



# Global dynamics for Lotka–Volterra systems with infinite delay and patch structure



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## ABSTRACT

We study some aspects of the global dynamics of an  $n$ -dimensional Lotka–Volterra system with infinite delay and patch structure, such as extinction, persistence, existence and global asymptotic stability of a positive equilibrium. Both the cases of an irreducible and reducible linear community matrix are considered, and no restriction on the signs of the intra- and inter-specific delayed terms is imposed. Although the system is not cooperative, our approach often uses comparative results with an auxiliary cooperative system. Some models in recent literature are generalized, and results improved.

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## 1. Introduction

In recent years, mathematicians and biologists have been analyzing biological models given by systems of differential equations with time-delays and patch-structure. On one hand, models with patch-structure are frequently quite realistic, for example in population dynamics, when the growth of single or multiple species populations depends on the resources of each particular patch of an heterogeneous environment, or on other biological features such as age or size. Therefore, the populations are distributed over several different patches or classes, with interactions and migration among them. Additionally, time-delays are very often present in models from population dynamics, neurosciences, ecology, epidemiology, chemistry and other sciences. Moreover, infinite delays have been considered in equations used in mathematical biology since the works of Volterra, to translate the cumulative effect of the past history of a system. Typically, the “memory functions” appear as integral kernels and, although defined in the entire past, the delay should be introduced in such a way that its effect diminishes when going back in time.

In this paper, the following patch-structured Lotka–Volterra system with both infinite distributed and discrete delays is considered:

$$x'_i(t) = x_i(t) \left( \beta_i - \mu_i x_i(t) - \sum_{j=1}^n a_{ij} \int_0^\infty K_{ij}(s) x_j(t-s) ds \right) + \sum_{j \neq i, j=1}^n d_{ij} x_j(t - \tau_{ij}), \quad i = 1, \dots, n. \quad (1.1)$$

Here,  $\beta_i \in \mathbb{R}$ ,  $\mu_i > 0$ ,  $a_{ij} \in \mathbb{R}$ ,  $d_{ij} \geq 0$ ,  $\tau_{ij} \geq 0$ ,  $i, j = 1, \dots, n$ ; the kernels  $K_{ij} : [0, \infty) \rightarrow [0, \infty)$  are  $L^1$  functions, normalized so that

$$\int_0^\infty K_{ij}(s) ds = 1, \quad \text{for } i, j = 1, \dots, n. \quad (1.2)$$

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Moreover, we suppose that for all  $i$  the linear operators defined by  $L_{ii}(\varphi) = \int_0^\infty K_{ii}(s)\varphi(-s)ds$ , for  $\varphi : (-\infty, 0] \rightarrow \mathbb{R}$  bounded, are non-atomic at zero, which amounts to have  $K_{ii}(0) = K_{ii}(0^+)$ .

We have in mind to apply our results to the concrete model

$$x'_i(t) = x_i(t) \left( b_i - \mu_i x_i(t) - \sum_{j=1}^n a_{ij} \int_0^\infty K_{ij}(s)x_j(t-s)ds \right) + \sum_{j \neq i, j=1}^n (\varepsilon_{ij} \alpha_{ij} x_j(t - \tau_{ij}) - \alpha_{ji} x_i(t)), \quad i = 1, \dots, n, \quad (1.3)$$

where,  $\mu_i > 0$ ,  $b_i, a_{ij} \in \mathbb{R}$ , and, for  $i \neq j$ ,  $\alpha_{ij} \geq 0$ ,  $\tau_{ij} \geq 0$ ,  $\varepsilon_{ij} \in (0, 1]$ , and the kernels  $K_{ij}$  are as above. Denoting

$$d_{ij} := \varepsilon_{ij} \alpha_{ij} \text{ for } i \neq j, \quad \beta_i := b_i - \sum_{j \neq i} \alpha_{ji},$$

(1.3) reads as (1.1). System (1.3) serves as a population model for the growth of single or multiple species gathered in  $n$  different patches or classes:  $x_i(t)$  is the density of the population on patch  $i$ , with  $b_i$  and  $\mu_i$  as its usual Malthusian growth rate and (instantaneous) self-limitation coefficient, respectively;  $a_{ii}$  and  $a_{ij}$  ( $i \neq j$ ) are respectively the intra- and inter-specific delayed acting coefficients;  $\alpha_{ij}$  ( $i \neq j$ ) are the dispersal rates of populations moving from patch  $j$  to patch  $i$ , and  $\tau_{ij}$  the times taken during this dispersion; the coefficients  $\varepsilon_{ij} \in (0, 1]$  appear to account for some loss of the populations during migration from one patch to another. Frequently, one takes  $\varepsilon_{ij} = e^{-\gamma_{ij}\tau_{ij}}$  for some  $\gamma_{ij} > 0$ ,  $i, j = 1, \dots, n$ ,  $i \neq j$ , cf. e.g. [20].

Here, some aspects of the asymptotic behavior of solutions to delayed Lotka–Volterra systems (1.1) will be analyzed. Although not very meaningful in biological terms, all the techniques and results in this paper apply to more general systems with several bounded delays or even infinite delays in the migration terms, of the form

$$x'_i(t) = x_i(t) \left( \beta_i - \mu_i x_i(t) - \sum_{j=1}^n a_{ij} \int_0^\infty x_j(t-s) d\eta_{ij}(s) \right) + \sum_{j \neq i, j=1}^n \sum_{p=1}^m d_{ij}^{(p)} x_j(t - \tau_{ij}^{(p)}), \quad i = 1, \dots, n, \quad (1.4)$$

or

$$x'_i(t) = x_i(t) \left( \beta_i - \mu_i x_i(t) - \sum_{j=1}^n a_{ij} \int_0^\infty x_j(t-s) d\eta_{ij}(s) \right) + \sum_{j \neq i, j=1}^n d_{ij} \int_0^\infty x_j(t-s) dv_{ij}(s), \quad i = 1, \dots, n, \quad (1.5)$$

where  $d_{ij}^{(p)}, \tau_{ij}^{(p)} \geq 0$ , the other coefficients are as in (1.1), and  $\eta_{ij}, v_{ij} : [0, \infty) \rightarrow \mathbb{R}$  are bounded and non-decreasing functions with total variation one, for all  $i, j$ . Most of our techniques also apply to non-autonomous systems with time-dependent bounded delays  $\tau_{ij}(t) \geq 0$ .

Due to the biological interpretation of the model, only positive or non-negative solutions should be considered admissible. On the other hand, there are natural constraints on admissible phase spaces for functional differential equations (FDEs) with infinite delay (cf. Section 2): not only a careful choice of a so-called ‘admissible space’ as a phase space is in order, see e.g. [11,12], but also one must consider *bounded* initial conditions. Thus, solutions of (1.1) are required to have initial conditions of the form

$$x_i(\theta) = \varphi_i(\theta), \quad \theta \in (-\infty, 0], \quad i = 1, \dots, n, \quad (1.6)$$

where  $\varphi_i$  are non-negative, bounded continuous functions on  $(-\infty, 0]$ . For the framework of Sections 4 and 5, additionally the functions  $\varphi$  are supposed to be bounded away from zero on  $(-\infty, 0]$ .

There is an immense literature on FDEs of the Lotka–Volterra type, and it is impossible to mention all the relevant contributions. The present investigation was motivated by several papers, among them those of Takeuchi et al. [19,20], Liu [15], and Faria [3,4]. For other related papers, we refer to [2,5,16,21], also for further references.

In [15], Liu considered a cooperative model for a species following a delayed logistic law, with the population structured in several classes and no delays in the migration terms, of the form

$$x'_i(t) = x_i(t) \left[ b_i - \mu_i x_i(t) + \sum_{p=1}^m c_i^{(p)} x_i(t - \sigma_i^{(p)}) \right] + \sum_{j=1}^n d_{ij} x_j(t), \quad i = 1, \dots, n, \quad (1.7)$$

where  $\mu_i, b_i > 0$  and  $c_i^{(p)}, d_{ij}, \sigma_i^{(p)} \geq 0$  for  $i, j = 1, \dots, n, p = 1, \dots, m$ . In [15] only the case of  $D = [d_{ij}]$  an irreducible matrix was studied. Furthermore, the quite restrictive conditions  $(b_i + \sum_{j=1}^n d_{ij}) / (\mu_i - \sum_{p=1}^m c_i^{(p)}) = k$  for  $1 \leq i \leq n$  ( $k$  a positive constant) were imposed, so that  $x^* = (k, \dots, k)$  is an equilibrium. On the other hand, Takeuchi et al. [20] studied the system

$$x'_i(t) = x_i(t) (b_i - \mu_i x_i(t)) + \sum_{j \neq i, j=1}^n (e^{-\gamma_{ij}\tau_{ij}} \alpha_{ij} x_j(t - \tau_{ij}) - \alpha_{ji} x_i(t)), \quad i = 1, \dots, n, \quad (1.8)$$

where  $\mu_i > 0$ ,  $b_i \in \mathbb{R}$  and  $\alpha_{ij}, \tau_{ij}, \gamma_{ij} \geq 0$  for  $i, j = 1, \dots, n, j \neq i$ . Note that (1.3) is a natural generalization of (1.8), obtained by the addition of interacting terms with infinite delay. Again, only the case of an irreducible matrix  $D = [d_{ij}]$ , where now  $d_{ij} = e^{-\gamma_{ij}\tau_{ij}} \alpha_{ij}$ ,  $d_{ii} = 0$ , was studied in [20].

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