longrightarrow \infty} TP(D) > k_1 + k_2.$$

If $r_1 < r_2$, $TP(D)$ is greater than $k_1 + k_2$ for small values of D. Collecting all the information, if $r_1 < r_2$ and $r_2/k_2 > r_1/k_1$, $TP(D)$ is greater than $k_1 + k_2$ for small values of D and $TP(D) < k_1 + k_2$ for large values of D. See Section 2 in [4] for a detailed discussion.

3   Results for the metacommunity model

For each $D \geq 0$, we assume that there exists an equilibrium $(g_1(D), g_2(D), g_3(D))$ (that depends on D) that is a global attractor of (2.1) for every non-trivial initial condition. The case of coexistence of multiple attractors in (2.1), for instance, $aR > 1$ and $bk_2 > 1$ in the next system, will be analyzed in forthcoming papers. To analyze the influence on the overall population size of each species in (2.1), we will study how

$$TP_1(D) = g_1(D) + g_2(D)$$

and

$$TP_2(D) = g_3(D)$$

vary according to the dispersal rate. In fact, the aim of this paper is to study if increasing D benefits/damages $TP_1(D)$ and $TP_2(D)$ for small dispersal rates.

Model (2.1) is studied by using analytical results that are presented in several appendices. In the next figures, we will draw the asymptotic value of the solutions using $t = 100$, (more time does not modify the figures).

3.1   The competitive case

Consider

$$\begin{cases} x_1' = r_1x_1 \left(1 - \frac{x_1}{k_1} \right) + D(x_2 - x_1) \\ x_2' = r_2x_2 \left(1 - \frac{x_2}{k_2} - ay \right) + D(x_1 - x_2) \\ y' = sy \left(1 - \frac{y}{R} - bx_2 \right). \end{cases} \tag{3.1}$$

where all the parameters are strictly positive. The influence of D on the total biomass of each species depends on the dynamical behaviour of the species in patch 2 in the absence of dispersal, *i.e.*

$$\begin{cases} x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2} - ay\right) \\ y' = sy \left(1 - \frac{y}{R} - bx_2\right). \end{cases} \tag{3.2}$$

Next, we discuss the possible behaviours of $TP_1(D)$ and $TP_2(D)$ depending on the competition outcomes of (3.2).

Case 1: Exclusion of species 1 in patch 2, ($aR > 1$ and $bk_2 < 1$).

In this landscape, patch 1 is a source and patch 2 is a sink for species 1, whereas patch 2 is a source for species 2 (the sedentary species). At a local scale, the movement of species 1 increases species diversity in patch 2 via rescue effects, by which migrants re-establish the local population that had been driven to extinction. The mobility of species 1 also leads to an increment in the interspecific competition on species 2. As a result, the density of population of species 2 always decreases by increasing D, (see Fig. 1, and Case 1 of Section 5.2.1). However, the influence of D on the overall population of species 1 is more subtle. We have proved in Appendix 2 (case 1 of Section 5.2.1) that

$$TP_1'(0) = k_1 \left(\frac{-1}{r_1} + \frac{1}{r_2(aR - 1)}\right).$$

Therefore, if

$$r_1 > r_2(aR - 1), \tag{3.3}$$

there is a range of dispersal rates that generate an increase of the total population size of species 1, (see Fig. 1 (A)). Note that inequality (3.3) is satisfied if r_1 is large or if $aR \approx 1$. The benefits of D on the population size of species 1 for large values of r_1 is a consequence of the exploitation of a high quality patch without interspecific competition. On the other hand, the positive influence when $aR \approx 1$ fits directly with the analysis on the impact of a concrete route discussed in [36]. Specifically, if a sink is close to becoming a source, the connection is highly recommended.

Negative values of $TP_1'(0)$ appear provided

$$r_2(aR - 1) > r_1.$$

This inequality is verified, for instance, if the competition rate a or the maximum growth rate of species 2 are large (see Fig. 1(B)). In other words, patch 2 is a sink in which the survival of species 1 is extremely challenging due to the interspecific competition.

An apparently paradoxical effect is the possibility of a detrimental impact of the movement of species 1 on the overall population size of both species (See Fig. 1 (B)). To understand this effect, we remark that increasing D promotes the presence of species 1 in patch 2, increasing inter-specific competition on species 2. In turn the negative effect on species 1 emerges when the recolonization in patch 2 does not compensate for the loss of migration in patch 1. In more mathematical terms, if

$$p_1(D) + p_2(D) < k_1$$

in spite of the fact that

$$0 < p_2(D).$$

Note that $p_1(0) = k_1$ and $p_2(0) = 0$.
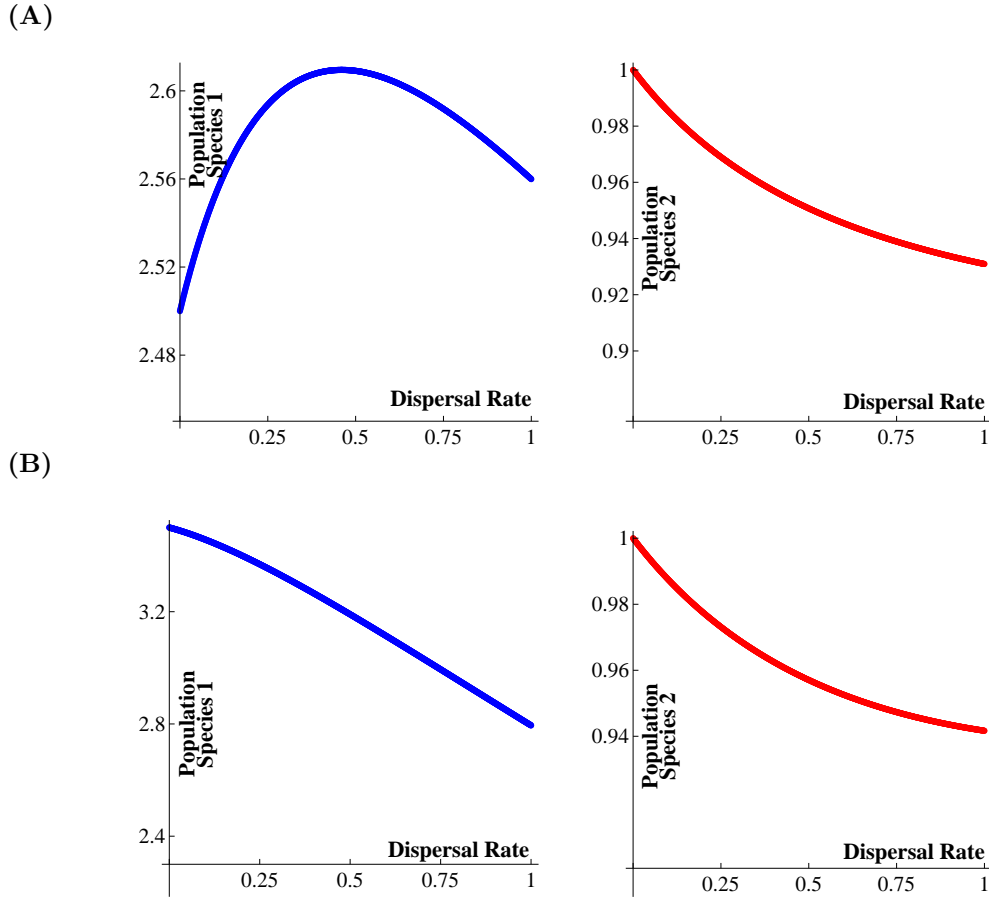
(A)

(B)

Figure 1: Representation of $TP_1(D)$ and $TP_2(D)$ in system (3.1) when $aR > 1$ and $bk_2 < 1$ (Case 1). (A) The parameters employed are: $r_1 = 2.5$, $r_2 = 3$, $k_1 = 2.5$, $k_2 = 4$, $s = 1$, $a = 1.5$, $b = 0.1$, $R = 1$. Notice that $r_1 > r_2(aR - 1)$. We can observe the positive influence on $TP_1(D)$ for $D \in (0, 0.5)$. In fact, function $TP_1(D)$ is unimodal. On the other hand, $TP_2(D)$ is a decreasing function. We emphasize that $TP_1'(0)$ and $TP_2'(0)$ give information only for small values of D. (B) The parameters employed are: $r_1 = 2$, $r_2 = 5$, $k_1 = 3.5$, $k_2 = 4$, $s = 1$, $a = 1.5$, $b = 0.1$, $R = 1$. Note that $r_1 < r_2(aR - 1)$. In this case, both functions are strictly decreasing. For species 1, patch 2 is a sink in which the growth rate of the superior competitor is moderately high.

Case 2: Exclusion of species 2 in patch 2, ($aR < 1$ and $bk_2 > 1$).
The dynamical behaviour of species 1 is essentially the same as in the absence of species 2 i.e., system (2.2), (see Appendix 2, section 5.2.1, Case 2). In fact,

$$TP_1'(0) = \left(\frac{1}{r_2} - \frac{1}{r_1} \right) (k_1 - k_2).$$

A notable result is that the random dispersal of species 1 cannot produce the coexistence of both species despite species 2 being sedentary, (see Proposition 5.1 and Remark 5.1). This fact seems to contrast with the coexistence mechanism coined as emigration mediated coexistence by Amarasekare [1]. A natural guess would be that the mobility of the superior competitor from a much higher quality patch could weaken interspecific competition and so, would allow the persistence of

the inferior competitor. Although patch 2 could be of a much higher quality, we do not see the emigration mediated coexistence in (3.1) because patch 1 is always a source. Actually, the impact of maladaptive emigration is not so strong as to enable the survival of the inferior competitor.

Case 3: Coexistence of both species in patch 2, ($aR < 1$ and $bk_2 < 1$).
Under a positive $r - k$ relationship of type

$$r_1 > r_2 \quad \text{and} \quad k_1 > k_2,$$

the movement of species 1 always has a positive influence on its own overall population size and a detrimental effect on the other species (see Proposition 5.2). Roughly speaking, the expected response of the classical metapopulation theory when dispersal is rare is preserved for species 1. The benefits on species 1 are simply a result of the exploitation of a high quality patch without interspecific competition. In turn, species 2 is subject to a higher competition pressure, leading to a decrease in population abundance, (see Fig. 2(A)).

The influence of D under a positive $r - k$ relationship of type

$$r_1 < r_2 \quad \text{and} \quad k_1 < k_2,$$

is more complex. In Appendix 2 (case 3 Section 5.2.1), we have deduced that

$$TP_1'(0) = \left(\frac{1}{r_2} - \frac{1 - aR}{r_1} \right) \left(\frac{k_1}{1 - aR} - \frac{k_2}{1 - abRk_2} \right)$$

and

$$TP_2'(0) = \frac{bR}{r_2} \left(\frac{k_2}{1 - abRk_2} - \frac{k_1}{1 - aR} \right).$$

Thus, the possible responses of D depend on the thresholds

$$\alpha = k_2(1 - aR) - k_1(1 - abRk_2)$$

and

$$\beta = r_1 - r_2(1 - aR).$$

If $\alpha > 0$ (resp. < 0), there is a positive (resp. negative) effect of the dispersal rate of species 1 on the population abundance of species 2. On the other hand, the influence of D on species 1 relies on the sign of $\alpha \cdot \beta$. A notable finding is that, in general, the presence of a competitor in patch 2 does not preserve the positive influence of D on species 1 predicted by the metapopulation theory, (see Fig.2). Another marked result is that we can see, at the same time, a negative (resp. positive) effect of the diffusion of species 1 on the population abundance of both species. See Fig. 2 (A)-(B).

3.2 The Consumer-Resource case

Here we assume an interaction of consumer-resource type between species 1 and 2. Most phenomena of this subsection have already emerged in the competitive case. Therefore, we will omit some similar discussions.

3.2.1 Species 1 is a consumer

Consider

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1} \right) + D(x_2 - x_1) \\ x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2} + ay \right) + D(x_1 - x_2) \\ y' = sy \left(1 - \frac{y}{R} - bx_2 \right). \end{cases} \tag{3.4}$$
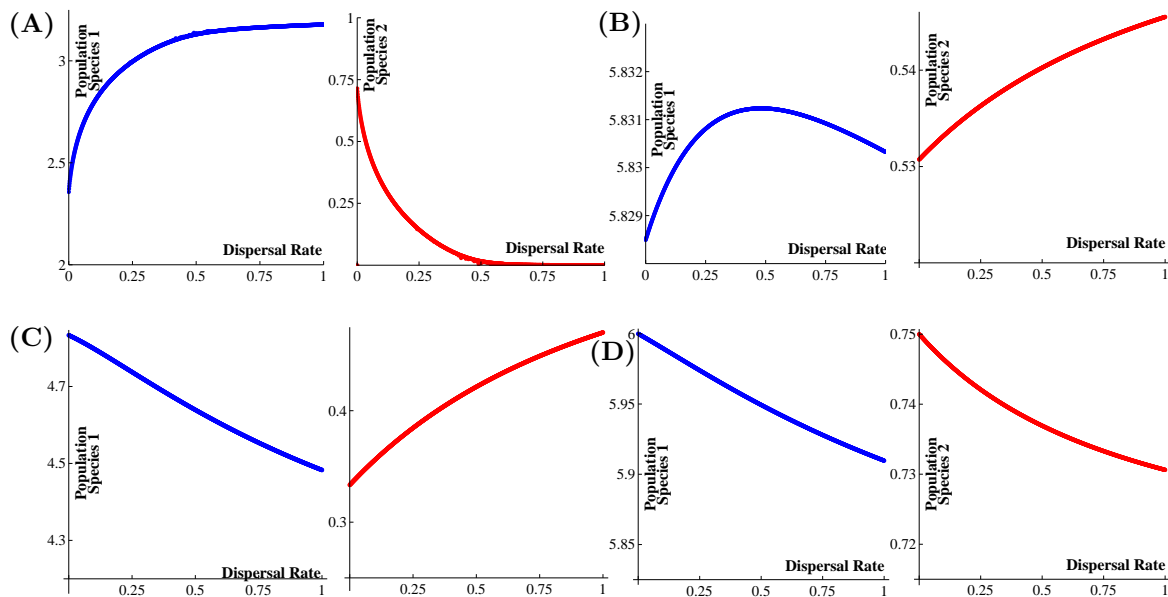
Figure 2: Representation of $TP_1(D)$ and $TP_2(D)$ in system (3.1) when $aR < 1$ and $bk_2 < 1$ (Case 3). (A) We have the positive correlation $r_1 > r_2$ and $k_1 > k_2$. The parameters employed are: $r_1 = 3$, $r_2 = 1$, $k_1 = 2$, $k_2 = 1$, $s = 1$, $a = 0.9$, $b = 0.8$, $R = 1$. We observe that $TP_1(D)$ increases whereas $TP_2(D)$ decreases. In fact, the negative effect of dispersal drives to the extinction to species 2. In (B)-(C)-(D), we analyze the positive correlation $r_1 < r_2$ and $k_1 < k_2$. (B) $\alpha > 0$ and $\beta > 0$. The parameters employed are: $r_1 = 2.2$, $r_2 = 3$, $k_1 = 2.7$, $k_2 = 3.5$, $s = 1$, $a = 0.2$, $b = 0.15$, $R = 1$. The interspecific competition rates are moderately small. The benefit of dispersal on species 2 is a consequence of the fact that there is a reduction of population of species 1 in patch 2. For species 1, we see the expected unimodal response of the classical metapopulation theory. (C) $\alpha > 0$ and $\beta < 0$. The parameters employed are: $r_1 = 2$, $r_2 = 3$, $k_1 = 1.5$, $k_2 = 4$, $s = 1$, $a = 0.5$, $b = 0.25$, $R = 1$. Roughly speaking, this response appears when there is coexistence of both species but the population abundance of species 2 in patch 2 is larger than that of species 1. (D) $\alpha < 0$ and $\beta > 0$. The parameters employed are: $r_1 = 2$, $r_2 = 5$, $k_1 = 3.5$, $k_2 = 4$, $s = 1$, $a = 0.5$, $b = 0.1$, $R = 1$. This response appears when there is coexistence of both species and there is not a clear winner in the competition. Notice that the parameters are close to satisfy $aR > 1$ and $bk_2 > 1$, (the situation that guarantees the saddle point dynamics in (3.1)).

As above, the influence of D relies on the dynamics of the subsystem

$$\begin{cases} x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2} + ay\right) \\ y' = sy \left(1 - \frac{y}{R} - bx_2\right). \end{cases} \tag{3.5}$$

Case 1: Coexistence of both species in patch 2, $(bk_2 < 1)$.
As in the competitive case, if there exists a positive $r - k$ relationship of type $r_1 < r_2$ and $k_2 < k_1$, the diffusion of the consumer will always have a positive effect on its own density of population and a negative effect on the population of the resource (see Appendix 2, Proposition 5.3). In fact, the positive influence that comes from single-metapopulation models is magnified by the presence of a new resource. Nevertheless, under the other positive $r - k$ relationship, we can have any response to D. Specifically, we have deduced in Appendix 2, (Case 1, Section 5.2.2), that

$$TP_1'(0) = \left(\frac{1}{r_2} - \frac{1 + aR}{r_1}\right)\left(\frac{k_1}{1 + aR} - \frac{k_2}{1 + abRk_2}\right)$$

and

$$TP_2'(0) = \frac{bR}{r_2}\left(\frac{k_2}{1 + abRk_2} - \frac{k_1}{1 + aR}\right).$$

From these expressions, we can observe that the signs of

$$\alpha = k_2(1 + aR) - k_1(1 + abRk_2),$$

$$\beta = r_1 - r_2(1 + aR)$$

determine the response of the dispersal rate of the consumer. Specifically, if $\alpha \cdot \beta < 0 \ (> 0)$, D has a positive (resp. negative) impact on the population abundance of the consumer. On the other hand, if $\alpha > 0$ (resp. < 0) D has a beneficial (resp. detrimental) influence for the population size of the resource.

Case 2: Exclusion of species 2 in patch 2 ($bk_2 > 1$).
This case (see Appendix 2, Section 5.2.2, Case 2) is similar to that of the competitive case. On the one hand, D has a positive influence on the overall population size of species 1 under a positive $r - k$ correlation. On the other hand, a noteworthy result is the impossibility for the resource to be rescued by the movement of the consumer. As suggested in [1, 33], random dispersal reduces the strength of predation in patch 2 provided the consumer is mobile, the resource is immobile, and patch 2 is of higher productivity than patch 1. However, this cannot cause the persistence of the prey in our model. The rescue mentioned in [1, 33] would appear when the predator can not survive in patch 2 in the absence of prey.

3.2.2 Species 1 is a mobile resource

System (2.1) now takes the form

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) + D(x_2 - x_1) \\ x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2} - ay\right) + D(x_1 - x_2) \\ y' = sy \left(1 - \frac{y}{R} + bx_2\right). \end{cases} \tag{3.6}$$

The influence of D on each species depends on the local dynamics in patch 2, namely

$$\begin{cases} x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2} - ay\right) \\ y' = sy \left(1 - \frac{y}{R} + bx_2\right). \end{cases} \tag{3.7}$$

Case 1: Coexistence of both species in patch 2 ($aR < 1$).
Contrary to the competitive case, under a positive $r - k$ correlation of type $r_1 > r_2$ and $k_1 > k_2$, there is a positive influence of D on the total population size of both species, (see Proposition 5.4 in Appendix 2). In contrast, under the other positive correlation, the influence of the dispersal rate of the resource depends on the thresholds

$$\alpha = k_2(1 - aR) - k_1(1 + abRk_2),$$

$$\beta = r_1 - r_2(1 - aR).$$

These expressions are derived from

$$TP_1'(0) = \left(\frac{1}{r_2} - \frac{1 - aR}{r_1} \right) \left(\frac{k_1}{1 - aR} - \frac{k_2}{1 + abRk_2} \right)$$

and

$$TP_2'(0) = \frac{bR}{r_2} \left(\frac{k_1}{1 - aR} - \frac{k_2}{1 + abRk_2} \right),$$

(see Appendix 2, case 1, section 5.2.3).

There is a negative (resp. positive) impact of the movement of the resource on its own population abundance if $\alpha \cdot \beta < 0$ (> 0). On the other hand, it is beneficial (resp. detrimental) for the population size of the consumer, if $\alpha > 0$ (resp. $\alpha < 0$), (see Appendix 2, section 5.2.3 Case 1).

Case 2: Extinction of species 2 in patch 2 ($aR > 1$).
In this case, patch 1 is a refuge for the resource. As expected, the movement of the resource promotes the coexistence of both species in patch 2, also producing an increment of population abundance of the consumer, (see Appendix 2, section 5.2.3 Case 2). Furthermore, it is deduced in this appendix that

$$TP_1'(0) = -k_1 \left(\frac{1}{r_1} - \frac{1}{r_2(aR - 1)} \right).$$

Therefore, the influence of D on the overall population size of the resource depends on the threshold

$$\alpha = r_1 - r_2(aR - 1).$$

Specifically, there is a beneficial (resp. detrimental) effect provided $\alpha > 0$ (resp. $<$), (see Appendix 2, section 5.2.3 Case 2).

3.3 Adding a new region in model (2.1)

We know that under a positive $r - k$ correlation, dispersal has a positive influence on the overall population size in single-species metapopulation models. However, how this biological result is preserved when two patches are placed into a complex metacommunity is not well understood. Here, we study this issue in the landscape illustrated in Fig. 3.
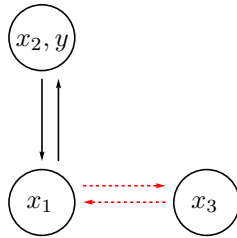

Figure 3: Pictorial illustration of a landscape studied in Section 3.3.

The motivation from researching this issue also comes from population management. To reduce the possible damages mentioned in Sections 3.1 and 3.2, a natural management strategy could be the linkage, if possible, of an isolated region.

In our metacommunity, species 1 can occupy the three patches. The maximum growth rate and carrying capacity for species 1 in patch i are r_i and k_i resp. for $i = 1, 2, 3$. Within patch 2, species 1 is subject to the interaction of a sedentary species (as in (2.1)). A simple model for the situation described takes the form

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) + D(x_2 + x_3 - 2x_1) \\ x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2} + \lambda y\right) + D(x_1 - x_2) \\ x_3' = r_3 x_3 \left(1 - \frac{x_3}{k_3}\right) + D(x_1 - x_3) \\ y' = sy \left(1 - \frac{y}{R} + \mu x_2\right) \end{cases} \tag{3.8}$$

Implicit in (3.8), we assume that an individual has no predilection for choosing a route (if it exists). Moreover, the introduction of a new route increases the probability of dispersal. Another natural scenario would be that the probability to stay in patch 1 is independent of the number of routes leaving patch 1. In such a case, the model would be

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) + D(x_2 + x_3 - x_1) \\ x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2} + \lambda y\right) + D(0.5x_1 - x_2) \\ x_3' = r_3 x_3 \left(1 - \frac{x_3}{k_3}\right) + D(0.5x_1 - x_3) \\ y' = sy \left(1 - \frac{y}{R} + \mu x_2\right) \end{cases} \tag{3.9}$$

As expected, the influence of D in both systems is quite similar. The reader can consult [42, 43] for a similar model with 12 patches.

In Appendix 3, we prove that

$$\widetilde{TP}_1'(0) = TP_1'(0) + (k_3 - k_1)\left(\frac{1}{r_1} - \frac{1}{r_3}\right) \tag{3.10}$$

where $TP_1(D)$ is the total population size of species 1 in model (2.1). Since the second term of (3.10) is always positive under a positive $r - k$ relationship, any possible dispersal damage could be regulated. Roughly speaking, (3.10) suggests that in the network presented in Fig.3, the dispersal response in each route has to be analyzed in an independent manner. Then, both quantities are averaged as indicated by (3.10), (see Fig. 4).
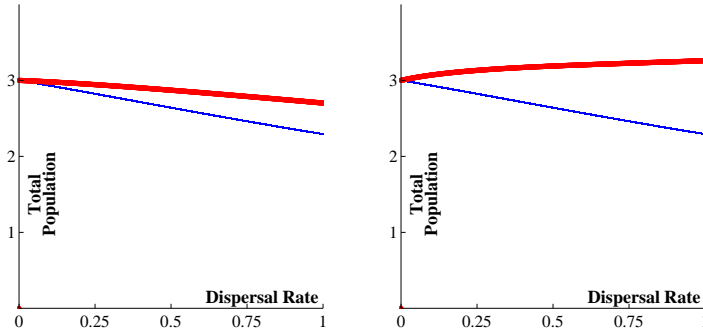
Figure 4: Behaviour of the total population size in systems (3.8) (left) and (3.9) (right). The red (thick) line represents the asymptotic value of the total population size of species 1 in the landscape with the topology illustrated in Fig. 3 (with the red linkage). The blue line represents the asymptotic value of the total population in the metapopulation with the topology illustrated in Fig. 3 (without the connection). The parameters are $r_1 = 1$, $r_2 = 3$, $r_3 = 2$, $k_1 = 1$, $k_2 = 2$, $k_3 = 2$, $s = 1$, $a = 2$, $\lambda = -2$, $\mu = 0.4$, $R = 1$. In this case, the addition of a new region compensates the negative effects of dispersal by the predation in patch 2.

It is well known that the arrangement of source and sink patches in a network has important dynamical properties in the fate of the whole population, see [34]. We have discussed the topology illustrated in Fig. 3 for simplicity. However, the arguments exposed in Appendix 3 could be adapted to the network illustrated in figure 5, namely
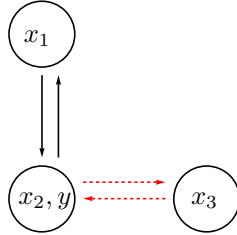

Figure 5: Pictorial illustration of a landscape studied in Section 3.3.

$$\widetilde{TP}_1'(0) = TP_1'(0) + \widehat{TP_1}'(0) \tag{3.11}$$

where $\widehat{TP_1}(D)$ is the total population size of species 1 in model (2.1) considering patches 2 and 3.

4 Discussion

Dispersal between subpopulations is widespread in nature and has been recognized as a remarkable factor in the dynamics and distribution of individuals [1, 10, 19]. The primary effect of diffusion is associated with rescue events that promote the coexistence of species at local scale. With competition among species, obvious benefits of dispersal are the use of refugia and the exploitation of new resources for a limited group of competitors [1]. However, dispersal can also play a negative role. For instance, random movements can drive the individuals to lower quality patches, reducing their individual fitness [4,15], (see [6] for experimental results in this direction). Understanding the

multiple implications of the movement of species in a metacommunity is, nowadays, a fundamental issue in population and community ecology [1, 11, 12, 23]. Nevertheless, despite considerable theoretical and empirical advances, many important questions remain unsolved. The present paper can be seen as a step toward a systematic comprehension of how the dispersal rate affects the population abundance of the species in simple metacommunities. Our analysis was based on a two patch model of Lotka-Volterra type that comprises a mobile species and a sedentary species. The use of Lotka-Volterra models has been debated in a spatial context, see [5, 31, 40]. However, the simplicity of the formulation allows to suggest simple management guides and to draw new biological insights that complement recent promising experimental work [9, 42, 43].

A noteworthy phenomenon in metapopulations is that population abundance in a fragmented landscape can exceed the sum of local carrying capacities [4, 15, 30, 42]. For a landscape made of two sources, this result requires a suitable positive correlation, namely, the carrying capacity and the maximum growth rate of a source must be larger than those in the other source [4, 42]. One of the main goals of this paper was to investigate when this property is preserved in a metacommunity. In the competitive case, if there are two different sources with growth rates and carrying capacities which are positively correlated, the introduction of an immobile competitor into the lower quality source maintains the positive effect of dispersal on the mobile species. However, if we introduce the competitor into the source of a higher quality, the response may be beneficial or detrimental, depending on the precise thresholds given in Section 3.1. Analogously, in a consumer-resource system, the introduction of a sedentary resource into the source of a high quality preserves the beneficial dispersal response predicted by the classic metapopulation theory. Nevertheless, a more subtle response emerges when the limited resource is added to the lower quality region. Very recently, Zhang *et al.* [43] suggested that the positive dispersal influence is not preserved in metacommunities of consumer-resource type. Note that our results are in agreement with [43] because we have shown situations in which it is and is not preserved.

In a recent review, Amarasekare [1], (see also [33]) described some coexistence mechanisms for food-webs of two or three species. A mechanism coined as emigration-mediated coexistence consists of the persistence of an inferior competitor as a result of the mobility of a superior competitor to a lower quality patch. Specifically, the mobility of the superior competitor reduces the interspecific competition rate and allows the survival of the inferior competitor when it is immobile. In our paper, we have not detected this mechanism because both patches are sources and the possible maladaptive movement is not so severe. The occurrence of emigration-mediated coexistence in (2.1) would require patch 1 to be a sink.

A marked finding of this study is that increasing the dispersal rate of a competitor can produce, at the same time, an increment (resp. decrease) of the total population size of both competitors. Although this result seems somewhat paradoxical, a detailed analysis of the local populations clarifies it: In a landscape of two different patches, the mobility of a competitor could imply the exploitation of new resources and reduction of the interspecific competition on a sedentary competitor. Certainly, these two phenomena together lead to an increment of the population of both competitors. The discussion of a negative influence on both competitors would be analogous, simply introducing a maladaptive movement in the mobile competitor. As suggested in Section 3.2, these phenomena also appear in consumer-resource systems. In this case, the introduction of a limited resource could provoke a negative effect of dispersal on the population abundance of the consumer. We emphasize that the complete classification of the possible effects of diffusion in (2.1) is provided. These results have implications on conservation management. Regarding the rescue effect, increasing dispersal rates is generally associated with an increment of the degree of synchrony [12]. Classical metapopulation models suggest that this negative effect could be compensated by an increment of the overall population size, especially in the connection of two different sources [15]. In metacommunities, this property deserves some caution since the movement

between sources can have a negative impact on the species depending on the type of species inhabiting the patches.

Ecological corridors are a popular management strategy designed to reduce the effects of habitat fragmentation [7, 39]). However, the provision of a corridor could be a double-edged sword [12, 15, 21, 22, 38]: Extinction risks can be reduced though the colonisation of new regions, regulating the loss of other local populations. On the other hand, corridors can endanger the viability of the population by synchrony events of by increments of predation forces. Regarding this strategy, our results emphasize that its success in terms of the increase of the total population size depends on the intrinsic features of the patches and the type of interaction between the involved species. As in the context of metapopulations [36], an efficient design of corridors is often one that involves source-sink systems with the sink close to becoming a source (or viceversa). In our context, a sink appears when the species can not survive the inter-specific competition of the other species.

One of the main concerns of conservationists is the isolation of subpopulations [3, 13]. The addition of an isolated region in a landscape is commonly suggested as a mechanism that suppresses local extinctions [15]. However, its performance in real problems is a matter of debate. An obvious benefit is the possibility of compensating for the predation or competition damages mentioned in Section 3. Our results support this compensation mechanism and suggest that managers should analyze the influence of each route in an independent manner, according to the results of Section 3; and then averaging both thresholds according to (3.10). Certainly, the expected regulation behaviour mentioned above will appear under a positive $r - k$ correlation between the introduced region and the region without interspecific competition, (patches 1 and 3 in (3.8)).

In summary, our results have shown a source of rich new phenomena in metacommunities, which are beyond the possible biological insights of models that neglect spatial variables. We conclude that dispersal has, in general, neither a detrimental nor beneficial impact on the population abundance of the species in a metacommunity. In fact, the influence of dispersal depends on the identity of the species and the quality of the patches. The next step will be to analyze the situation where both species co-exist in any patches. Despite its apparent simplicity, a new mathematical analysis is required. Presumably, new surprising phenomena could emerge in this biological scenario.

5 Appendices

5.1 Appendix 1

Consider

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) + D(x_2 - x_1) \\ x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2}\right) + D(x_1 - x_2). \end{cases} \quad (5.1)$$

To evaluate the influence on the population abundance of the dispersal rate, we have to analyze such a dependence on the steady state. Let us denote $TP(D)$ as the total population size of (5.1) depending on D. Mathematically, $TP(D) = p_1(D) + p_2(D)$ with

$$\begin{cases} 0 = r_1 p_1(D) \left(1 - \frac{p_1(D)}{k_1}\right) + D(p_2(D) - p_1(D)) \\ 0 = r_2 p_2(D) \left(1 - \frac{p_2(D)}{k_2}\right) + D(p_1(D) - p_2(D)). \end{cases} \quad (5.2)$$

and $(p_1(D), p_2(D))$ a global attractor of (5.1) for any initial condition in $\{(x_1, x_2) : x_1 > 0, x_2 > 0\}$. Notice that $TP(0) = k_1 + k_2$.

Theorem 5.1. *The function $TP(D)$ is derivable in a neighborhood of zero and*

$$TP'(0) = \left(\frac{1}{r_2} - \frac{1}{r_1} \right)(k_1 - k_2)$$

Proof. Consider $G = (G_1, G_2) : \mathbb{R}^3 \longrightarrow \mathbb{R}^2$ defined as

$$G(x_1, x_2, D) = \left(r_1 x_1 \left(1 - \frac{x_1}{k_1} \right) + D(x_2 - x_1), r_2 x_2 \left(1 - \frac{x_2}{k_2} \right) + D(x_1 - x_2) \right).$$

Observe that $G(k_1, k_2, 0) = (0, 0)$. Since the matrix

$$A = \left(\begin{array}{cc} \frac{\partial G_1}{\partial x_1}(k_1, k_2, 0) & \frac{\partial G_1}{\partial x_2}(k_1, k_2, 0) \\ \frac{\partial G_2}{\partial x_1}(k_1, k_2, 0) & \frac{\partial G_2}{\partial x_2}(k_1, k_2, 0) \end{array} \right) = \left(\begin{array}{cc} -r_1 & 0 \\ 0 & -r_2 \end{array} \right)$$

has

$$det A \neq 0,$$

the Implicit Function Theorem (see [6]) guarantees the existence of a smooth map $(\phi_1(D), \phi_2(D))$ defined in I, a neighbourhood of zero, satisfying that

$$(\phi_1(0), \phi_2(0)) = (k_1, k_2),$$

$$G(\phi_1(D), \phi_2(D), D) = (0, 0) \tag{5.3}$$

for all $D \in I$. Differentiating implicitly (5.3) and evaluating at $D = 0$, we obtain that

$$\left(\begin{array}{c} \phi_1'(0) \\ \phi_2'(0) \end{array} \right) = -A^{-1} \left(\begin{array}{c} k_2 - k_1 \\ k_1 - k_2 \end{array} \right) = \left(\begin{array}{c} \frac{1}{r_1}(k_2 - k_1) \\ \frac{1}{r_2}(k_1 - k_2) \end{array} \right).$$

Consequently,

$$TP'(0) = \phi_1'(0) + \phi_2'(0) = \left(\frac{1}{r_2} - \frac{1}{r_1} \right)(k_1 - k_2).$$

$\square$

5.2 Appendix 2

First, we recall the version of the Implicit Function Theorem (see [6]) that we employ in the results of Section 3.

Theorem 5.2. *Consider $F(x_1, x_2, y, D) = (F_1, F_2, F_3) : \mathbb{R}^4 \longrightarrow \mathbb{R}^3$ a map of class $\mathcal{C}^1$. Let $(x_1^*, x_2^*, y^*, 0)$ be a point that satisfies $F(x_1^*, x_2^*, y^*, 0) = (0, 0, 0)$. If $\det(A) \neq 0$ with*

$$A = \left(\begin{array}{ccc} \frac{\partial F_1}{\partial x_1}(x_1^*, x_2^*, y^*, 0) & \frac{\partial F_1}{\partial x_2}(x_1^*, x_2^*, y^*, 0) & \frac{\partial F_1}{\partial y}(x_1^*, x_2^*, y^*, 0) \\ \frac{\partial F_2}{\partial x_1}(x_1^*, x_2^*, y^*, 0) & \frac{\partial F_2}{\partial x_2}(x_1^*, x_2^*, y^*, 0) & \frac{\partial F_2}{\partial y}(x_1^*, x_2^*, y^*, 0) \\ \frac{\partial F_3}{\partial x_1}(x_1^*, x_2^*, y^*, 0) & \frac{\partial F_3}{\partial x_2}(x_1^*, x_2^*, y^*, 0) & \frac{\partial F_3}{\partial y}(x_1^*, x_2^*, y^*, 0) \end{array} \right).$$

then there is a smooth map $g(D) = (g_1(D), g_2(D), g_3(D))$ defined in an interval of the form $(-\widetilde{D}, \widetilde{D})$ with $\widetilde{D} > 0$ such that

$$F(g(D), D) = (0, 0, 0)$$

for all $D \in (-\widetilde{D}, \widetilde{D})$ with $g(0) = (x_1^*, x_2^*, y^*)$. Moreover,

$$(g_1'(0), g_2'(0), g_3'(0))^t = -A^{-1} \cdot \frac{\partial F}{\partial D}(x_1^*, x_2^*, y^*, 0)^t. \tag{5.4}$$

Note that for a system of differential equations of the form

$$\begin{cases} x_1' = F_1(x_1, x_2, y, D) \\ x_2' = F_2(x_1, x_2, y, D) \\ y' = F_3(x_1, x_2, y), \end{cases} \tag{5.5}$$

the equilibria are the points that satisfy

$$F(x_1, x_2, y, D) = (0, 0, 0).$$

Assume that (x_1^*, x_2^*, y^*) is an equilibrium of (5.5) for $D = 0$ that is a global attractor for all initial conditions in $Int\mathbb{R}_+^3 := \{(x_1, x_2, y) : x_1 > 0, x_2 > 0, y > 0\}$. To analyze the effect of diffusion on the total population size, we are going to study how $(g_1(D), g_2(D), g_3(D))$ varies with respect to D. We remark that the total population sizes of species 1 and 2 are given by

$$TP_1(D) = g_1(D) + g_2(D),$$

$$TP_2(D) = g_3(D).$$

Therefore, for small dispersal rates, the quantities

$$TP_1'(0) = g_1'(0) + g_2'(0), \tag{5.6}$$

$$TP_2'(0) = g_3'(0), \tag{5.7}$$

determine if increasing D is beneficial or detrimental for the total population size of the species. In more mathematical terms, there is a range of dispersal rates that generates an increase of the total population size of species 1, if $TP_1'(0) > 0$ and the total population size of species 1 decreases, if $TP_1'(0) < 0$. On the other hand, $TP_2'(0)$ indicates whether the dispersal rate of species 1 is beneficial or harmful for the total biomass of species 2. In the rest of this appendix, we will compute (5.6) and (5.7) in the systems of Sections 3.1 and 3.2. In these systems,

$$\frac{\partial F}{\partial D}(x_1^*, x_2^*, y^*, 0) = (x_2^* - x_1^*, x_1^* - x_2^*, 0).$$

5.2.1 The competitive case

Consider

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) + D(x_2 - x_1) \\ x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2} - ay\right) + D(x_1 - x_2) \\ y' = sy \left(1 - \frac{y}{R} - bx_2\right). \end{cases} \tag{5.8}$$

Next we discuss the possible dynamical behaviours of (5.8) for $D = 0$.

Case 1: $1 < aR$ and $bk_2 < 1$.
The equilibrium $(k_1, 0, R)$ is a global attractor in system (5.8) for $D = 0$. After some tedious but simple computations,

$$A^{-1} = \begin{pmatrix} \frac{-1}{r_1} & 0 & 0 \\ 0 & \frac{1}{r_2(1-aR)} & * \\ 0 & \frac{bR}{r_2(aR-1)} & * \end{pmatrix}.$$

In this case,

$$TP_1'(0) = k_1 \left(\frac{-1}{r_1} + \frac{1}{r_2(aR - 1)}\right)$$

and

$$TP_2'(0) = k_1 \frac{bR}{r_2(1 - aR)}.$$

Notice that $TP_2'(0)$ is always negative.

Case 2: $aR < 1$ and $bk_2 > 1$.
The equilibrium $(k_1, k_2, 0)$ is a global attractor in system (5.8) for $D = 0$. We have that

$$A^{-1} = \begin{pmatrix} \frac{-1}{r_1} & 0 & 0 \\ 0 & \frac{-1}{r_2} & * \\ 0 & 0 & * \end{pmatrix}.$$

In this case

$$TP_1'(0) = (k_2 - k_1) \left(\frac{1}{r_1} - \frac{1}{r_2} \right)$$

and $TP_2'(0) = 0$. Note that $TP_1'(0)$ is the same in (5.8) and (5.1).

Proposition 5.1. *If* $TP_2(0) = TP_2'(0) = 0$ *with* $1 - bg_2(0) \neq 0$, *then the derivative of any order at zero is zero, that is*

$$TP_2^{n)}(0) = 0$$

for all $n \in \mathbb{N}$.

Proof. By definition, $TP_2(D) = g_3(D)$ (the coordinate of the equilibrium associated with species 2) satisfies that

$$0 = sTP_2(D) \left(1 - \frac{TP_2(D)}{R} - bg_2(D) \right).$$

Differentiating implicitly this expression, we have that

$$0 = sTP_2'(D) \left(1 - \frac{TP_2(D)}{R} - bg_2(D) \right) + sTP_2(D) \left(-\frac{TP_2'(D)}{R} - bg_2'(D) \right).$$

Now, if we differentiate this expression and evaluate at $D = 0$, we obtain

$$0 = sTP_2''(0) \left(1 - \frac{TP_2(0)}{R} - bg_2(0) \right) + sTP_2'(0)(\star) + sTP_2(0)(\star).$$

($\star$ denotes a suitable mathematical expressions that does not affect in the discussion). Since $1 - bg_2(0) \neq 0$, we deduce that $TP_2''(0) = 0$. We conclude the proof by arguing in an inductive way. $\qquad \square$

Remark 5.1. *Since* $TP_2(D)$ *is a real analytic function, the previous proposition implies that* $TP_2(D) = 0$ *for all* $D \in [0, 1]$.

Case 3: $aR < 1$ and $bk_2 < 1$.
The equilibrium

$$\left(k_1, \frac{-k_2 + aRk_2}{-1 + abRk_2}, \frac{R(-1 + bk_2)}{-1 + abRk_2} \right)$$

is a global attractor in (5.8) for $D = 0$. We have that

$$A^{-1} = \begin{pmatrix} \frac{-1}{r_1} & 0 & 0 \\ 0 & \frac{1}{r_2(aR-1)} & * \\ 0 & \frac{bR}{r_2(1-aR)} & * \end{pmatrix}.$$

In this case, we obtain

$$TP_1'(0) = \left(\frac{1}{r_2} - \frac{1-aR}{r_1} \right) \left(\frac{k_1}{1-aR} - \frac{k_2}{1-abRk_2} \right)$$

and

$$TP_2'(0) = \frac{bR}{r_2} \left(\frac{k_2}{1-abRk_2} - \frac{k_1}{1-aR} \right).$$

Proposition 5.2. *Assume that* $0 < aR < 1$ *and* $0 < bk_2 < 1$. *If* $r_2 < r_1$ *and* $k_2 < k_1$ *then* $TP_1'(0) > 0$ *and* $TP_2'(0) < 0$.

Proof. Using that $aR < 1$, then $0 < 1 - aR < 1$. On the other hand, $r_2 < r_1$ implies that

$$\frac{1}{r_1} < \frac{1}{r_2}.$$

Collecting these two facts, we deduce that

$$\frac{1-aR}{r_1} < \frac{1}{r_2}$$

or equivalently

$$\frac{1}{r_2} - \frac{1-aR}{r_1} > 0. \tag{5.9}$$

Next, since $0 < bk_2 < 1$, we have that

$$abRk_2 < aR.$$

This leads to $0 < 1 - aR < 1 - abRk_2 < 1$. Now, using that $k_2 < k_1$, we can deduce that

$$\frac{k_2}{1-abRk_2} < \frac{k_1}{1-aR}. \tag{5.10}$$

Finally, (5.9) and (5.10) imply that

$$TP_1'(0) > 0 \quad \text{and} \quad TP_2'(0) < 0.$$

$\square$

Case 4: $1 < aR$ and $bk_2 > 1$.
In this case, system (5.8) exhibits bi-stability for $D = 0$. Specifically, there is a coexistence of two stable attractors, namely $(k_1, 0, R)$ and $(k_1, k_2, 0)$.

5.2.2 Species 1 is a predator and Species 2 is a prey

Consider

$$
\begin{cases}
x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) + D(x_2 - x_1) \\
x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2} + ay\right) + D(x_1 - x_2) \\
y' = sy \left(1 - \frac{y}{R} - b x_2\right).
\end{cases}
\tag{5.11}
$$

Next we discuss the possible dynamical behaviours of (5.11) for $D = 0$.

Case 1: $bk_2 < 1$.
The equilibrium

$$
\left(k_1, \frac{k_2(1 + aR)}{1 + abRk_2}, \frac{-R(-1 + bk_2)}{1 + abRk_2}\right)
$$

is a global attractor in system (5.11) for $D = 0$. We find

$$
A^{-1} = \begin{pmatrix}
\frac{-1}{r_1} & 0 & 0 \\
0 & \frac{-1}{r_2(1+aR)} & * \\
0 & \frac{bR}{r_2(1+aR)} & *
\end{pmatrix}.
$$

In this case,

$$
TP_1'(0) = \left(\frac{1}{r_2} - \frac{(1 + aR)}{r_1}\right)\left(-\frac{k_2}{1 + abRk_2} + \frac{k_1}{1 + aR}\right)
$$

and

$$
TP_2'(0) = \frac{bR}{r_2}\left(\frac{k_2}{1 + abRk_2} - \frac{k_1}{1 + aR}\right).
$$

Proposition 5.3. *Suppose that $bk_2 < 1$. If $r_1 < r_2$ and $k_1 < k_2$ then $TP_1'(0) > 0$ and $TP_2'(0) < 0$.*

Proof. Using $bk_2 < 1$, then $abk_2 R < aR$. Hence,

$$
\frac{1}{1 + abRk_2} > \frac{1}{1 + aR}.
$$

Since $k_2 > k_1$, we conclude that

$$
\frac{k_2}{1 + abRk_2} > \frac{k_1}{1 + aR}.
\tag{5.12}
$$

This inequality implies that $TP_2'(0) < 0$ because $\frac{bR}{r_2} > 0$. On the other hand, $1 < 1 + aR$ and

$$
\frac{1}{r_2} < \frac{1}{r_1}
$$

hold. Therefore,

$$
\frac{1}{r_2} < \frac{1 + aR}{r_1}.
\tag{5.13}
$$

By using (5.12) and (5.13), we conclude that $TP_1'(0) > 0$. $\qquad\square$

Case 2: $bk_2 > 1$.
The equilibrium $(k_1, k_2, 0)$ is a global attractor in (5.8) for $D = 0$. Now,

$$
A^{-1} = \begin{pmatrix}
\frac{-1}{r_1} & 0 & 0 \\
0 & \frac{-1}{r_2} & * \\
0 & 0 & *
\end{pmatrix}.
$$

In this case,

$$TP_1'(0) = (k_2 - k_1)\left(\frac{1}{r_1} - \frac{1}{r_2}\right)$$

and

$$TP_2^{n)}(0) = 0$$

for any order n. As in the competitive case, this implies that the branch $TP_2(D)$ is identically zero, see Proposition 5.1.

5.2.3   Species 1 is a Prey and Species 2 is a Predator

Consider

$$\begin{cases} x_1' = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) + D(x_2 - x_1) \\ x_2' = r_2 x_2 \left(1 - \frac{x_2}{k_2} - ay\right) + D(x_1 - x_2) \\ y' = sy \left(1 - \frac{y}{R} + by\right). \end{cases} \tag{5.14}$$

Next we discuss the possible dynamical behaviours of (5.14) for $D = 0$.

Case 1: $aR < 1$.

The equilibrium

$$\left(k_1, \frac{k_2(1 - aR)}{1 + abRk_2}, \frac{R(1 + bk_2)}{1 + abRk_2}\right)$$

is a global attractor in (5.14) for $D = 0$. We have that

$$A^{-1} = \begin{pmatrix} \frac{-1}{r_1} & 0 & 0 \\ 0 & \frac{-1}{r_2(1 - aR)} & * \\ 0 & \frac{bR}{(-1 + aR)r_2} & * \end{pmatrix}$$

In this case,

$$TP_1'(0) = \left(\frac{1}{r_2} - \frac{1 - aR}{r_1}\right)\left(\frac{k_1}{1 - aR} - \frac{k_2}{1 + abRk_2}\right)$$

and

$$TP_2'(0) = \frac{bR}{r_2}\left(\frac{k_1}{1 - aR} - \frac{k_2}{1 + abRk_2}\right).$$

Proposition 5.4. *Assume that $aR < 1$. If $r_2 < r_1$ and $k_2 < k_1$ then $TP_1'(0) > 0$ and $TP_2'(0) > 0$.*

Proof. It is clear that

$$1 - aR < 1 + abRk_2.$$

Using that $k_2 < k_1$, we have that

$$\frac{k_1}{1 - aR} > \frac{k_2}{1 + abRk_2}. \tag{5.15}$$

This inequality implies that $TP_2'(0) > 0$. On the other hand, using $r_2 < r_1$, we get

$$\frac{1}{r_2} > \frac{1 - aR}{r_1}.$$

Collecting all the information, it is concludes that $TP_1'(0) > 0$. $\square$

Case 2: $aR > 1$.

The equilibrium $(k_1, 0, R)$ is a global attractor in (5.14) for $D = 0$. We have that

$$A^{-1} = \begin{pmatrix} \frac{-1}{r_1} & 0 & 0 \\ 0 & \frac{1}{r_2(1-aR)} & * \\ 0 & \frac{bR}{r_2(1-aR)} & * \end{pmatrix}.$$

In this case,

$$TP_1'(0) = -k_1 \left(\frac{1}{r_1} - \frac{1}{r_2(aR-1)} \right)$$

and

$$TP_2'(0) = k_1 \frac{bR}{r_2(-1+aR)}.$$

Observe that $TP_2'(0)$ is always positive.

5.3 Appendix 3

We consider a metacommunity model of the general form

$$\begin{cases} y' = H_1(y, x_1, x_2, D) \\ x_1' = H_2(y, x_1, x_2, D) \\ x_2' = H_3(y, x_1, x_2, D), \end{cases} \tag{5.16}$$

such as those considered in Sections 3.1 and 3.2. For instance, in the competitive case,

$$\begin{cases} H_1(y, x_1, x_2, D) = sy \left(1 - \frac{y}{R} - bx_2 \right) \\ H_2(y, x_1, x_2, D) = r_1 x_1 \left(1 - \frac{x_1}{k_1} \right) + D(x_2 - x_1) \\ H_3(y, x_1, x_2, D) = r_2 x_2 \left(1 - \frac{x_2}{k_2} - ay \right) + D(x_1 - x_2). \end{cases} \tag{5.17}$$

We have written the equation associated with y at the beginning for convenience of the presentation. After adding a new patch to (5.16), (as system (3.8)), we have a system of the form

$$\begin{cases} y' = H_1(y, x_1, x_2, D) \\ x_1' = H_2(y, x_1, x_2, D) + D(x_3 - x_1) \\ x_2' = H_3(y, x_1, x_2, D) \\ x_3' = r_3 x_3 \left(1 - \frac{x_3}{k_3} \right) + D(x_1 - x_3). \end{cases} \tag{5.18}$$

Note that if (y^*, x_1^*, x_2^*) is a global attractor of system (5.16) for $D = 0$, then (y^*, x_1^*, x_2^*, k_3) is a global attractor of system (5.18) for $D = 0$ as well.

Denote by

$$P(y, x_1, x_2, x_3, D) = (P_1(y, x_1, x_2, x_3, D), P_2(y, x_1, x_2, x_3, D), P_3(y, x_1, x_2, x_3, D), P_4(y, x_1, x_2, x_3, D))$$

with

$$P_1(y, x_1, x_2, x_3, D) = H_1(y, x_1, x_2, D),$$

$$P_2(y, x_1, x_2, x_3, D) = H_1(y, x_1, x_2, D) + D(x_3 - x_1),$$

$$P_3(y, x_1, x_2, x_3, D) = H_3(y, x_1, x_2, D)$$

$$P_4(y, x_1, x_2, x_3, D) = r_3 x_3 \left(1 - \frac{x_3}{k_3} \right) + D(x_1 - x_3).$$

Note that

$$
B = \begin{pmatrix} \frac{\partial P_1}{\partial y}(y^*,x_1^*,x_2^*,k_3,0) & \frac{\partial P_1}{\partial x_1}(y^*,x_1^*,x_2^*,k_3,0) & \frac{\partial P_1}{\partial x_3}(y^*,x_1^*,x_2^*,k_3,0) & \frac{\partial P_1}{\partial x_3}(y^*,x_1^*,x_2^*,k_3,0) \\ \frac{\partial P_2}{\partial y}(y^*,x_1^*,x_2^*,k_3,0) & \frac{\partial P_2}{\partial x_1}(y^*,x_1^*,x_2^*,k_3,0) & \frac{\partial P_2}{\partial x_3}(y^*,x_1^*,x_2^*,k_3,0) & \frac{\partial P_2}{\partial x_3}(y^*,x_1^*,x_2^*,k_3,0) \\ \frac{\partial P_3}{\partial y}(y^*,x_1^*,x_2^*,k_3,0) & \frac{\partial P_3}{\partial x_1}(y^*,x_1^*,x_2^*,k_3,0) & \frac{\partial P_3}{\partial x_3}(y^*,x_1^*,x_2^*,k_3,0) & \frac{\partial P_3}{\partial x_3}(y^*,x_1^*,x_2^*,k_3,0) \\ 0 & 0 & 0 & -r_3 \end{pmatrix} =
$$

$$
= \begin{pmatrix} A & 0 \\ 0 & -r_3 \end{pmatrix}
$$

with

$$
A = \begin{pmatrix} \frac{\partial H_1}{\partial y}(y^*,x_1^*,x_2^*,0) & \frac{\partial H_1}{\partial x_1}((y^*,x_1^*,x_2^*,0)) & \frac{\partial H_1}{\partial x_2}(y^*,x_1^*,x_2^*,0) \\ \frac{\partial H_2}{\partial y}(y^*,x_1^*,x_2^*,0) & \frac{\partial H_2}{\partial x_1}((y^*,x_1^*,x_2^*,0)) & \frac{\partial H_2}{\partial x_2}(y^*,x_1^*,x_2^*,0) \\ \frac{\partial H_3}{\partial y}(y^*,x_1^*,x_2^*,0) & \frac{\partial H_3}{\partial x_1}((y^*,x_1^*,x_2^*,0)) & \frac{\partial H_3}{\partial x_2}(y^*,x_1^*,x_2^*,0) \end{pmatrix}.
$$

Observe that A is of the form

$$
\begin{pmatrix} * & 0 & * \\ 0 & -r_1 & 0 \\ * & 0 & * \end{pmatrix}.
$$

On the other hand,

$$
\frac{\partial P}{\partial D}(y^*,x_1^*,x_2^*,k_3,0) = (0, \frac{\partial H_2}{\partial D}(y^*,x_1^*,x_2^*,0) + (k_3 - x_1^*), \frac{\partial H_3}{\partial D}(y^*,x_1^*,x_2^*,0), x_1^* - k_3).
$$

Collecting these computations, we can formulate:

Theorem 5.3. *Let $(y^*,x_1^*,x_2^*,0)$ be a point that satisfies $H(y^*,x_1^*,x_2^*,0) = (0,0,0)$. If $\det(A) \neq 0$ with*

$$
A = \begin{pmatrix} \frac{\partial H_1}{\partial y}(y^*,x_1^*,x_2^*,0) & \frac{\partial H_1}{\partial x_1}(y^*,x_1^*,x_2^*,0) & \frac{\partial H_1}{\partial x_2}(y^*,x_1^*,x_2^*,0) \\ \frac{\partial H_2}{\partial y}(y^*,x_1^*,x_2^*,0) & \frac{\partial H_2}{\partial x_1}(y^*,x_1^*,x_2^*,0) & \frac{\partial H_2}{\partial x_2}(y^*,x_1^*,x_2^*,0) \\ \frac{\partial H_3}{\partial y}(y^*,x_1^*,x_2^*,0) & \frac{\partial H_3}{\partial x_1}(y^*,x_1^*,x_2^*,0) & \frac{\partial H_3}{\partial x_2}(y^*,x_1^*,x_2^*,0) \end{pmatrix}.
$$

then there is a smooth map $h(D) = (h_1(D), h_2(D), h_3(D), h_4(D))$ defined in an interval of the form $(-\widetilde{D}, \widetilde{D})$ with $\widetilde{D} > 0$ such that

$$
P(h(D), D) = (0,0,0,0)
$$

for all $D \in (-\widetilde{D}, \widetilde{D})$ with $h(0) = (y^*,x_1^*,x_2^*,k_3)$. Moreover,

$$
(h_1'(0), h_2'(0), h_3'(0), h_4'(0))^t = - \begin{pmatrix} A & 0 \\ 0 & -r_3 \end{pmatrix}^{-1} \frac{\partial P}{\partial D}(y^*,x_1^*,x_2^*,k_3,0)^t. \tag{5.19}
$$

According to (5.19),

$$
\widetilde{TP}_1'(0) = h_2'(0) + h_3'(0) + h_4'(0) \tag{5.20}
$$

determines if D is beneficial or harmful for the total biomass of species 1. Specifically, if $\widetilde{TP}_1'(0) > 0$ (resp. $\widetilde{TP}_1'(0) < 0$) there is a range of dispersal rates that generates an increase (resp. decrease) in the total population size of species 1. Note that

$$
\widetilde{TP}_1'(0) = TP_1'(0) + (k_3 - k_1)\left(\frac{1}{r_1} - \frac{1}{r_3}\right). \tag{5.21}
$$

where $TP_1'(0)$ is defined in Appendix 2.

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