The limits of fast and slow symmetric dispersal in single-species discrete diffusion system

Bilel Elbetch, Tounsia Benzekri, Daniel Massart, Tewfik Sari

The limits of fast and slow symmetric dispersal in single-species discrete diffusion system

Bilel Elbetch[1], **Tounsia Benzekri** [2], **Daniel Massart** [3], **Tewfik Sari** [4]

[1] Department of Mathematics, University Dr. Moulay Tahar of Saida, Algeria,
[2] Department of Mathematics, USTHB, Bab Ezzouar, Algiers, Algeria,
[3] IMAG, Univ Montpellier, CNRS, Montpellier, France,
[4] ITAP, Univ Montpellier, INRAE, Institut Agro, Montpellier, France.

[1]bilel.elbetch@univ-saida.dz, [2]tbenzekri@usthb.dz,
[3]daniel.massart@umontpellier.fr, [4]tewfik.sari@inrae.fr.

ABSTRACT

The paper considers a n-patch model with migration terms, where each patch follows a logistic law. In the case of perfect mixing, i.e when the migration rate tends to infinity, the total population follows a logistic law with a carrying capacity which in general is different from the sum of the n carrying capacities.

1. Introduction

Population dynamics is a wide field of mathematics, which contains many problems, for example fragmentation of population and the effect of migration in the general dynamics of population. Bibliographies can be found in the work of Levin [7, 8] and Holt [6]. There are ecological situations that motivate the representation of space as a finite set of patches connected by migrations, for instance an archipelago with bird population and predators. It is an example of insular bio-geography. The standard question in this type of biomathematical problems, is to study the effect of migration on the general population dynamics, and the consequences of fragmentation on the persistence or extinction of the population. Our aim is to extend some of the results in [1, 2, 3, 4] to the more general case of the n-patch model:

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta \sum_{j=1, j\neq i}^{n} \gamma_{ij}\left(x_j - x_i\right), \qquad i = 1, \cdots, n. \tag{1.1}$$

where n is the number of the patches in the system. The parameter β represents the dispersal rate of the population; $\gamma_{ij} = \gamma_{ji} \geq 0$ denotes the flux between patches j and i, for $j \neq i$. Note that if $\gamma_{ij} > 0$ there is a flux of migration between patches i and j and if $\gamma_{ij} = 0$ there is no migration. In the case where $\beta = 0$, there is no migration , and the system (1.1) admits $(K_1, \cdots, K_n)$ as a non trivial equilibrium point, which furthermore is globally asymptotically stable (GAS). The problem is whether or not, the equilibrium continues to be positive and GAS for any $\beta > 0$. In this work our aim is to study the behavior of the system (1.1) for large migration rate, i.e when $\beta \to \infty$.

2. Mathematical model

We consider the model of multi-patch logistic growth, coupled by symmetric migration terms (1.1). This system of differential equations can be written:

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) + \beta \sum_{j=1}^{n} \gamma_{ij} x_j, \qquad i = 1, \cdots, n \tag{2.1}$$

where

$$\gamma_{ii} = -\sum_{j=1, j\neq i}^{n} \gamma_{ij}, \qquad i = 1, \cdots, n \tag{2.2}$$

denotes the outgoing flux of patch i. We denote by Γ the matrix

$$\Gamma := (\gamma_{ij})_{n\times n}. \tag{2.3}$$

Its columns sum to 0 since the matrix Γ is symmetric and the diagonal elements γ_{ii} are defined by (2.2) in such a way that each row sums to 0. The matrix

$$\Gamma_0 := \Gamma - \mathrm{diag}(\gamma_{11}, \ldots, \gamma_{nn}) \tag{2.4}$$

which is the same as Γ, except that the diagonal elements are 0, is called the connectivity matrix. It is the adjacency matrix of the weighted directed graph $\mathcal{G}$, which has exactly n vertices (the patches), and there is an arrow from patch j to patch i precisely when $\gamma_{ij} > 0$, with weight γ_{ij} assigned to the arrow.
We have the following result:

Proposition 2.1. *The domain*

$$\Omega = \{(x_1, \ldots, x_n) \in \mathbb{R}^n / x_i \geq 0, i = 1, \ldots, n.\}$$

is positively invariant for the system (1.1).

For the global stability of the model, we have the result:

Proposition 2.2. *Assume that the matrix $\Gamma := (\gamma_{ij})_{n\times n}$ (or equivalently, the connectivity matrix Γ_0) is irreducible. The model* (1.1) *has a unique positive equilibrium point which is GAS in the positive cone $\mathbb{R}^n_+ \setminus \{0\}$.*

Proof. The result follows from [9]. □

Remark 2.1. *The matrix Γ being irreducible means that the set of patches cannot be partitioned into two nonempty disjoint subsets, I and J, such that there is no migrations between a patch in subset I and a patch in subset J. The matrix Γ is assumed to be irreducible throughout the rest of the paper. Therefore species can reach any patch from any patch either directly or through other patches.*

In all of this work, the GAS equilibrium of the system (1.1), whose existence is shown in Proposition 2.2, is denoted by $E^*(\beta) = (x_1^*(\beta), \ldots, x_n^*(\beta))$ and the total equilibrium population by:

$$X_T^*(\beta) = x_1^*(\beta) + \cdots + x_n^*(\beta), \tag{2.5}$$

3. The limits of fast symmetric dispersal

In this section our aim is to study the behavior of the system (1.1) for large migration rate, i.e when $\beta \to \infty$. We need the following result:

Lemma 3.1. *The matrix Γ has rank $n-1$. Except 0 which is a simple eigenvalue of Γ, whose eigenvector is $u = (1, \ldots, 1)^T$, all other eigenvalues of Γ are negative.*

We have the following result:

Theorem 3.1. *We have*

$$\lim_{\beta \to +\infty} E^*(\beta) = \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n r_i/K_i}(1, \ldots, 1).$$

As a corollary of the previous theorem we obtain the following result which describes the total equilibrium population for perfect mixing:

Corollary 3.1. *We have*

$$X_T^*(+\infty) = \lim_{\beta \to +\infty} \sum_{i=1}^{n} x_i^*(\beta) = n\frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n r_i/K_i}. \tag{3.1}$$

Proposition 3.1. *If $\alpha_1 = \cdots = \alpha_n =: \alpha$, then $X_T^*(+\infty) = \sum_{i=1}^n K_i$.*

Proof. We use Equation (3.1) for $\alpha_1 = \cdots = \alpha_n =: \alpha$. □

We can use the theory of singular perturbations and theorem of Tikhonov [10, 11] to obtain a better understanding of the behaviour of the system in the case of perfect mixing.

Theorem 3.2. *Let $(x_1(t,\beta), \ldots, x_n(t,\beta))$ be the solution of the system* (1.1) *with initial condition $(x_{10}, \cdots, x_{n0})$ satisfying $x_{i0} \geq 0$ for $i = 1 \cdots n$. Let $Y(t)$ be the solution of the logistic equation*

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{nK}\right), \text{ where } r = \frac{\sum_{i=1}^n r_i}{n} \text{ and } K = \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n r_i/K_i}, \tag{3.2}$$

with initial condition $Y(0) = \sum_{i=1}^n x_{i0}$. Then, when $\beta \to \infty$, we have

$$\sum_{i=1}^{n} x_i(t,\beta) = Y(t) + o(1), \qquad \text{uniformly for } t \in [0, +\infty) \tag{3.3}$$

and, for any $t_0 > 0$, we have

$$x_i(t,\beta) = \frac{Y(t)}{n} + o(1), \quad i = 1, \ldots, n, \quad \text{uniformly for } t \in [t_0, +\infty). \tag{3.4}$$

In the case of fast dispersal, the approximation (3.3) shows that the total population behaves like the unique logistic equation (3.2) and then, when t and β tend to ∞, the total population $\sum x_i(t,\beta)$ tends toward $nK = n\sum r_i / \sum \alpha_i$, where $\alpha_i = r_i/K_i$, as stated in Corollary 3.1. The approximation (3.4) shows that, with the exception of a thin initial boundary layer, where the population density $x_i(t,\beta)$ quickly jumps from its initial condition x_{i0} to the average $Y(0)/n$, each patch of the n-patch model behaves like the single logistic equation

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right), \text{ where } r = \frac{1}{n}\sum_{i=1}^n r_i \text{ and } K = \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n r_i/K_i}. \tag{3.5}$$

Hence, when t and β tend to ∞, the population density $x_i(t,\beta)$ tends toward $K = \sum r_i / \sum \alpha_i$, as stated in Theorem 3.1.

Remark 3.1. *The single logistic equation (3.5) gives an approximation of the population density in each patch in the case of fast dispersal. The intrinsic growth rate r is the arithmetic mean of the local intrinsic growth rates r_i and the carrying capacity K is the weighted harmonic mean of the local carrying capacities K_i with weights the growth rates r_i.*

Remark 3.2. *Notice that if we use the r-α formalism for the logistic equation, instead of the r-K formalism, where $\alpha = r/K$ is the parameter quantifying intraspecific competition, then the n-patch model (1.1) becomes*

$$\frac{dx_i}{dt} = r_i x_i - \alpha_i x_i^2 + \beta \sum_{j=1, j\neq i}^{n} \gamma_{ij}\left(x_j - x_i\right), \qquad i = 1, \cdots, n.$$

The perfect mixing approximation (3.5) of each population x_i becomes

$$\frac{dx}{dt} = rx - \alpha x^2, \text{ where } r = \frac{1}{n}\sum_{i=1}^n r_i \text{ and } \alpha = \frac{1}{n}\sum_{i=1}^n \alpha_i,$$

which is a single logistic equation whose intrinsic growth rate r and intraspecific competition parameter α are the arithmetic means of the local r_i and α_i respectively.

4. conclusion

The goal of this paper was to generalize to a multi-patch model the results obtained in [1] for a two-patch model. The migration between patches is modeled by a symmetric Metzler matrix, called the connectivity matrix. When the connectivity matrix is irreducible, the system is shown (Prop. 2.2) to have a unique nontrivial equilibrium, which furthermore is globally asymptotically stable.
we looked at another particular case, that of perfect mixing, when the migration rate goes to infinity, in other words, when there is no restriction whatsoever on travel. We computed the equilibrium in this situation, and by perturbation arguments (see [10, 11]), we proved that the dynamics in this ideal case provide a good approximation to the case when the migration rate is large.

References

[1] R. Arditi, C. Lobry and T. Sari, In dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation, Theoretical Population Biology, **106** (2015), 45-59. http://doi:10.1016/j.tpb.2015.10.001.

[2] R. Arditi, C. Lobry and T. Sari, Asymmetric dispersal in the multi-patch logistic equation, Theoretical Population Biology, **120** (2018), 11-15. http://doi:10.1016/j.tpb.2017.12.006.

[3] D. L. DeAngelis and B. Zhang, Effects of dispersal in a non-uniform environment on population dynamics and competition: a patch model approach, Discrete Contin. Dyn. Syst. Ser. B, **19** (2014), 3087-3104. http://dx.doi.org/10.3934/dcdsb.2014.19.3087.

[4] D. L. DeAngelis, Wei-Ming Ni and B. Zhang, Effects of diffusion on total biomass in heterogeneous continuous and discrete-patch systems, Theoretical Ecology, **9** (2016), 443-453. http://doi10.1007/s12080-016-0302-3.

[5] B. Elbetch, T. Benzekri , D. Massart and T. Sari, The multi-patch logistic equation, Discrete and Continuous Dynamical System series B 22 (2020). http://dx.doi.org/10.3934/dcdsb.2021025

[6] R. D. Holt, Population dynamics in two patch environments: some anomalous consequences of an optimal habitat distribution, Theoretical Population Biology, **28** (1985), 181-201. http://dx.doi.org/10.1016/0040-5809(85)90027-9.

[7] S. A. Levin, Dispersion and population interactions, Amer. Natur, **108** (1974), 207-228. https://doi.org/10.1086/282900.

[8] S. A. Levin, Spatial patterning and the structure of ecological communities, in Some Mathematical Questions in Biology VII, Vol. **8**, Amer. Math. Sot., Providence, RI., 1976.

[9] Y. Takeuchi, Cooperative systems theory and global stability of diffusion models, Acta Applicandae Mathematicae, **14** (1989), 49–57. https://doi.org/10.1007/978-94-009-2358-4_6.

[10] A. N. Tikhonov, Systems of differential equations containing small parameters in the derivatives, Mat. Sb. (N.S.), **31** (1952), 575-586. http://refhub.elsevier.com/S0040-5809(15)00102-1/sbref18.

[11] W. R. Wasow, Asymptotic Expansions for Ordinary Differential Equations, Robert E. Krieger Publishing Company, Huntington, NY, 1976.