

# Conspecific Support in Competitive Systems as a Pattern Formation Mechanism

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**Abstract.** The long term properties, like co-existence and extinction, are usually determined by the demographics of the competing species or other competitive advantages. In this paper we consider the effect of conspecific support on the co-existence of species. We show that, even if the competing species have the same demographics and interaction, their co-existence can be destabilized by sufficient level of conspecific support. When considering large number of species the conspecific support destabilizes the co-existence equilibrium, thus producing a pattern of extinction and varied levels of existence. Upscaling the model to continuous space variable leads to model of pattern formation via local self-activation and lateral inhibition.

## Introduction

Conspecific support is common survival strategy used by living organisms. It is typically local and is manifested differently for different species, e.g. biofilms of bacteria, packs of dogs, herds of grazers, patches of grass in arid areas, patches of forest in savanna, etc. The basic mechanisms for conspecific support are joint defence, joint acquisition and retention of resources, better mating opportunities, etc. The conspecific support usually results in the so called Allee Effect - positive correlation between the per capita growth rate and the population density when the population density is sufficiently small, [8]. When conspecific support is essential for survival at low population density, we have a strong Allee Effect, characterised by the existence of minimum survival level, below which the species goes extinct.

In this paper we show the importance of conspecific support for competing species or subpopulation groups. More precisely, in the case of two competing species, the conspecific support may destabilize a qualified competition co-existence. In the case of  $n$  species the same mechanism leads to pattern of existence and extinction, which in essence is a mathematical representation of the Gierer-Meinhardt theory of pattern formation via local self-activation and lateral inhibition, [3], [6]. The model is upscaled from discrete to a continuous space variable by using nonlocal integral operators. The obtained model is already discussed in [4], [1]. It is interesting to establish the link with discrete space models with conspecific support.

## Model of two competing species

Let us consider first a general system of two competing species of Kolmogorov-type

$$\frac{du}{dt} = ug_1(u, v), \quad (1)$$

$$\frac{dv}{dt} = vg_2(u, v), \quad (2)$$

where  $g_1$  and  $g_2$  are smooth real functions defined on  $\mathbb{R}_+^2$ . Competition of the species implies that  $g_1(u, v)$  is decreasing on  $v$  and that  $g_2(u, v)$  is decreasing on  $u$ . We study (1)–(2) as a dynamical system. A common references on the topic is [9]. Our main interest is in the existence or extinction of any the species. We recall the following definition.

**Definition 1** A population with size or spatial density  $u = u(t)$ ,  $t \in [0, +\infty)$  is said to be uniformly strongly persistent if there exists  $\varepsilon > 0$  such that for every  $u(0) > 0$  we have  $\liminf_{t \rightarrow +\infty} u(t) \geq \varepsilon$ , [7].

Equivalently, uniform strong persistence of a population means that for any positive initial state the populations are uniformly bounded away from zero for sufficiently large  $t$ .

We make the following *assumption* regarding the two populations modelled in (1)–(2):

*Each population in the absence of the other has a unique positive equilibrium, which is globally asymptotically stable on  $(0, +\infty)$ .* (3)

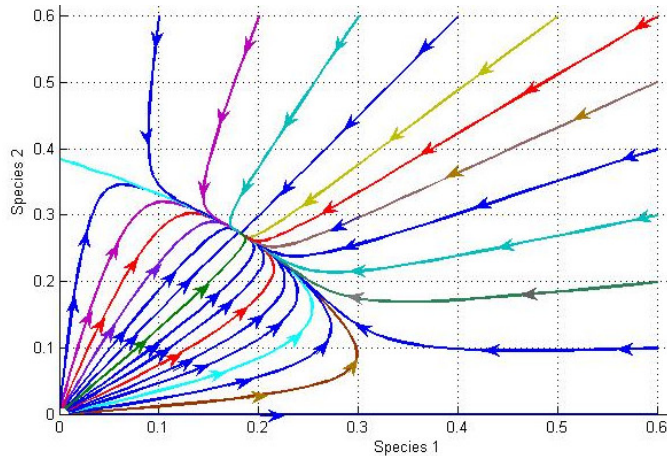
We denote these equilibria by  $p$  and  $q$ , respectively.

**Theorem 1** The model (1)–(2) defines a positive dynamical system on  $\mathbb{R}_+^2$ . Further, both populations uniformly strongly persist if and only if  $g_1(0, q) > 0$  and  $g_2(p, 0) > 0$ .

**Proof:** The proof comprises the following three steps:

- (i) The coordinate axes are invariant set. Hence, so is  $\mathbb{R}_+^2$ .
- (ii) It follows from the assumption (3) that the set  $[0, p] \times [0, q]$  is positively invariant and attractive.
- (iii) Using the condition on  $g_1$  and  $g_2$  given in the theorem and the competition assumption, we obtain that the interval  $[0, p]$  on the  $x$ -axis and the interval  $[0, q]$  on the  $y$ -axis are both positively invariant and repelling subsets of  $[0, p] \times [0, q]$ . The uniform persistence then follows from the compactness of  $[0, p] \times [0, q]$ .

□



**FIGURE 1.** Typical trajectories of the solutions of (4)–(5) under qualified competition.

**Example:** The system with linear per capita growth rate [2, Section 5.1].

$$\frac{du}{dt} = u(1 - au - bv), \quad (4)$$

$$\frac{dv}{dt} = v(1 - cu - dv), \quad (5)$$

where  $a, b, c, d$  are positive constants. For this system the competition is called *qualified* or *weak* if  $a > c$  and  $d > b$ . As an easy consequence of Theorem 1 we obtain that if the competition is qualified, then both species uniformly strongly persist. Indeed, for this example we have  $g_1(u, v) = 1 - au - bv$ ,  $g_2(u, v) = 1 - cu - dv$ ,  $p = \frac{1}{a}$ ,  $q = \frac{1}{d}$ . Hence,  $g_1(0, q) = 1 - \frac{b}{d} > 0$  and  $g_2(p, 0) = 1 - \frac{c}{a} > 0$ . Therefore, Theorem 1 applies. Further, one can also show that, the system has a positive equilibrium, which is globally asymptotically stable on the interior of  $\mathbb{R}_+^2$ , as illustrated in Figure 1.

### Model of two competing species with conspecific support

We model the conspecific support multiplying the per capita growth rate by a linear factor. We exclude from this operation the density independent mortality rate, which reflects the maximum life-span of the species and is independent of conditions or support. In this way we obtain from (1)–(2) the following system

$$\frac{du}{dt} = u(1 + \beta_1 u)(g_1(u, v) + \mu_1) - \mu_1 u, \quad (6)$$

$$\frac{dv}{dt} = v(1 + \beta_2 v)(g_2(u, v) + \mu_2) - \mu_2 v, \quad (7)$$

where  $\beta_1, \beta_2$  are coefficients in the respective linear factors and  $\mu_1, \mu_2$  are the density independent death rates of the two species. For  $\beta_1 = \beta_2 = 0$  the system (6)–(7) is exactly (1)–(2). For positive values of  $\beta_1$  and/or  $\beta_2$  the model (6)–(7) is of the same form as (1)–(2) with right-hand sides

$$\begin{aligned}\tilde{g}_1(u, v) &= (1 + \beta_1 u)(g_1(u, v) + \mu_1) - \mu_1, \\ \tilde{g}_2(u, v) &= (1 + \beta_2 v)(g_2(u, v) + \mu_2) - \mu_2.\end{aligned}$$

It is easy to see that if  $\beta_1$  is sufficiently large then for small population the per-capita growth rate of the first species increases as  $x$  increases. This is the so called Allee Effect. More precisely, due to the specific form chosen for representing the conspecific support, we have a weak Allee Effect, since there is no additional positive equilibrium generated by the conspecific support. Similar argument holds for the second species. Let us note that in the strong Allee Effect we have an unstable positive equilibrium referred to as a minimum survival density. We show that a type of conspecific support resulting only in weak Allee Effect may destabilize the co-existence of the species. Indeed,  $\tilde{g}_1(x, 0)$  has a root  $\tilde{p}(\beta_1, \mu_1) > p$ . Then, if  $g_2$  is unbounded below and  $\tilde{p}(\beta_1, \mu_1)$  is sufficiently large, we have  $\tilde{g}_2(\tilde{p}, 0) = g_2(\tilde{p}, 0) < 0$ , that is, the second species does not persist uniformly.

Similar consideration holds for the root  $\tilde{q}(\beta_2, \mu_2)$  of  $\tilde{g}_2(0, y)$  and the persistence of first species.

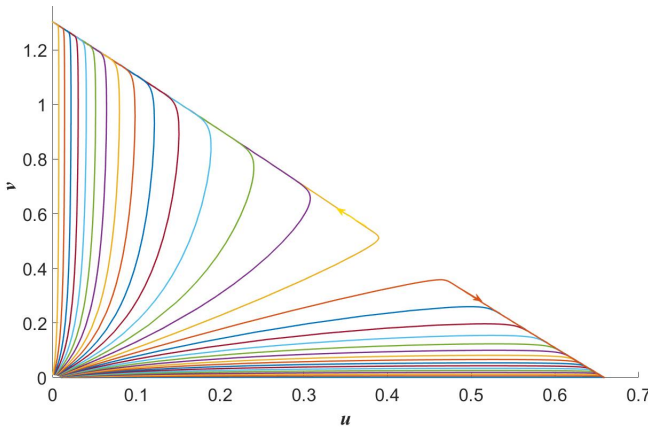
**Example:** Destabilizing the qualified competition equilibrium.

The model (6)–(7) in the case of the example (4)–(5) has the form

$$\begin{aligned}\frac{du}{dt} &= u(1 + \beta u)(1 + \mu - au - bv) - \mu u, \\ \frac{dv}{dt} &= v(1 + \beta v)(1 + \mu - cu - dv) - \mu v.\end{aligned}\tag{8}$$

We deliberately choose the constants related to conspecific support to be the same for the two species in order to illustrate that the destabilization of co-existence is not a result of any competitive advantage of one over species the other.

**Theorem 2** *If  $\mu > \frac{a}{c} - 1 > 0$ , there exists  $\beta_{crit}$  such that for the model (8)–(9) we have  $\tilde{g}_2(\tilde{p}(\beta, \mu), 0) < 0$  and  $\tilde{g}_1(0, \tilde{q}(\beta, \mu)) < 0$  for  $\beta > \beta_{crit}$ .*



**FIGURE 2.** Typical trajectories of the solutions of (8)–(9) for  $\beta > \beta_{crit}$ . Parameter values:  $a = 2.1$ ,  $c = 2$ ,  $d = 1.1$ ,  $b = 1$ ,  $\beta = 5$ ,  $\mu = 0.5$ .

Similarly, there exists  $\beta_{crit}^{(2)}$  such that  $\tilde{g}_1(0, \tilde{q}(\beta)) < 0$  for  $\beta > \beta_{crit}^{(2)}$ . Then  $\beta_{crit} = \max\{\beta_{crit}^{(1)}, \beta_{crit}^{(2)}\}$  is the threshold value of  $\beta$  required in the statement of the theorem.  $\square$

Typical set of trajectories when  $\beta > \beta_{crit}$  is presented on Figure 2.

**Proof:** Let  $\mu > \frac{a}{c} - 1 > 0$ , be fixed. Then the unique positive root of  $\tilde{g}_1(x, 0) = 0$  is

$$\tilde{p}(\beta) = \frac{\mu + 1}{2a} - \frac{1}{2\beta} + \sqrt{\left(\frac{\mu + 1}{2a} - \frac{1}{2\beta}\right)^2 + \frac{1}{a\beta}}.$$

Through standard techniques one can see that  $\tilde{p}$  is in increasing function of  $\beta$  and we have

$$\lim_{\beta \rightarrow 0} \tilde{p}(\beta) = \frac{1}{a} = p, \quad \lim_{\beta \rightarrow +\infty} \tilde{p}(\beta) = \frac{\mu + 1}{a}.$$

Hence,

$$\tilde{g}_2(\tilde{p}(\beta), 0) = 1 - c\tilde{p}(\beta),$$

considered as a function of  $\beta$ , decreases from  $1 - \frac{c}{a} > 0$  to  $1 - \frac{c}{a}(\mu + 1) < 0$ . Therefore, there exists  $\beta_{crit}^{(1)} \in (0, +\infty)$  such that  $\tilde{g}_2(\tilde{p}(\beta_{crit}^{(1)}), 0) = 0$  and  $\tilde{g}_2(\tilde{p}(\beta), 0) < 0$  for  $\beta > \beta_{crit}^{(1)}$ .

## Model of $n$ competing species

In this section we show that the destabilization of co-existence due to conspecific support in the case of two species may lead to pattern formation in the case of many species. We consider  $n$  species, arranged in the order of their indexes, where every species interact competitively with its two neighbours. To avoid the influence of other factors, we consider that all species have the same vital dynamics. In fact, we can also consider them groups of the same species, e.g. packs of dogs, prides of lions, patches of grass. Then a model with linear per capita growth rate can be written in the form

$$\frac{du_i}{dt} = u_i(k - \alpha u_i - u_{i-1} - u_{i+1}), \quad i = 1, \dots, n, \quad (10)$$

where  $u_i$  is the size of the  $i$ th species/population group. As usual in the search for pattern formation, we use periodic boundary condition, that is

$$u_{n+1} = u_1.$$

**Theorem 3** *If  $\alpha > 2$ , then all  $n$  species uniformly strongly persist.*

**Proof:** Similar to Theorem 1 we establish that the model (10) defines a dynamical system on  $\mathbb{R}_+^n$  and that the set  $\Omega = \left[0, \frac{k}{\alpha}\right]^n$  is positively invariant and attractive. Hence it is enough to consider the model on  $\Omega$ . For every  $i \in \{1, 2, \dots, n\}$  we have on the set  $\Omega$  the following inequality

$$\frac{du_i}{dt} \geq u_i \left( k - \alpha u_i - \frac{k}{\alpha} - \frac{k}{\alpha} \right) = u_i \left( \frac{(\alpha - 2)k}{\alpha} - u_i \right).$$

Therefore,

$$\liminf_{t \rightarrow +\infty} u_i(t) \geq \frac{(\alpha - 2)k}{\alpha} > 0.$$

□

Including conspecific support for each individual species or population group similar to (6)–(7 and (8)–(9) we obtain the following system

$$\frac{du_i}{dt} = u_i(1 + \beta u_i)(k + \mu - \alpha u_i - u_{i-1} - u_{i+1}) - \mu u_i, \quad i = 1, \dots, n, \quad u_{n+1} = u_1. \quad (11)$$

**Theorem 4** *Let  $\alpha > 2$ . If  $\mu > (\alpha - 2)\frac{k}{2}$ , there exists  $\beta_{crit}$  such that for  $\beta > \beta_{crit}$  the system (11) has attractive boundary equilibria.*

**Proof:** We will give the proof in the case when  $n$  is even. The proof for when  $n$  is odd is slightly more technically complicated but uses essentially the same argument.

Let  $\varphi(\theta) = (1 + \beta\theta)(k + \mu - \alpha\theta) - \mu$ . It is easy to see that  $\varphi$  has a unique positive root, which we denote by  $\theta^*$ . Clearly,

$$\varphi'(\theta^*) < 0. \quad (12)$$

Further, we have

$$\varphi\left(\frac{k}{2}\right) = (1 + \beta\frac{k}{2})(\mu - (\alpha - 2)\frac{k}{2}) - \mu.$$

Taking into account the inequality given for  $\mu$ ,  $\varphi(\frac{k}{2})$  is linear increasing function of  $\beta$ . Therefore, there exists  $\beta_{crit}$  such that

$$\beta > \beta_{crit} \implies \varphi\left(\frac{k}{2}\right) > 0. \quad (13)$$

Further, one can observe that since  $\varphi$  is a quadratic function of  $\theta$ , (13) implies that

$$\beta > \beta_{crit} \implies \theta^* > \frac{k}{2}. \quad (14)$$

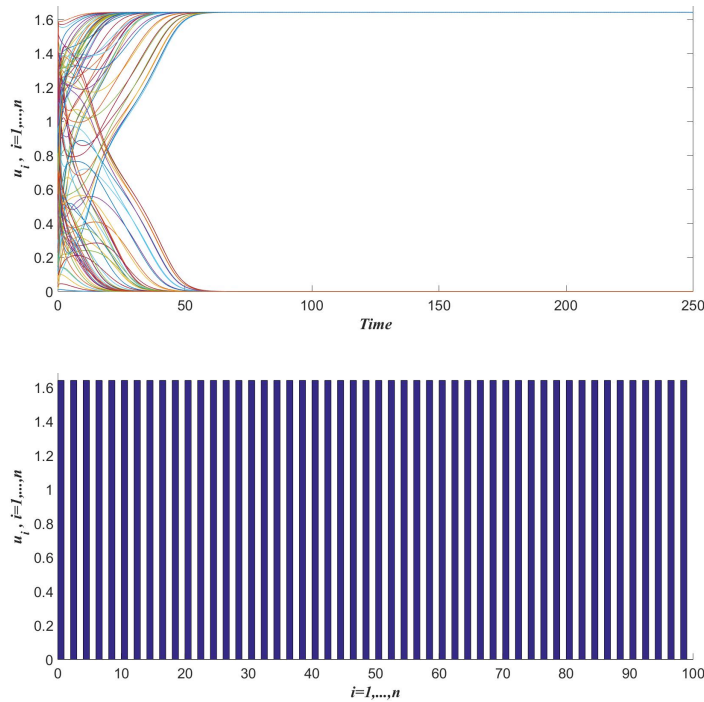
We will show that for  $\beta > \beta_{crit}$  the system has an attractive boundary equilibrium.

Let  $\beta > \beta_{crit}$  and let us consider the equilibrium

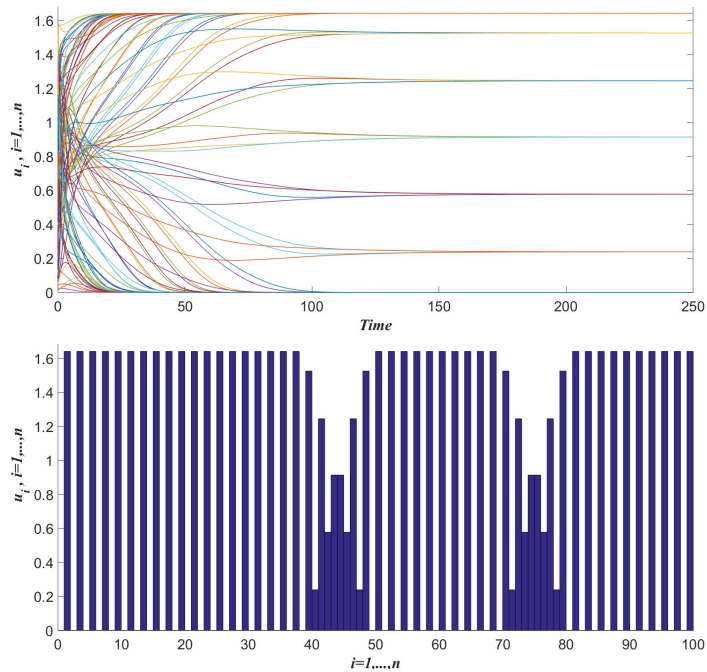
$$x^* = (\theta^*, 0, \theta^*, 0, \theta^*, \dots, \theta^*, 0).$$

Every even row of the Jacobian of the right hand side of (11) at  $x^*$  contains a single nonzero entry, which is at the diagonal and is equal to  $k - 2\theta^*$ . Therefore, the Jacobian has  $\frac{n}{2}$  eigenvalues equal to  $k - 2\theta^*$ , which due to (14) are negative. After these rows and respective columns are removed, the remaining submatrix is diagonal with diagonal values equal to  $\theta^*\varphi(\theta^*)$ . Therefore, the remaining  $\frac{n}{2}$  eigenvalues are all equal to  $\theta^*\varphi(\theta^*)$ , which is negative due to (12). Hence, the equilibrium  $x^*$  is stable and attractive.  $\square$

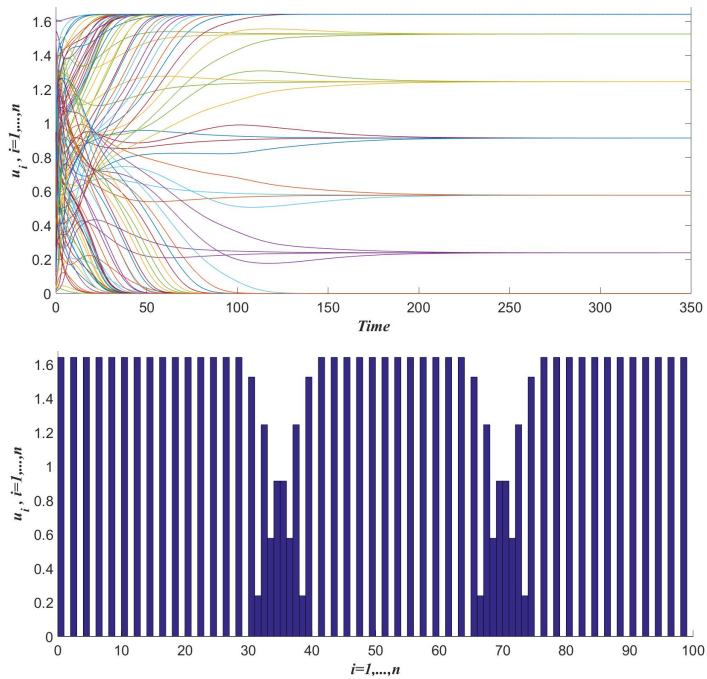
Theorem 4 shows that at least for  $\beta > \beta_{crit}$  there is no uniform strong persistence of all species. This property opens the possibility for emergence of patterns involving extinction of some species. The simulations presented on Figures 3–5 were implemented with  $k = 3$ ,  $\alpha = 2.1$ ,  $\mu = 0.5$ ,  $\beta = 5$ ,  $n = 100$ . In every figure we have time diagram (above) and a "space" diagram (below). In every figure the time diagram indicates that the equilibrium for each species is obtained. Further, it indicates that the obtained equilibrium of the model is stable with respect to small perturbations, e.g. at least of the size of the roundoff error. The "space" diagram represents the sizes of each species that the obtained equilibrium in a bar-chart, where the species are arranged in the order of their indexes. The initial condition is a random vector, every coordinate uniformly distributed in  $[0.01, 1.01]$ . We note that different pattern are obtained in different runs. Three pattern are given on Figures 3–5.



**FIGURE 3.** Pattern 1 of  $n$  competing species with conspecific support. Regular sequence of persistence and extinction as given in  $x^*$ .



**FIGURE 4.** Pattern 2 of  $n$  competing species with conspecific support.



**FIGURE 5.** Pattern 3 of  $n$  competing species with conspecific support.

## Upscaling from discrete to continuous model

For large  $n$  the vector  $(u_1(t), u_2(t), \dots, u_n(t))$  is often modelled as a function  $u(t, x)$ , where  $x$  is a continuous variable in a real interval  $\Omega$ . Further, for large  $n$  one can assume interaction not only with the immediate neighbours, but with their neighbours and beyond. Then the analogy of the growth limiting factor in (11) is an integral of the form

$$I(u; t, x) = \int_{\Omega} \psi(y-x)(k + \mu - \alpha u(t, y)) dy,$$

where the support and the shape of the kernel  $\psi$  determines the span and type of interaction. Similarly, the growth with conspecific support factor in the case of a continuous variable  $x$  is modelled as

$$A(u; t, x) = \int_{\Omega} \phi(y-x)u(t, y)(1 + \beta u(t, y)) dy,$$

where the support and shape of  $\phi$  determines the span and type of conspecific support for growth. We may assume that  $\phi$  and  $\psi$  are normalized so that

$$\int_{\Omega} \phi(x) dx = \int_{\Omega} \psi(x) dx = 1. \quad (15)$$

For simplicity we also assume that they have compact support. Naturally, the  $\text{supp}(\phi)$  is expected to be much smaller than  $\text{supp}(\psi)$ .

The upscaling of the model (11) to continuous space variable is of the general form

$$\frac{\partial u(t, x)}{\partial t} \propto A(u; t, x) \times I(u; t, x) - \mu u(t, x). \quad (16)$$

Further, we need to take into account that the growth limiting factor  $I(u; t, x)$  could be negative, while  $u(t, x) = 0$  and  $u(t, x)$  is nonnegative over  $\Omega$ . Hence, with a modification to exclude the possibility of obtaining negative values the model is

$$\frac{\partial u(t, x)}{\partial t} = \begin{cases} r \int_{\Omega} \phi(y-x)u(t, y)(1 + \beta u(t, y)) dy \times \int_{\Omega} \psi(y-x)(k + \mu - \alpha u(t, y)) dy - \mu u(t, x) & \text{if } u(t, x) > 0, \\ \max \left\{ r \int_{\Omega} \phi(y-x)u(t, y)(1 + \beta u(t, y)) dy \times \int_{\Omega} \psi(y-x)(k + \mu - \alpha u(t, y)) dy - \mu u(t, x), 0 \right\} & \text{otherwise,} \end{cases} \quad (17)$$

where  $r$  is a positive constant.

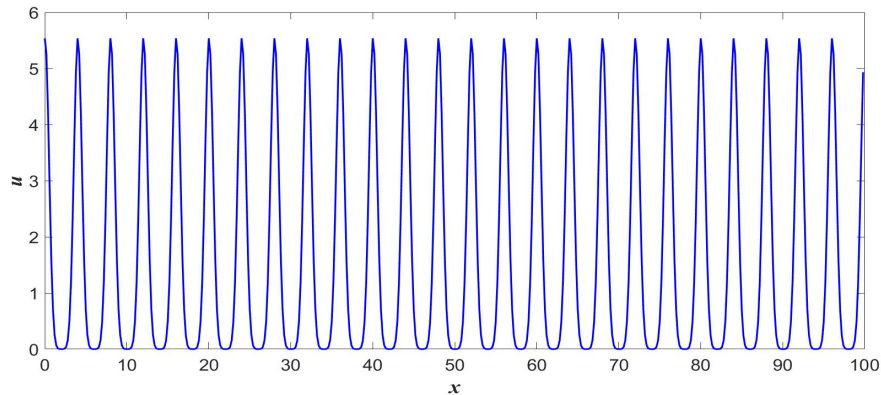
The model (16) was first introduced in [4] to model patterns in tiger bush. The model (17) was used in [1] for modeling the algae *Anabaena*. It is quite interesting that these models can be linked to models like (11) of competing species with conspecific support and, in fact, can be derived through upscaling of (11) from discrete to continuous space variable.

For the simulations in Figures 6 and 7 we use the same values of the parameters as for the simulation on Figures 3–5 with the kernels  $\phi$  and  $\psi$  given in the form

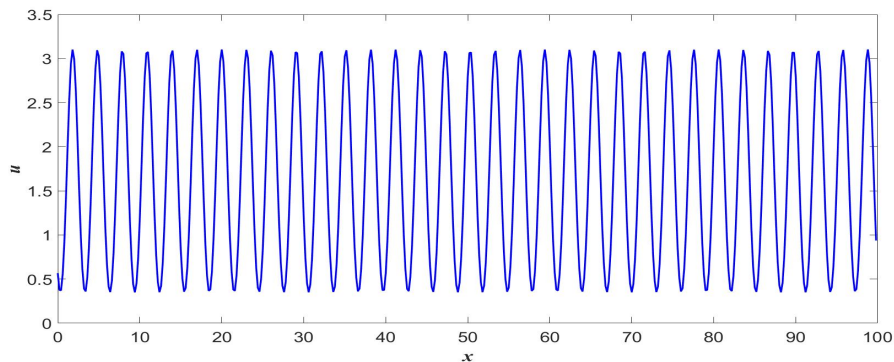
$$\phi(x) = \begin{cases} (L_1 - x)L_1^{-2} & \text{if } |x| \leq L_1 \\ 0 & \text{if } |x| > L_1 \end{cases}, \quad \psi(x) = \begin{cases} (L_2 - x)L_2^{-2} & \text{if } |x| \leq L_2 \\ 0 & \text{if } |x| > L_2 \end{cases},$$

where  $L_1$  and  $L_2$  are positive reals such that  $L_1 < L_2$ . The simulations are run until a stable pattern occurs. Figure 6 is obtained for  $L_1 = 0.8$  and  $L_2 = 4$ . The pattern is very similar to the one in Figure 3. For smaller ratio  $L_2 : L_1$  we obtained wave-like patterns not involving any local extinction. No similar patterns were obtained for the model (11). In Figure 7 we present a pattern obtained for  $L_1 = 1$  and  $L_2 = 3$ .

We need to remark that these patterns are formed essentially through the Gierer-Meinhard [3] mechanism of self-activation, represented by the operator  $A$ , and lateral inhibition, represented by the operator  $I$ . Typically, this mechanism is represented mathematically via a system of reaction diffusion equations satisfying the Turing instability condition [10], [6]. Here we show, among other things, that different mathematical representations of the Gierer-Meinhard theory of pattern formation are possible.



**FIGURE 6.** Stable pattern obtained for  $L_1 = 0.8$  and  $L_2 = 4$ .



**FIGURE 7.** Stable pattern obtained for  $L_1 = 1$  and  $L_2 = 3$ .

## Conclusion

It is widely accepted that the Turing mechanism for systems of reaction-diffusion equations is appropriate way for modeling pattern formation, [10]. In fact, it seems that it is widely believed that it is the only way, particularly given that Gierer and Meinhardt derived independently the same model to represent their theory of biological pattern formation, [5].

We propose two alternative mechanisms for pattern formation, one in a discrete-space model and one in a continuous-space model. In both cases the pattern formation is due to local self-activation (conspecific support) and lateral inhibition by exhausting the resource.

## ACKNOWLEDGMENTS

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