Coexistence and superior competitor exclusion in the Leslie-Gower competition model with fast dispersal

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October 9, 2014

Abstract

In this work we study a nonlinear two time scales discrete competition model. Specifically, we deal with a spatially distributed Leslie-Gower competition model with fast dispersal. After building up the corresponding two time scales model, we have used approximate aggregation techniques to derive a lower dimensional, reduced system. When the ratio between time scales is large enough, the aggregated system can be used to analyze the two time scales model.

As a result, we have found trade-off mechanisms between fast dispersal and competition under spatial homogeneity conditions. When the environment is heterogeneous, we have found that under asymmetric dispersal, whether competitive coexistence or competitive exclusion occurs depends on the initial population sizes of the two species.

Keywords: Leslie-Gower model; Survival strategies; Dispersal; Aggregation methods; Individual behavior; bi-stability; tri-stability.

1 Introduction.

The analysis of the mechanisms underlying coexistence in patchy environments is an important issue in theoretical ecology [17, 18, 16]. Essentially, species competition and individuals dispersal are taken into account and the interest relies on the interplay between both processes.

One of its paradigms, the Patch Occupancy Metapopulation Theory (POT) [10], explores population persistence and species coexistence in patchy landscapes using the competition-colonization trade-off as its basis. The POT focuses on the presence of local populations in habitat patches and it does not include any description of local dynamics. The POT implicitly recognizes that competition operates at a much faster time scale than colonization-extinction processes. All these assumptions preclude, in fact, local coexistence and imply that migration cannot influence local competitive interactions. The POT and its predictions are, nevertheless, at odds with some empirical data [11] due to the implicit separation of time scales.

In [1] it is set up a metapopulation model considering dispersal and competition within the same time scale. Under this assumption, the authors shown that in a spatially homogeneous competitive environment differences in species dispersal are not enough to explain coexistence with the absence of a refuge for the weaker competitor. Besides, they considered spatial heterogeneity either by allowing for species refuges or by assuming variations in competitive rankings over space such that the superior competitor in some parts of the landscape becomes the inferior competitor in the remnant landscape. The heterogeneity is concreted in spatial variance in fitness that leads to a source- sink dynamics framework enabling coexistence.

Finally, the puzzle was completed in [22] where dispersal was assumed to be much faster that competition. Under this settings, the authors shown that there is a trade-off between fast dispersal and competition when the environment is homogeneous. In particular, appropriate dispersal rates may allow the weaker competitor to survive and even to exclude the stronger competitor.

The approaches presented in [10] and [22] share the feature that competition and dispersion occur at different time scales. Understanding how ecological phenomena interact across temporal scales is crucial in theoretical ecology [16, 12], since it is known that differences in process time scales may be critical for system dynamical behaviour [20, 12, 15].

The aim of this work is to analyze the interplay of species competition and fast individuals dispersal in a metapopulation, in the sense that we seek trade-off mechanism between these two processes related to species coexistence. We also study the role of spatial heterogeneity in the aforementioned compensation mechanism. Here, we focus on the impact of dispersal on local populations with discrete non-overlapping generations. This situation can be found in a range of evolutionary and ecological processes in which gene flow and dispersal rate due to non sedentary habits can operate at a fast scale relative to selection or population interaction processes [22]. The corresponding mathematical models adopt the form of systems of difference equations [31]. The study of the role of dispersal in continuous-time metapopulation models is extensive [16, 2, 4, 22].

The paradigms of competition models are the Lotka-Volterra model in the continuous case and the Leslie-Gower model [13] in the discrete case. The latter played a fundamental role in laboratory experiments with the flour beetle (of the genus *Tribolium*) that give rise to the competitive exclusion principle that is one of the important tenets in ecology [23, 24, 25, 26, 13]. The Leslie-Gower model consists of two Beverton-Holt equations with the adding of the interspecific competition.

The proposed model considers two competing species inhabiting an environment consisting of p different patches. The model couples local Leslie-Gower competition dynamics with linear (constant rates) individuals dispersal between patches. Dispersal is assumed to be faster than competition, which yields a system of $2p$ difference equations with two time scales. Taking advantage of the time scales separation the system can be studied in terms of a two dimensional system for the total densities of the two species. This reduction is performed with the help of the so-called approximate aggregation of variable technique [3, 5]. The form of the reduced system is that of a discrete competition model different from the Leslie-Gower model and with a richer dynamics.

The Leslie-Gower model exhibits the same dynamics [6, 19] than the Lotka-Volterra model. Weak species competition leads to a coexistence equilibrium state while strong species competition makes competitive exclusion to occur: which species gets extinct either depends on priority effects (the excluded species depend on the initial amount of individuals, the species that gains an early advantage wins) or do not. The laboratory results with the flour beetle where mostly supported by the Leslie-Gower competition model. Nevertheless, data from one of those experiments was at odds with this model, since in this experiment whether competitive coexistence occurred or competitive exclusion occurred depended on the initial population numbers of the two species [6]. In [6, 7] an explanation to this data is proposed in terms of an age structured population model by introducing a Ricker-type nonlinearity and found multiple mixed-type attractors. Instead, the model that we propose keeps as local dynamics the simple Leslie-Gower model but we find that together with fast dispersal there exist scenarios displaying multiple equilibrium attractors that compatible with the data observed in the experiments with the flour beetle and are different from those displayed in [6, 7] (see section 4).

This work is organized as follows: in section 2 we set up a slow-fast Leslie-Gower spatially distributed competition model. The habitat consists of p patches and there individuals dispersal. The system consists of $2p$ equations and we sketch both a dimension reduction procedure as well as the kind of information that produces. Section 3 is devoted to the analysis of the reduced system. We derive general conditions for species viability, species coexistence or species extinction. Nevertheless, under the most general settings, the model depends on so many parameters to perform a complete analysis. In section 3.1 we deal with the important case of an a 2 patches environment. In this case we show that fast dispersal in heterogeneous environments may lead to scenarios with two and even three stable equilibrium points (bi-stability and tri-stability), while it is not possible if both patches are homogeneous. Besides, we highlight a trade-off mechanism between dispersal and competition. We discuss the previous results in section 4 and section 5 contains the conclusions of this work. The appendix section A devoted to prove the mathematical results completes the manuscript.

2 Methods

In this section we set up a difference equation (discrete time) model that accounts species competition along with fast dispersal. After building the slow fast model, the separation of time scales allows us to apply the results sketched in Appendix A and get a less dimensional system. The section finishes with a result which describes which kind of information about the slow fast system can be retrieved from the reduced system.

2.1 Presentation of the model.

We consider two competing species inhabiting an environment divided into p patches. Let $n_i^j(t)$ be the number of individuals of species $i = 1, 2$ in patch $j = 1, \ldots, p$ at time t. We denote $N_i(t) = (n_i^1(t), n_i^2(t), \ldots, n_i^p(t))$, the spatial distribution of individuals of each species and the population vector

$$N(t) = (N_1(t), N_2(t))^T \,,$$

where the superscript T stands for transposition. We assume that individual displacements between patches is faster than the local community dynamics. Following appendix A both processes, dispersal and local dynamics, are represented by two mappings F (for fast) and S (for slow), respectively. The time unit of the system is that of the the slow process and the effect of the fast dynamics is represented by the k-th iterate of mapping F, $F^{(k)}$, with k being an approximation of the time scales ratio. Thus, we set the so called complete system that combines both processes, fast and slow, and that reads as follows:

$$N(t+1) = S\left(F^{(k)}\left(N(t)\right)\right) \tag{1}$$

Next, we explicitly define the mappings F and S.

We assume that dispersal rates are constant and we denote f_i^{rs} the fraction of individuals of species i moving from patch s to patch r. Gathering these coefficients we define the dispersal matrices $\mathcal{F}_i = (f_i^{rs})$, $i = 1, 2$, that are stochastic. For further purposes, we also assume that they are regular. The definition of mapping F representing dispersal is thus

$$F(N) = \begin{pmatrix} \mathcal{F}_1 & 0 \\ 0 & \mathcal{F}_2 \end{pmatrix} \begin{pmatrix} N_1^T \\ N_2^T \end{pmatrix} = \mathcal{F} N \tag{2}$$

The local species competition in each patch $j = 1, \cdots, p$ is represented by the Leslie-Gower model [6]. If n_1^j and n_2^j are the number of individuals of both species in patch j, after a time unit they become, respectively

$$\begin{cases} \dfrac{b_1^j}{1 + c_{11}^j n_1^j + c_{12}^j n_1^j} n_1^j = s_1^j(n_1^j, n_2^j), \\ \dfrac{b_2^j}{1 + c_{21}^j n_2^j + c_{22}^j n_2^j} n_2^j = s_2^j(n_1^j, n_2^j), \end{cases}$$

where b_i^j is the intrinsic growth rate of species i in patch j (that is, the growth rate without taken into account density dependent effects) and c_{rs}^j measures the competitive effect of species s on species r in patch j. growth rate in the absence of the other competitor Denoting $S_i(N(t)) = (s_i^1(n_1^1, n_2^1), \ldots, s_i^p(n_1^p, n_2^p))$ the mapping S representing the local dynamics is defined by

$$S(N) = (S_1(N), S_2(N))^T \tag{3}$$

Summing up, it the complete system (1) $S\left(F^{(k)}\left(N(t)\right)\right) = S\left(\mathcal{F}^k N(t)\right)$

2.2 Reduction of the model.

We use the method described in appendix A to reduce the system (1). The procedure follows from the usual assumption for slow fast system that fast dynamics attains an stable equilibrium state "instantaneously" fast, which is equivalent to assume that the ratio between time scales, k, is large. Mathematically, the fact that $\mathcal{F}_i$ are regular and stochastic means [29] that, associated to the eigenvalue 1, there exist positive eigenvectors $\mathbf{v}_i = (v_{i1}, \ldots, v_{ip})$ and $\mathbf{1} = (1, \ldots, 1) \in \mathbb{R}^p$ such that $\mathbf{1}\mathbf{v}_i^T = 1$ and such that

$$\lim_{k\to\infty} \mathcal{F}_i^k = \mathbf{v}_i^T \mathbf{1}. \tag{4}$$

The vector $\mathbf{v}_i$ represents the stable distribution of individuals of species i among the p different patches, that is, the dispersal process drives both species to attain stable distributions given by $\mathbf{v}_i$ at the fast time scale. From (4) it is straightforward that

$$\lim_{k\to\infty} \mathcal{F}^k N = \begin{pmatrix} \mathbf{v}_1^T \mathbf{1} N_1^T \\ \mathbf{v}_2^T \mathbf{1} N_2^T \end{pmatrix} = \bar{\mathcal{F}} N,$$

where $\bar{\mathcal{F}}$ is that in hypothesis A.1 and $N(t+1) = S\left(\bar{\mathcal{F}}\left(N(t)\right)\right)$ is the auxiliary system (13) in appendix A which approaches the complete system (1) for k large enough. The dimension reduction is possible provided a suitable decomposition $\bar{\mathcal{F}} = E \circ G$ as prescribed in hypothesis A.2, which is fulfilled by defining

$$G\left(N\right) = \begin{pmatrix} \mathbf{1} & 0 \\ 0 & \mathbf{1} \end{pmatrix} N = \left(\sum_{j=1}^{p} n_1^j, \sum_{j=1}^{p} n_2^j\right)^T, \qquad E\left(y_1, y_2\right) = \left(\mathbf{v}_1 y_1, \mathbf{v}_2 y_2\right)^T$$

The existence of the mapping G is is equivalent to the existence of the so-called global variables of the system, that are constant for the fast dynamics and become the state variables of the reduced system. In this case, the global variables are the total number of individuals of each species that, obviously, do not change with dispersal and we denote them $y_i = \sum_{j=1}^{p} n_i^j$, $i = 1, 2$. The mapping E describes the asymptotic distribution of individuals between regions. Note that the equilibria of fast dynamics depend on the global variables and the stable distributions of individuals of each species among the p different patches.

With the help of mappings G and E we can build up the aggregated system (14) for the global variables, which reads as follows

$$\begin{cases} y_1(t+1) = f_1(y_1(t), y_2(t)), \\ y_2(t+1) = f_2(y_1(t), y_2(t)). \end{cases} \tag{5}$$

where

$$f_1(y_1(t), y_2(t)) = \sum_{j=1}^{p} \frac{b_1^j v_{1j} y_1(t)}{1 + c_{11}^j v_{1j} y_1(t) + c_{12}^j v_{2j} y_2(t)} := \phi_1(y_1(t), y_2(t)) y_1(t),$$

$$f_2(y_1(t), y_2(t)) = \sum_{j=1}^{p} \frac{b_2^j v_{2j} y_2(t)}{1 + c_{21}^j v_{1j} y_1(t) + c_{22}^j v_{2j} y_2(t)} := \phi_2(y_1(t), y_2(t)) y_2(t). \tag{6}$$

The definition of the mapping $\mathcal{F}$ (see equation 2) imply that hypotheses of theorem A.1 are met. Thus, important features of the asymptotic behavior of the solutions of system (1) can be studied through the corresponding analysis of the reduced system (5). The next result is a contextualized version of the main general aggregation theorem A.1 from the appendix A.

Theorem 2.1 *Consider the general model* (1). *Let* $Y^* = (y_1^*, y_2^*) \in [0, \infty) \times [0, \infty)$ *be a hyperbolic equilibrium point of the aggregated system* (5). *Then there exists* $k_0 \in \mathbb{N}$ *such that for each* $k \geq k_0$ *there exists a hyperbolic equilibrium point* X_k^* *of system (1) satisfying*

$$\lim_{k \to \infty} X_k^* = X^* = (\mathbf{v}_1 y_1^*, \mathbf{v}_2 y_2^*)$$

where $\mathbf{v}_1$ *and* $\mathbf{v}_2$ *stand for the asymptotic spatial distribution of individuals of each due to the dispersal process.*

1. *If* y^* *is asymptotically stable then* X_k^* *is asymptotically stable for each* $k \geq k_0$*, and the basins of attraction of each* X_k^* *can be described in terms of the basins of attraction of* Y^**.*

2. *If* y^* *is unstable then* X_k^* *is unstable, for each* $k \geq k_0$*.*

Proof.– We have already proved that system (1) fulfills hypotheses A.1 and A.2 that lead to theorem A.1. To prove that limits (15) are uniform on compact sets, see [28], proposition 3.10. ■

Therefore, whenever the time scales ratio is large enough, the behavior of the complete system (1) can be described in terms of the equilibrium points (y_1^*, y_2^*) of the aggregated system (5) and the asymptotic stable distribution of individuals among patches $\mathbf{v}_1$ and $\mathbf{v}_2$. That is, the larger is the time scales ratio, the better the solutions of the complete system approach $(\mathbf{v}_1 y_1^*, \mathbf{v}_2 y_2^*)$.

3 Results

In this section we analyze the reduced system (5). In the first instance, there are three important kind of equilibrium states: the trivial equilibrium $(0,0) \in \mathbb{R}^2$, that stands for global extinction, the semi trivial equilibrium points $E_1^* = (y_1^*, 0)$, $E_2^* = (0, y_2^*) \in \mathbb{R}^2$, $y_1^* \neq 0$, $y_2^* \neq 0$ that correspond with the state in which on species gets extincted and, finally, coexistence equilibrium states of the form $E^* = (y_1^*, y_2^*) \in \mathbb{R}^2$, $y_1^* \neq 0$, $y_2^* \neq 0$. Of course, discrete systems may exhibit many other long term behavior different from approaching one of these equilibrium states, including convergence to periodic states or chaotic orbits. The aim of this section is to determine which behavior admit the solutions of system 5 and which are the conditions enabling it.

We prove first that the reduced system (5) is well defined and that it is competitive [30]. This is an important feature since, as we will see soon, it entails that any solution of the aggregated system converges to an equilibrium state in the form of an equilibrium point. This fact allows us to take full advantage of theorem (2.1). We denote the positive cone by $\mathbb{R}_+^2 = (0, \infty) \times (0, \infty)$.

Proposition 3.1 *Consider the aggregated system* (5)*. Then*

1. *The positive cone as well as* $(0,\infty)\times\{0\}$ *and* $\{0\}\times(0,\infty)$ *are forward invariant.*
2. *All solutions in* $[0,\infty)\times[0,\infty)$ *are forward bounded:*

$$y_1(t) \le \sum_{j=1}^{p} b_1^j/c_{11}^j, \qquad y_2(t) \le \sum_{j=1}^{p} b_2^j/c_{22}^j, \qquad \textit{for } t = 1,2,\cdots$$

3. *The system is competitive, meaning that if*

$$y_1 < y_1' \ \textit{ and } \ y_2' < y_2$$

then

$$f_1(y_1,y_2) < f_1(y_1',y_2') \ \textit{ and } \ f_2(y_1',y_2') < f_2(y_1,y_2).$$

Proof.–: It can be easily accomplished by direct calculation. ■

It is immediate that $(0,0)$ is an equilibrium point of system (5) regardless of the value of the parameters of the model, while this is not the case of the semi trivial equilibrium points. The following result relates conditions for global extinction of both species with conditions that assure the existence of the semi trivial equilibrium points. The key parameter is *the global growth rate* of species i, $\phi_i(0,0) = \sum_j^p v_{ij} b_i^j$, that is, the sum of the local growth rates weighted by the asymptotic distribution of individuals among patches.

Proposition 3.2 *Consider system* (5) *and* ϕ_i, *the function defined in* (6). *Then,*

1. *The trivial equilibrium is a global attractor if, and only if,* $\phi_i(0,0) \le 1$ *for* $i = 1,2$.
2. *For each* $i = 1,2$, *there exists* E_i^* *if, and only if,* $\phi_i(0,0) > 1$. *In this case,* y_i^* *is the unique positive value satisfying* $\phi_i(E_i^*) = 1$.

Proof.– See appendix A.2 ■

Corollary 3.3 *All solutions of system* (5) *in* $[0,\infty)\times[0,\infty)$ *converge eventually to an equilibrium point.*

Proof: See appendix A.2. ■

For each species, the existence of the semi trivial equilibrium is closely related to its ability to survive in the absence of the other species. The following result establishes that species i can survive if $\phi_i(0,0) \leq 1$ but $\phi_j(0,0) > 1$, with $i \neq j$.

Proposition 3.4 *Consider system* (5) *and* ϕ_i*, the function defined in* (6). *Then*

1. *Species i gets globally extinct if, and only, if $\phi_i(0,0) \leq 1$.*
2. *Assume that $\phi_1(0,0) > 1$ and $\phi_2(0,0) \leq 1$. Then, for any solution $(y_1(t), y_2(t))$ of system (5) such that $y_1(0) > 0$ it follows that $\lim\limits_{t\to\infty}(y_1(t), y_2(t)) = E_1^*$.*
3. *If, instead, $\phi_1(0,0) \leq 1$ and $\phi_2(0,0) > 1$ then, for any solution $(y_1(t), y_2(t))$ of system (5) such that $y_2(0) > 0$ it follows that $\lim\limits_{t\to\infty}(y_1(t), y_2(t)) = E_2^*$.*

Proof.– See appendix A.2 ■

Nevertheless, when both species have the potential to survive (i.e., $\phi_i(0,0) > 1$ for $i = 1,2$) the effect of species competition must be taken into account and condition $\phi_i(0,0) > 1$ does not guarantees anymore that species i will survive. We carry on the analysis by assuming that $\phi_i(0,0) > 1$ for $i = 1,2$ and we seek for conditions leading to either one species exclusion or species coexistence.

Proposition 3.5 *Consider system* (5) *and assume that* $\phi_i(0,0) > 1$ *for* $i = 1,2$*, so that the semi trivial equilibrium points* E_i^*, $i = 1,2$*, exist. Then,* E_i^* *is locally asymptotically stable if*

$$\phi_j(E_i^*) < 1, \qquad j \neq i \tag{7}$$

and unstable if

$$\phi_j(E_i^*) > 1, \qquad j \neq i. \tag{8}$$

Proof: It follows from the usual analysis of the eigenvalues of the corresponding Jacobian matrix. Standard calculations lead to the desired results just keeping in mind that y_i^* solves the equation $1 = \phi_i(E_i^*)$. ■

A direct consequence of proposition 3.5 is the following

Corollary 3.6 *Consider system* (5) *and assume that* $\phi_i(0,0) > 1$ *for* $i = 1,2$*. If condition* $\phi_j(E_i^*) > 1$ *holds for* $i,j = 1,2$ $j \neq i$*, then there is species coexistence.*

Proof: ■

Condition (7) in proposition 3.5 provides also sufficient conditions for species extinction via priority effects:

Corollary 3.7 *Consider system* (5) *and assume that* $\phi_i(0,0) > 1$ *for* $i = 1,2$*. If condition* $\phi_j(E_i^*) < 1$ *holds for* $i,j = 1,2$ $j \neq i$*, then exist neighborhoods* $\mathcal{U}_i$ *of* E_i^* *such that or any initial condition in* $(y_1^i(0), y_2^i(0)) \in \mathcal{U}_i \cap \mathbb{R}_+^2$ *the corresponding solutions* $(y_1^i(t), y_2^i(t))$ *converges to* E_i^*

Proof: ■

We have found conditions entailing species coexistence and we already know that any solution converges to an stable equilibrium state. The focus is now on determine the structure of these stable states: number, distribution, and so on. Note that the coexistence states are the positive roots of a system of the form

$$\begin{cases} P_1(y_1, y_2) = 0, \\ P_2(y_1, y_2) = 0, \end{cases}$$

being P_i polynomials on y_1 and y_2 of degree p, the number of patches. To our knowledge, there is no general criterion to determine the number of coexistence states for an arbitrary $p \geq 5$ (taking into account that these polynomials are not general ones, since there are constrains imposed by equations (5)). That fact prevents us from obtaining general results. Of course, positive solutions can be numerically calculated for a given a concrete set of parameter values. It is important to recall that the aggregated model is a 2 dimensional one, so that the stability of the positive equilibrium points can be easily analyzed, for instance, via linearization.

3.1 Two patches environment

In this section we set a two patches environment, that is simpler but still meaningful setting. The previous section left open the door to find multi attractor scenarios and one of the purposes of this section is to illustrate this fact. The other aim of this section is to get an insight in the role of fast dispersal in competition on homogeneous environments.

Note that the aggregated system still depends on 16 parameters, which makes any try of performing an exhaustive classification of all the possible outcomes of the model to be beyond the aims of this work. Therefore, we adopt either a numerical approach to show the existence of multi attractor scenarios or further "homogenizer" assumptions on the coefficients of the system to enable an analytical approach.

3.1.1 Multi stability results in heterogeneous environments.

A serial of numerical experiments yielded, along with the classic dynamical outcomes, 2 and even 3 attracting equilibrium points. We display now an example in which whether competitive coexistence or competitive exclusion occurs depends on the initial population sizes of the two species.

Figure 1 displays the case where the semi trivial equilibrium $E_2^* = (0, y_2^*)$ and a positive equilibrium $E^* = (y_1^*, y_2^*)$ are locally AS, whereas the semi trivial equilibrium $E_1^* = (y_1^*, 0)$ is unstable. Then, species 2 always survives while species 1 may get extinct or may persist (coexistence) depending on the initial population values. Symmetric results exchanging the roles of $E_1^*$and E_2^* exists.

Instead, Figure 2 displays a more complex situation. There, both semi trivial equilibriums $E_1^* = (y_1^*, 0)$ and $E_2^* = (0, y_2^*)$ and a positive equilibrium $E^* = (y_1^*, y_2^*)$ are locally asymptotically stable, while there are another two unstable positive equilibrium points. In this case, coexistence or one species exclusion (having quite different competitive abilities) may arise.

In both cases the outcome depends exclusively on the initial population values. Note that in both cases the asymmetric distribution of individuals. It is important to point out that, from extensive numerical experiments, we have found that for moderate dispersal rates the aggregated model behaves as the non spatially distributed one.

3.1.2 Competition-dispersal trade-off.

Now we investigate the *net* effect of individual displacements between patches on the outcome of the competition process. Thus, we set homogeneous conditions among patches, meaning that at patch $j = 1, 2$,

$$b_1^j = b_1, \quad b_2^j = b_2 \quad c_{11}^j = 1, \quad c_{22}^j = 1, \quad c_{12}^j = c_{12}, \quad c_{21}^j = c_{21}. \tag{9}$$

Furthermore, in order to avoid the extinction of both species we suppose

$$b_1,\, b_2 > 1 \tag{10}$$

Thus, the aggregated system is

$$\left\{ \begin{array}{l} y_1(t+1) = \dfrac{b_1 v_1 y_1(t)}{1 + v_1 y_1(t) + c_{12} v_2 y_2(t)} + \dfrac{b_1(1-v_1) y_1(t)}{1 + (1-v_1) y_1(t) + c_{12}(1-v_2) y_2(t)}, \\ y_2(t+1) = \dfrac{b_2 v_2 y_2(t)}{1 + c_{21} v_1 y_1(t) + v_2 y_2(t)} + \dfrac{b_2(1-v_2) y_2(t)}{1 + c_{21}(1-v_1) y_1(t) + (1-v_2) y_2(t)}. \end{array} \right. \tag{11}$$

where we have written v_1 and v_2 instead of v_{11} and v_{21}, respectively. In what follows, keeping in mind the aforementioned homogeneity conditions, we are interested in two questions. On the one hand, are there multiattractors in a homogeneous environment? or, in other words, is spatial heterogeneity a necessary condition for the existence of multiattractors? And, on the other hand, regardless of the previous question, is there any dispersal strategy allowing the inferior competitor survive (when it would get extincted if patches were isolated)?

The following result lightens the first question

Proposition 3.8 *Consider that the aggregated system* (11) *fulfills conditions (9) and (10). Then. there exists, at most, a single positive equilibrium point.*

Proof.– See appendix A.2 ■

Next, we establish conditions describing all the possible outcomes of system (11) under homogeneity conditions.

Proposition 3.9 *Consider that the aggregated system* (11) *fulfills conditions (9), (10) and* $\phi_i(0,0) > 1$.

1. *If* $\phi_i(E_j^*) > 1$ *for* $i, j = 1, 2$, $i \neq j$ *then, there exists a single coexistence state* $E^* \in \mathbb{R}_+^2$ *which attracts any solution with initial values in* $(0, \infty) \times (0, \infty)$.

2. *If* $\phi_i(E_j^*) < 1$ *for* $i, j = 1, 2$, $i \neq j$ *then, there exists a single coexistence equilibrium point* E_u^* *which is unstable. Any solution of the system aggregated system with initial values* $y_1(0), y_2(0) \neq E_u^*$ *converges either to* E_1^* *or* E_2^*. *Indeed,* E_u^* *is a saddle and its stable manifold divides the positive cone in two regions, each of them being the basins of attraction of one semi trivial equilibrium point.*

3. *Assume now that* $\phi_i(E_j^*) > 1$ *but* $\phi_j(E_i^*) < 1$. *Then,*

   (a) *It there exists a coexistence state* E^**, then it is a saddle any solution of the system aggregated system with initial values* $y_1(0), y_2(0) \neq E^*$ *and* $y_j(0) \neq 0$ *converges to* E_j^*.

   (b) *It there exists no coexistence state, then any solution of the system aggregated system with initial values such that* $y_j(0) \neq 0$ *converges to* E_j^*.

Proof.– It follows from corollary 3.3, which assures that any solution converges to an equilibrium point, proposition 3.8, where it is shown that there is at most one coexistence state and conditions on $\phi_i(E_j^*)$, that are related with the local stability of the semi trivial equilibrium points. ■

The following result corroborates the intuition that there are always dispersal rates allowing species coexistence. An obvious choice consists of dividing the arena between species, setting dispersal rates so that each species occupies a different patch (but there will be no competition). This result will turn out interesting (and non obvious) situations.

Proposition 3.10 *Consider the aggregated system* (11) *and assume also condition* (10). *Then, for any fixed values* $b_1 > 1$, $b_2 > 1$, c_{12} *and* c_{21}, *there exist dispersal rates* v_{11} *and* v_{21} *fulfilling conditions* $\phi_i(E_j^*) > 1$, *for* $i \neq j$, $i, j = 1, 2$.

Proof.– See appendix A.2 ■

A first comment on the previous result is that strong (and not only extreme) asymmetric dispersal rates allows population coexistence. Besides, from the proof we get the following upper bounds for the population size after a transient time.

Corollary 3.11 *Under the hypotheses of proposition 11, after a transient time the population is bounded from above by* $(2(b_1 - 1), 2(b_2 - 1))$.

Proof.– It follows from direct calculations. ■

We conclude this section with numerical simulations (figure 3) that illustrate the possible outcomes of the competition process for different dispersal strategies. We use the explicit conditions achieved in section 3.1.2 to compute conditions (7) and (8). We consider an homogeneous environment (in the sense of (9)) and set coefficients so that species 1 would drive species 2 to extinction if patches were isolated. The outcome of the model in case of asymptotic symmetrical distribution of individuals, that is, around the line $\nu_1 = \nu_2$, is the same as if patches were isolated (blue region). On the contrary, in case of strong asymmetric dispersal, there is species coexistence (white region). When species competition abilities are similar, appropriate dispersal rates allow the weaker to out compete the stronger species (green region). As the difference in competitive abilities become larger, the weaker competitor is more likely to disappear.

4 Discussion of results

Our results highlight the key role of fast dispersal for species competition in patchy habitats. In this case, dispersal becomes important not only to find new resources, but also to avoid patches where competitive pressure is high.

From an applied point of view, the construction of corridors between patches allowing individuals to migrate is a popular management tool used in the design of species conservation or species control strategies [27]. Our results suggest how important is for management purposes controlling not only these corridors and the dispersal rates through them, but also local intrinsic growth rates. Aided by parameter $\phi(0,0)$ managers can analyze and decide the most efficient strategy to enable one species extinction.

We must point out that there is controversy surrounding the effects of connecting or not connecting patches, since there are experiments demonstrating beneficial and negative effect of dispersal on the size of the metapopulation [4]. This apparent contradiction is faced in [8] considering a single species in a two patches environment, and our results can be used to to extend their findings to habitats consisting of an arbitrary number of patches connected by fast dispersal.

As we have pointed out, when species competition effects are taken into account, $\phi_i(0,0) > 1$ is a necessary but not sufficient condition for species i to survive. We have derived explicit conditions (based on the values of $\phi_i(E_j^*)$) entailing species extinction due to priority effects or species coexistence. Our results preclude the existence of neither periodic nor chaotic behavior in the evolution of the competing species. On the contrary, we found that the total amount of individuals of each species converges eventually to an equilibrium value.

This results are somehow at odds with those found in [6, 7] used to explain the unexpected (and unexplained) laboratory data obtained in the experiments with flour beetles (see the Introduction section)performed by Park [23, 24, 25, 26]. Data from this experiment showed that whether competitive coexistence occurred or competitive exclusion occurred was due to priority effects. In [6, 7] the authors proposed age structured specific models for the flour beetle that produced multiple mixed type attractors compatible with the aforementioned data. In particular, the coexistence state is a two cycle. We have found also (see section 3.1.1) multi attractor scenarios consisting of two or three equilibrium states which are also compatible with the aforementioned data. However, even if the experiments designed by Park and his collaborators did not take into account space, subsequent studies pointed out in the opposite direction.

In [9] it is reported a behavioral dissimilarity between the two species of triboulim (T) used by Park: T. castaneum was repelled by conditioned flour while T. confusum was strongly attracted by conditioned flour. Flour medium is conditioned by beetles living in and involves different factors, as depletion of the nutritive value of the medium or, most markedly, accumulation of the quinones given off by T. imagoes and taken up by the flour. In [21] it is reported that the average mobility of T. confunsum is about 9 cm per day. To contextualize these results, we recall that Park established the cultures in glass containers of either 9.5×2.5 cm or 10×7 cm and that the medium was changed every 30 days. Summing up, during each 30 days period tribolium can conditioned the environment (which is equivalent to consider a two patches environment) and cultures location can evolve towards an asymmetric distribution due to medium preference along with high mobility rates (when compared with the size of the glass containers). And those are the ingredients allowing figures 1 and 2. Unfortunately we can not compare the model with real data since dispersal data was not recorded (as it was not part of the experiment).

In the particular case of a two patches homogeneous environment with local Lotka-Volterra competition and fast linear dispersal was analyzed in [22]. The authors found an upper bound for the weaker competitor competitive abilities below which it will get extinct regardless of the dispersal rates that, however, does not exist in our model. Strong asymmetrical dispersal rates divide the arena: each patch is mainly occupied by one of the species and interaction becomes very low, so that the effects of competition are negligible. The underlaying mathematical reason for these incompatible results is that system (5) displays functional and dynamical emergence (see [3]) while its counterpart in [22] does not.

5 Conclusions

Our results highlight that fast dispersal is a trade-off mechanism in competing species dynamics, and it should be accounted along with the life history trade-offs pointed out in [2] among those relevant processes in metapopulation theory.

Even in the simplest environment consisting of two patches, and despite of being homogeneous or heterogeneous, we have proved that coexistence is always possible provided appropriate dispersal rates. Indeed, it follows from our results that manipulating local intrinsic growth rates and/or dispersal rates are effective steps to promote coexistence or one species exclusion and thus, are useful from the management point of view.

Furthermore, as the number of sites increases, the topology of the patchy environment becomes more and more complex. We hope that this work will serve as first step to deepen in the interplay between the topological structure (distribution of corridors and dispersal rates) and the local processes (local growth rate and competition effects) that define patchy environments.

Acknowledgements.– Authors are partially supported by Ministerio de Ciencia e Innovación (Spain), projects MTM2011-24321 and MTM2011-25238.

A Appendices

A.1 Approximate aggregation of nonlinear discrete systems

We briefly describe the approximate aggregation procedure presented in [28] where details can be found. We consider a population divided into groups, and each of these groups divided into several subgroups. The state at time t of the population with q groups is represented by a vector $X(t) := (\mathbf{x}^1(t), \dots, \mathbf{x}^q(t))^\mathsf{T} \in \mathbb{R}^N$, where every vector $\mathbf{x}^i(t) := (x^{i1}(t), \dots, x^{iN^i}(t))^\mathsf{T} \in \mathbb{R}_+^{N^i}$, $i = 1, \dots, q$, represents the state of the i group which is divided into N^i subgroups, with $N = N^1 + \cdots + N^q$.

The evolution of the population is driven by two processes which characteristic time scales are very different from each other. These two processes, fast and slow, are defined by two mappings

$$F, S : \Omega_N \longrightarrow \Omega_N \quad ; \quad F, S \in C^1(\Omega_N),$$

where $\Omega_N \subset \mathbb{R}^N$ is a nonempty open set.

We use as the time unit of the system coupling both processes that corresponding to the slow process. We approximate the effect of the fast dynamics over a time interval much longer than its own by means of the k-th iterate of mapping F, $F^{(k)}$, where k represents the time scales ratio. Thus, the complete system is defined by

$$X_k(t+1) = S(F^{(k)}(X_k(t))) := H_k(X_k(t)), \tag{12}$$

In order to proceed to the approximate reduction of the system (12) we assume the following two hypotheses on F:

Hypothesis A.1 *The sequence of iterates of* F, $\{F^{(k)}\}_{k\in\mathbb{N}}$, *converges pointwise on* Ω_N *to a mapping* $\bar{F} : \Omega_N \to \Omega_N$, *such that* $\bar{F} \in C^1(\Omega_N)$.

Hypothesis A.2 *There exist a non-empty open subset* $\Omega_q \subset \mathbb{R}^q$ *with* $q < N$ *and two mappings* $G : \Omega_N \longrightarrow \Omega_q$ *and* $E : \Omega_q \longrightarrow \Omega_N$ *with* $G \in C^1(\Omega_N)$, $E \in C^1(\Omega_q)$, *such that the mapping* $\bar{F}$ *of Hypothesis A.1 can be expressed as* $\bar{F} = E \circ G$.

We first define the auxiliary system which approximates (12) when $k \to \infty$, i.e., when the fast process has attained its equilibrium. Denoting its vector state at time t by X_t, this auxiliary system is

$$X(t+1) = S(\bar{F}(X(t))) = (S \circ E \circ G)(X(t)), \tag{13}$$

second, we define the global variables through

$$Y := G(X) \in \mathbb{R}^q.$$

and applying G to both sides in (13) we obtain the so-called aggregated system associated to system (12)

$$y(t+1) = (G \circ S \circ E)(y(t)) := \bar{s}(y(t)). \tag{14}$$

The next theorem relates the asymptotic behavior of systems (12) and (14) for large enough values of parameter k.

Theorem A.1 *Let us assume that F verify Hypotheses A.1 and A.2, and that*

$$\lim_{k \longrightarrow \infty} F^{(k)} = \bar{F} \text{ and } \lim_{k \longrightarrow \infty} DF^{(k)} = D\bar{F} \tag{15}$$

uniformly on any compact set $K \subset \Omega_N$.

Let $y^* \in \mathbb{R}^q$ be a hyperbolic equilibrium point of (14). Then there exists $k_0 \in \mathbb{N}$ such that for each $k \geq k_0$ there exists a hyperbolic equilibrium point X_k^* of (12) satisfying

$$\lim_{k \to \infty} X_k^* = X^*$$

where $X^* = E(y^*)$. Moreover,

1. *If y^* is asymptotically stable then X_k^* is asymptotically stable for each $k \geq k_0$, and if $X_0 \in \mathbb{R}^N$ is such that $\lim_{n \longrightarrow \infty} \bar{s}^{(n)}(y_0) = y^*$, where $y_0 = G(X_0)$, then*

$$\lim_{n \longrightarrow \infty} H_k^{(n)}(X_0) = X_k^*.$$

2. *If y^* is unstable then X_k^* is unstable, for each $k \geq k_0$.*

A.2 Appendix 2. Proofs.

Proof of proposition 3.2.- 1.- Consider any solution $(y_1(t), y_2(t))$ of the aggregated (5) such that $y_1(0) \neq 0$, $y_2(0) \neq 0$. The conditions $\phi_i(0,0) \leq 1$ imply that $0 < \phi_i(y_1, y_2) < 1$, so that $(y_1(t), y_2(t))$ is a strictly decreasing sequence bounded from below. Therefore, there exist $\tilde{y}_i = \lim_{t\to\infty} y_i(t)$. If $\tilde{y}_i \neq 0$, then $1 = \phi_i(\tilde{y}_1, \tilde{y}_2)$, which in contradiction with $\phi_i(0,0) \leq 1$. Thus $\tilde{y}_i = 0$ for $i = 1, 2$.

2.- Without lost of generality, we assume that $i = 1$. The fixed point equation is $1 = \phi_1(y_1, 0)$ and the conclusion follows from the fact that $\phi_1(y_1, 0)$ is a strictly decreasing function such that $\lim_{y_1\to\infty} \phi_1(y_1, 0) = 0$ ■

Proof of corollary 3.3.– We already know from proposition 3.2 that corollary 3.3 holds when $\phi_i(0,0) \leq 1$ for $i = 1, 2$.

Therefore, let us assume that $\phi_i(0,0) > 1$ for $i = 1$ or $i = 2$. In this case the desired result follows from theorem 5.2 in [30], and we proceed by showing that system (5) fulfills the hypotheses H1 up to H4 required there. Using the notation introduced in [30], we define $a = \sum_{j=1}^{p} b_1^j / c_{11}^j$ and $b = \sum_{j=1}^{p} b_1^j / c_{22}^j$ (so that $J = [0, a] \times [0, b]$) and $P(u, v) = (f_1(u, v), f_2(u, v)) : [0, \infty) \times [0, \infty) \to [0, \infty) \times [0, \infty)$ that is continuous.

Hypothesis H1 requires system (5) to be strictly competitive on J and strongly competitive on the interior of J (see page 338 in [30] for the precise definitions) which follow from statement 3 in proposition 3.1. Hypothesis H2 states that $(0, 0)$ is a repellor, which holds since $\phi_i(0,0) > 1$ for $i = 1, 2$. Hypothesis H3 is also meet by defining $\hat{u} = y_1^*$ and $\hat{v} = y_2^*$. Finally, from 2 in proposition 3.1 we get that $(f_1, f_2) : J \to J$ which yields hypothesis H4. ■

Proof of proposition 3.4.- Statement 1 follows easily using the proof of proposition 3.2 and corollary 3.3.

Regarding statement 2, thanks to corollary 3.3 we know that any solution $(y_1(t), y_2(t))$ of the aggregated system (5) converges to an equilibrium point (y_1^*, y_2^*). Condition $\phi_2(0,0) \leq 1$ implies that $y_2^* = 0$ and that it is the unique possible value for y_2^*. Therefore, the only possible equilibrium points of the reduced system are $(0, 0)$ and E_1^*. Note that $y_1(0) > 0$ implies that $y_1(t) > 0$ for all $t \geq 0$. Being ϕ_1 continuous in the positive cone, there exists $\delta > 0$ such that $\phi_1(y_1, y_2) > 1$ for all $(y_1, y_2) \in A =$

$\left\{0 < y_1,\, 0 < y_2, \quad 0 < \sqrt{y_1^2 + y_2^2} < \delta\right\}$. It means that $y_1(t)$ can not converge to 0 since, as soon as $(y_1(t), y_2(t)) \in A\; y_1(t{+}1) = \phi_1(y_1(t), y_2(t))y_1(t) > y_1(t)$. Therefore, E_1^* attracts any solution such that $y_1(0) \neq 0$.
A similar reasoning leads to prove statement 3. ■

Proof of proposition 3.8.– The proof is not difficult but laborious. The first equation of the fixed point equation associated to system (11) is equivalent to

$$\begin{aligned} &v_1(1-v_1)y_1^2 + \left[c_{12}(v_1+v_2-2v_1v_2)y_2 + 1 - 2b_1v_1(1-v_1)\right]y_1 \\ &+v_2(1-v_2)(c_{12})^2y_2^2 + c_{12}\left[1 - b_1(v_1+v_2-2v_1v_2)\right]y_2 + 1 - b_1 = 0. \end{aligned} \tag{16}$$

Given that $v_1(1-v_2) > 0$ we argue on the sign coefficient of y_1 and the intercept. We analyze first with the sign of the intercept of equation (16): let us consider

$$v_2(1-v_2)(c_{12})^2y_2^2 + c_{12}\left[1 - b_1(v_2+v_2-2v_1v_2)\right]y_2 + 1 - b_1 = 0. \tag{17}$$

It is straightforward than this equation (in y_2) has one positive root and one negative root too, since $v_2(1-v_2)(1-b_1) < 0$.

Then, we assume that the left hand side of (17) (the intercept of (16)) is negative for any positive values of y_2. Then, Descarte's rule implies that equation (16) possesses, at most, one positive solution, since $v_1(1-v_1) > 0$.

Instead, we assume now that the left hand side of (17) is positive and we focus on the sign of the coefficient of y_1 in equation (16)

$$c_{12}(v_1+v_2-2v_1v_2)y_2 + 1 - 2b_1v_1(1-v_1). \tag{18}$$

If it is positive, then there the real solutions of equation (16) are negative, if any. Otherwise equation (16) possesses up to two positive solutions. Still, we are only interested in positive values of y_2, so that

$$y_2 > \hat{y}_2 = \frac{-[1-b_1(v_1+v_2-2v_1v_2)]+\sqrt{[v_1+v_2-b_1(1-2v_1v_2)]^2-4v_2(1-v_2)(1-b_1)}}{2c_{12}v_2(1-v_2)} > 0.$$

Then, it follows from (18) that

$$\begin{aligned} &c_{12}(v_1+v_2-2v_1v_2)y_2 + 1 - 2b_1v_1(1-v_1) > \\ &c_{12}(v_1+v_2-2v_1v_2)\hat{y}_2 + 1 - 2b_1v_1(1-v_1) \end{aligned}$$

since $v_1 + v_2 - 2v_1v_2 > 0 \Leftrightarrow \frac{1}{v_1} + \frac{1}{v_2} > 2$, which always holds. The proof finishes by showing that

$$c_{12}(v_1 + v_2 - 2v_1v_2)\hat{y}_2 + 1 - 2b_1v_1(1 - v_1) > 0$$

which, replacing the $\hat{y}_2$ by its value, is equivalent to

$$\begin{aligned}&(v_1 + v_2 - 2v_1v_2)\left(b_1(v_1 + v_2 - 2v_1v_2) - 1\right)\\ &+(v_1 + v_2 - 2v_1v_2)\sqrt{\left[v_1 + v_2 - b_1(1 - 2v_1v_2)\right]^2 - 4v_2(1 - v_2)(1 - b_1)}\\ &+2v_2(1 - v_2)\left(1 - 2b_1v_1(1 - v_1)\right) > 0.\end{aligned}$$

The previous inequality holds if

$$(v_1 + v_2 - 2v_1v_2)\left(b_1(v_1 + v_2 - 2v_1v_2) - 1\right) + 2v_2(1 - v_2)\left(1 - 2b_1v_1(1 - v_1)\right) > 0.$$

Note that $v_1 + v_2 - 2v_1v_2 = v_1(1 - v_2) + v_2(1 - v_1)$ and, rearranging terms, the previous inequality is equivalent to

$$b_1(v_1(1 - v_2) - v_2(1 - v_1))^2 + (v_1 - v_2)(1 - 2v_2)) > 0$$

Finally, calculating the maximum and minimum of functions

$$\psi_1(v_1, v_2) = b_1(v_1(1 - v_2) - v_2(1 - v_1))^2, \qquad \psi_2(v_1, v_2) = (v_1 - v_2)(1 - 2v_2))$$

in the square $[0, 1] \times [0, 1]$ finishes the proof. ■

Proof of proposition 3.10.– Direct calculations show that one of the eigenvalues of the corresponding jacobian matrix is always in modulus less that 1 while and the other one

$$\lambda_1(v_1, v_2) := \frac{b_2v_2}{1 + c_{21}v_1y_1^*} + \frac{b_2(1 - v_2)}{1 + c_{21}(1 - v_1)y_1^*}, \tag{19}$$

where we have written $v_1 = v_{11}$ and $v_2 = v_{21}$, can be larger or less than 1. We can calculate explicitly y_1^*, that depends n v_1 and replace its expression in (19). It can be shown that $y_1^*(v_1)$ is symmetric in the $[0, 1]$ interval with respect to 1/2. Moreover, it is monotone increasing in $[0, 1/2]$,

$$\lim_{v_1 \to 0} y_1^*(v_1) = b_1 - 1 \qquad \text{and} \qquad \lim_{v_1 \to 1/2} y_1^*(v_1) = 2(b_1 - 1).$$

Then, it is straightforward that $\lambda_1(0,0) = \frac{b_2}{1+c_{12}(b_1-1)} = \lambda_1(1,1)$, $\lambda_1(1,0) = b_2 = \lambda_1(0,1) > 1$ while $\lambda_2(0,0) = \frac{b_1}{1+c_{21}(b_2-1)} = \lambda_2(1,1)$ and $\lambda_2(1,0) = b_1 = \lambda_2(0,1) > 1$. Then, there exist a neighborhood of $(v_1, v_2) = (1,0)$ and $(v_1, v_2) = (0,1)$ inside the unit square where conditions $\phi_i(E_j^*) > 1$, for $i \neq j$, $i, j = 1, 2$ hold. ■

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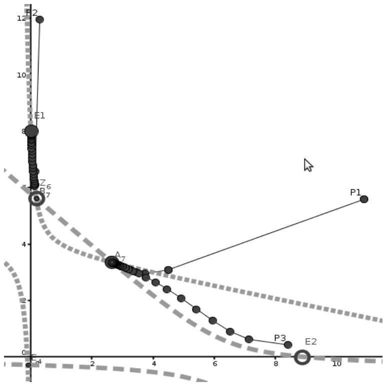


Figure 1: In gray, the nullclines. $E1$, $E5$ asymptotically stable equilibrium points. $E2$, $E3$ unstable equilibrium points. Each polygonal displays an orbit with initial values at P_1, P_2 and P_3, respectively. $b_1^1 = 7$, $b_1^2 = 8.5$, $b_2^1 = 1.5$, $b_2^2 = 5$, $c_{12}^1 = 5$, $c_{12}^2 = 4.5$, $c_{21}^1 = 13$, $c_{21}^2 = 3.5$, $v_{11} = 0.95$, $v_{21} = 0.2$.

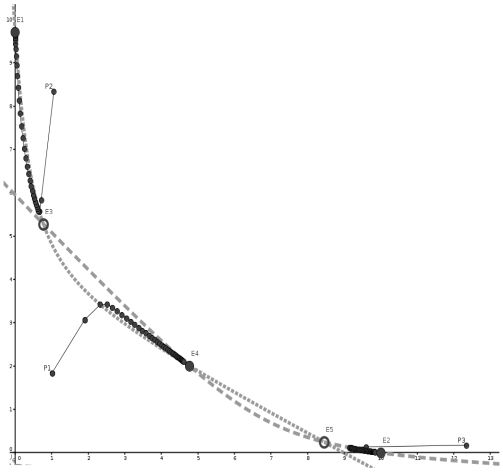
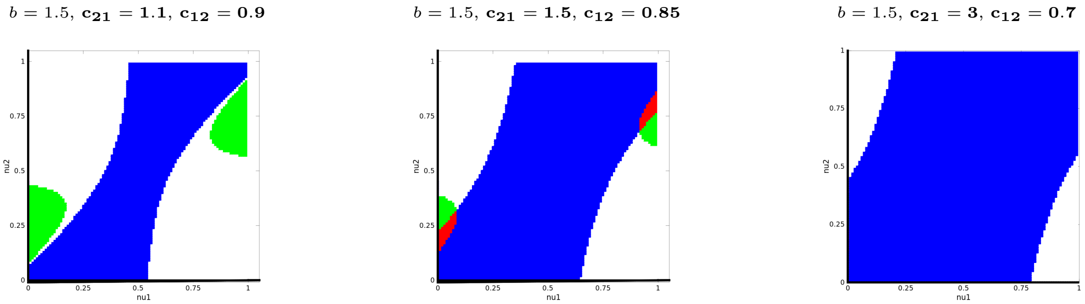


Figure 2: In gray, the nullclines. $E1$, $E2$, $E5$ asymptotically stable equilibrium points. $E3$, $E4$ unstable equilibrium points. Each polygonal displays an orbit with initial values at P_1, P_2 and P_3, respectively. $b_1^1 = 7.5$, $b_1^2 = 6.5$, $b_2^1 = 2$, $b_2^2 = 5$, $c_{12}^1 = 5$, $c_{12}^2 = 4.5$, $c_{21}^1 = 5.5$, $c_{21}^2 = 3.5$, $v_{11} = 0.9$, $v_{21} = 0.2$.



$b = 1.5$, $\mathbf{c_{21} = 1.1}$, $\mathbf{c_{12} = 0.9}$

$b = 1.5$, $\mathbf{c_{21} = 1.5}$, $\mathbf{c_{12} = 0.85}$

$b = 1.5$, $\mathbf{c_{21} = 3}$, $\mathbf{c_{12} = 0.7}$

Figure 3: Competition outcome as a function of asymptotic distribution of individuals. Parameter ν_i stands for the asymptotic fraction of individuals of species $i = 1, 2$ at patch i. In blue: species 2 exclusion, in white, coexistence, in red conditional extinction, in green species 1 exclusion.