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Nonlinear phenomena and resource exploitation in group living organisms

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Abstract

The proposed research project belongs to the broad area of nonlinear dynamics, self-organization and collective behavior in group living organisms confronted to the choice between different options. One of the most intensely studied examples of these phenomena is foraging recruitment and resource exploitation in social insects. It has been shown that this often involves a transition between individual random behavior and collective decision-making leading to different exploitation strategies induced by amplifying interactions between individuals.

In this work, a mathematical model of food recruitment in ants in the presence of communicating sources is developed. The aim is to analyze the effect of traffic between the sources using mean field approximation.

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1 Introduction

Self-organization[1,2] is a process in which pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of the system.

Self-organization includes a wide range of pattern-formation processes in both physical and biological systems[2], such as sand grains assembling into rippled dunes[3], chemical reactants forming swirling spirals (Belouzov-Zabotinsky), fish joining togather in schools[4–6], and cells making up highly structured tissues[7].

A pattern is a particular, organized arrangement of objects in space or time. i, e a school of fish, a raiding column of army ants *etc*. In a school of fish, for instance, each individual bases its behavior on its perception of the position and velocity of its nearest neighbors, rather than knowledge of the global behavior of the whole school. Similarly, an army ant within a raiding column bases its activity on local concentrations of pheromone laid down by other ants rather than on a global overview of the pattern of the raid.

The mechanisms of self-organization in biological systems differ from those in physical systems in two basic ways. The first is the greater complexity of the subunits in biological systems. The interacting subunits in physical systems are inanimate objects such as grains of sand or chemical reactants. In biological systems there is greater inherent complexity when the subunits are living organisms such as fish or ants. The second difference concerns the nature of the rules governing interactions among system components. In chemical and physical systems, pattern is created through interactions based solely on physical laws. For example, heat applied evenly to the bottom of a tray filled with a thin sheet of viscous oil transforms the smooth surface of the oil into an array of hexagonal cells of moving fluid called *Benard convection cells*[8]. The molecules of oil obey physical laws related to surface tension, viscosity, and other forces governing the motion of molecules in a heated fluid. Likewise, when wind blows over a uniform expanse of sand a pattern of regularly spaced ridges is formed through a set of forces attributable to gravity and wind acting on the sand particles[3,9] . Of course, biological systems obey the laws of physics, but in addition to these laws the physiological and behavioral interactions among the living components are influenced by the genitically controlled properties of the components.

Animals, most particular social insects live in groups. They make a collective decesion, through a mechanism of self-organization, when they have to go for food. It has been shown that, how groups make collective decisions to get food. The most common mechanisms leading to suitable collective decesion in group living insects are allelomimesis (what the neighbor is doing)[10–12].

The present work is concerned by recruirment in ant societies associated with foraging. More specifically, a mathematical model accounting for traffic of individuals between the available sources in the presence of two or more than two food sources is developed and analyzed. The basic mechanism of recruitment can be described as follows: An ant discovers food source, eats and returns to the nest laying down a chemical substance known as pheromone. This phenomenon has two roles[13]: First it stimulates inactive foragers waiting in the nest to leave it and second, it leads them to the food sources. On every trip, ants strengthen the pheromone trail.

The significant point is the understanding of the recruitment behavior has been the design of experiments is purposely idealized situation by which many of the problems can be fixed in the real world. The development of mathematical models ensure the facility that the parameters can be determined directly from the experiment. In this perceptive several authors through their various experimental studies have showed the surprising bahavior[14–16] when two food sources or two trails were made available at the same time. The competition between the two chemical trails gives rise to a variety of nonlinear phenomena which is related different types of traffic between the nest and the sources. In case of two identical food sources: When small amounts of pheromone drop on the path at per time, then it has an identical exploitation of the sources, which give rise to homogeneous state. After a threshold value of the parameter the system turns to a prefferred source through the bifurcation which rise to inhomogeneous states. These results have been adequately substantiate by experiment for the species *Lasius niger*. The procedure can also apply to other ant species by taking the different values of the parameters.

In section 2, a general model without traffic term is presented and analyzed in detail with a reference case. In section 3, a model with traffic term is analyzed and steady-state solutions in case of two and three identical and equidistant food sources. In section 4, the conclusions are summarized.

Fixed point and stability

A very general framework for ordinary differential equations is provided by the system[17]

$$\begin{aligned}\dot{x}_1 &= f_1(x_1, x_2, ..., x_n)\\ &\vdots\\ \dot{x}_n &= f_n(x_1, x_2, ..., x_n)\end{aligned} \tag{1}$$

Here the overdots denote differentiation with respect to t. Thus $\dot{x}_i = \frac{dx_i}{dt}$. The variables $x_1, ..., x_n$ might represent concentrations of chemicals in a reactor, populations of different species in an ecosystem, or the positions and velocities of the planets in the solar system. If $n = 2$, then eqs. (1) can be reduce as

$$\begin{aligned}\dot{x}_1 &= f_1(x_1, x_2)\\ \dot{x}_2 &= f_2(x_1, x_2)\end{aligned} \tag{2}$$

The nullcline is the set of points, which satisfy $f_1(x_1, x_2) = 0$ and $f_2(x_1, x_2) = 0$

The steady states are the points where the nullclines cross. The steady states of eqs. (2) are the constans (x_1^*, x_2^*), such that $f_1(x_1^*, x_2^*) = 0$ and $f_2(x_1^*, x_2^*) = 0$.

To find the stability of the steady states, we have to linearise eqs. (2),

Let $x_1 = x_1^* + X_1$ and $x_2 = x_2^* + X_2$, where X_1 and X_2 are the small perturbations. Now using Taylor's expansion, we obtain

$$\begin{cases}\dfrac{dX_1}{dt} = f_1(x_1^*, x_2^*) + X_1 \dfrac{\partial f_1}{\partial x_1}\Big|_{x_1=x_1^*, x_2=x_2^*} + X_2 \dfrac{\partial f_1}{\partial x_2}\Big|_{x_1=x_1^*, x_2=x_2^*}\\ \dfrac{dX_2}{dt} = f_2(x_1^*, x_2^*) + X_1 \dfrac{\partial f_2}{\partial x_1}\Big|_{x_1=x_1^*, x_2=x_2^*} + X_2 \dfrac{\partial f_2}{\partial x_2}\Big|_{x_1=x_1^*, x_2=x_2^*}\end{cases}$$

Since $f_1(x_1^*, x_2^*) = 0 = f_2(x_1^*, x_2^*)$

$$\begin{aligned}\frac{dX_1}{dt} &= a_{11}X_1 + a_{12}X_2\\ \frac{dX_2}{dt} &= a_{21}X_1 + a_{22}X_2\end{aligned}$$

Also, we can write

$$\begin{bmatrix} \dot{X}_1 \\ \dot{X}_2 \end{bmatrix} = A \begin{bmatrix} X_1 \\ X_2 \end{bmatrix}$$

Where

$$A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = A \begin{bmatrix} \frac{\partial f_1}{\partial x_1}\Big|_{x_1=x_1^*, x_2=x_2^*} & \frac{\partial f_1}{\partial x_2}\Big|_{x_1=x_1^*, x_2=x_2^*} \\ \frac{\partial f_2}{\partial x_1}\Big|_{x_1=x_1^*, x_2=x_2^*} & \frac{\partial f_2}{\partial x_2}\Big|_{x_1=x_1^*, x_2=x_2^*} \end{bmatrix}.$$

Now

$$\begin{bmatrix} X_1 \\ X_2 \end{bmatrix} = \mu e^{\lambda t}$$

Therefore

$$\lambda \mu = A \mu$$

or

$$(A - \lambda I)\mu = 0$$

λ are the eigenvalues of A, while μ is the associated eigenvector. By solving $det(A - \lambda I) = 0$, we get λ_1 and λ_2, which are the eigenvalues and

$$\begin{bmatrix} X_1 \\ X_2 \end{bmatrix} = c_1 \mu_1 e^{\lambda_1 t} + c_2 \mu_2 e^{\lambda_2 t} \tag{3}$$

where μ_1 and μ_2 are the associated eigenvectors and c_1 and c_2 are constants. By using eq. (3), we can observe the stability of the steady state.

A steady state (x_1^*, x_2^*), is an unstable node if λ_1 , $\lambda_2 > 0$ and, is stable if λ_1 , $\lambda_2 < 0$ and, is a saddle point if $\lambda_2 < 0 < \lambda_1$. If λ_1 and λ_2 are complex, then $\lambda_{1,2} = a + \iota b$, if $a > 0$ then the steady state is an unstable spiral and, if $a < 0$ then the steady state is a stable spiral and, if $a = 0$ then the staedy state is a centre.

Bifurcation

It is the abrupt transition of the entire system towards a new stable pattern when a threshold is crossed[18]. For example, at a critical temperature, a ferromagnet may become demagnetized due to the disordering effect of thermal forces. Upon variations of some control parameters a self-organized system will thus spontaneous present new types of structures whereby there is a discrete change from one state to another. Similar bifurcation phenomena are observed in ant societies which may take the form of symmetry-breaking as one observes the shift from an even exploitation of several food sources[19].

2 A reference case

A common ant in northern Europe is *Lasius niger*, also known as a black garden ant[18]. One can easily observe foraging in *L. niger* by setting out a dish of sugar solution in the vicinity of a nest. After some time, a forager will discover the sugar and shortly thereafter through a recruitment process, numerous additional foragers will appear at the food source. Observation reveals ants trafficking between the nest and the food source as if the creatures were following an invisible highway on the ground. The ants are moving along a chemical trail deposited by the ants. The ants reinforce this trail with additional pheromone both after they have ingested food and are returning to the nest, and when they are following the pheromone trail to return to the food source[14,20]. Each ant returning from the food source can stimulate many other nestmates to forage, these ants in turn stimulate still others, and so on.

An ant colony[13] has the choice between two identical, equidistant and non-communicating food sources. Ants leave the nest at a constant rate (the flux), ingest food, and return to the nest. The flux depends on the concentration of pheromone. In the experimental setup, ants have a choice between trail as shown in Fig.1 . We start our analysis by developing a mathematical relationship, which describes how ant chooses a path toward food sources .

Let c_i be the pheromone concentrations on trail $i = 1, 2, ..., s$ leading to the source. The rate of change of c_i with respect to time t, can be decomposed into two terms[11,21].

$$\frac{dc_i}{dt} = \phi q_i \frac{(k + c_i)^l}{\sum_{j=1}^{s}(k + c_j)^l} - \nu_i c_i \ , i = 1, 2, ..., s$$

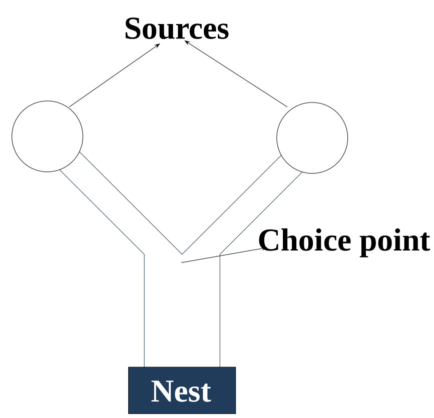

Figure 1: Experimental setup without communicating sources

The first, positive term describes the attractiveness of trail i over the others. The second, negative term describes the disappearance of the pheromone on the trail i through evaporation.

Here ϕ is the flow of the ants leaving the nest toward the trails (related to the size of the colony), q_i is the quantity of the pheromone (proportional to the richness of the food sources) dropped by ant on the trail i whose magnitude reflects the quality of source i , k is a threshold beyond which the pheromone dropped on the trail begins to be effective, l measures the sensitivity of the process of choice of a pareticular trail on the pheromonal concentration c_i present and will be therefore be referred to hereafter as "cooperativity parameter", ν_i is the disappearance of the pheromone on the trail i and s is the total number of sources visited by the ants.

Since food sources are identical and the paths leading the nest to the sources have the same characteristics, we can write $q_i = q$, $\nu_i = \nu$. For simplicity, we take $k = 1$, so

$$\frac{dc_i}{dt} = \phi q \frac{(1+c_i)^2}{\sum_{j=1}^{s}(1+c_j)^2} - \nu c_i \tag{4}$$

Where $l = 2$, will be fixed, which is well-matched with the experimental data for the ant species *L. niger*[22,23].

The solutions of eq. (4) depend on the parameters ϕq, ν and s.

For simplest case, when two identical and equidistant food sources ($s = 2$), then (4) can be written as

$$\begin{cases} \dfrac{dc_1}{dt} = \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2+(1+c_2)^2} - \nu c_1 \\ \dfrac{dc_2}{dt} = \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2} - \nu c_2 \end{cases} \tag{5}$$

We now find the steady states of eqs. (5), by setting the time derivatives equal to zero. We have two algebraic equations, which can be solved explicitly for c_1 and c_2.

$$\begin{cases} \dfrac{\nu}{\phi q} c_1 = \dfrac{(1+c_1)^2}{(1+c_1)^2+(1+c_2)^2} \\ \dfrac{\nu}{\phi q} c_2 = \dfrac{(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2} \end{cases} \tag{6}$$

Adding and dividing the two eqs. in (6), we have

$$c_1 + c_2 = \frac{\phi q}{\nu} \tag{7}$$

and

$$\frac{c_1}{c_2} = \frac{(1+c_1)^2}{(1+c_2)^2} \tag{8}$$

Solving eq. (7) and eq. (8) and after simplification, we get three steady states, which are

$$S_1 = \begin{bmatrix} \frac{\phi q}{2\nu} \\ \frac{\phi q}{2\nu} \end{bmatrix}$$

$$S_2 = \begin{bmatrix} \frac{\phi q/\nu + \sqrt{(\phi q/\nu)^2 - 4}}{2} \\ \frac{\phi q/\nu - \sqrt{(\phi q/\nu)^2 - 4}}{2} \end{bmatrix}, \quad S_3 = \begin{bmatrix} \frac{\phi q/\nu - \sqrt{(\phi q/\nu)^2 - 4}}{2} \\ \frac{\phi q/\nu + \sqrt{(\phi q/\nu)^2 - 4}}{2} \end{bmatrix}$$

To determine the stability of the steady states, we compute the Jacobian matrix associated to the right hand side of eqs. (5). For this, we define

$$f(c_1, c_2) = \phi q \frac{(1+c_1)^2}{(1+c_1)^2 + (1+c_2)^2} - \nu c_1$$
$$g(c_1, c_2) = \phi q \frac{(1+c_2)^2}{(1+c_1)^2 + (1+c_2)^2} - \nu c_2$$

The Jacobian is

$$J = \begin{bmatrix} \frac{\partial f}{\partial c_1} & \frac{\partial f}{\partial c_2} \\ \frac{\partial g}{\partial c_1} & \frac{\partial g}{\partial c_2} \end{bmatrix}.$$

Stability is determined by investigating the eigenvalues of the Jacobian at the steady states S_1, S_2, and S_3 as a function of ϕ. If $\phi \leq 0.2$ then we only have the steady state S_1, and if $\phi > 0.2$, we have the steady states S_1, S_2, and S_3. The eigenvalues of J evaluated at S_1 are both negative for $\phi \leq 0.2$ and of opposite sign for $\phi > 0.2$, hence S_1, is stable for $0 < \phi \leq 0.2$ and unstable for $\phi > 0.2$. At S_2 and S_3, the eigenvalues are negative, so these states are stable. The bifurcation diagram for c_1 with respect to ϕ is shown in Fig. 2a. The bifurcation diagram representing c_2 against ϕ is identical.

In the presence of a third identical and equidistant food source ($s = 3$), eq. (4) can be written as

$$\begin{cases} \dfrac{dc_1}{dt} = \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_1 \\ \dfrac{dc_2}{dt} = \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_2 \\ \dfrac{dc_3}{dt} = \phi q \dfrac{(1+c_3)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_3. \end{cases} \quad (9)$$

By solving the system of differential equations (9) as above, it is found that the homogeneous state loses its stability at $\phi = 0.3$. The new stable states emerge through limit point bifurcations in which the limit points are located at $\phi = 0.28$, dividing the solutions into four semi-inhomogeneous states, two of which are stable and two are unstable. At $0.28 < \phi < 0.3$, there are three stable states, which shows the coexistance between the homogeneous and inhomogeneous states, it means that mixed exploitation (exploitation of a single preferred source or an equal exploitation of multiple sources) occurs, as shown in Fig. 2b.

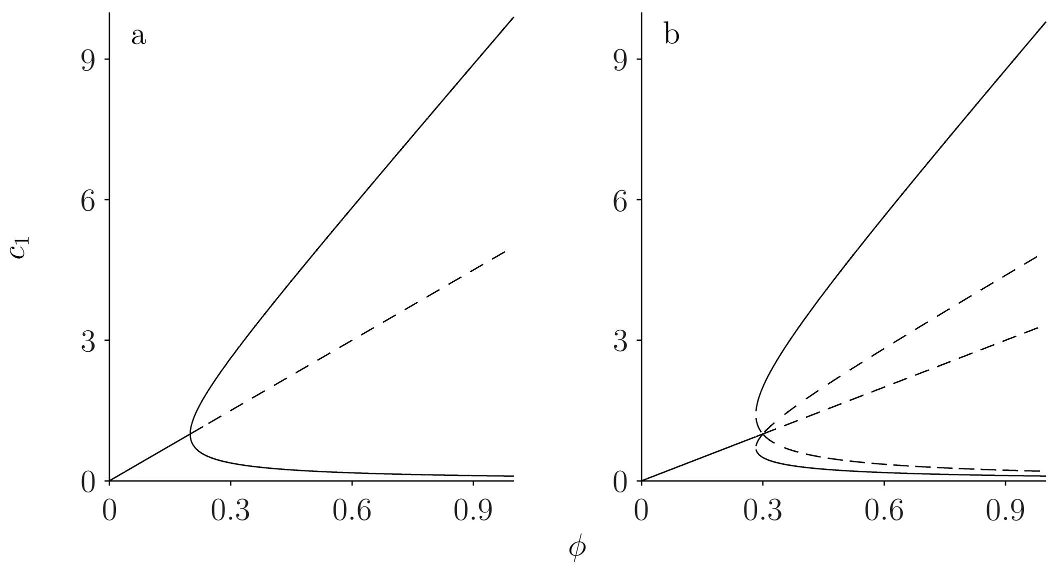

Figure 2: Bifurcation diagram of the steady-state solutions of eq. (4). $s = 2$ (a), $s = 3$ (b). Full and dashed lines shows the stable and unstable solution respectively. Other parameters values $\nu = 0.1$ and q=1

3 Modeling resource exploitation in the presence of traffic between sources

In this section, we shall discuss successively the mathematical model of ants in the presence of linear and nonlinear traffic between sources. Our goal is, to extend the results, which are analyzed in section 2.

3.1 Linear traffic term

We first consider an ant colony having the choice between two identical and equidistant food sources in the setup shown in Fig. 3, where food sources are now communicating with each other.

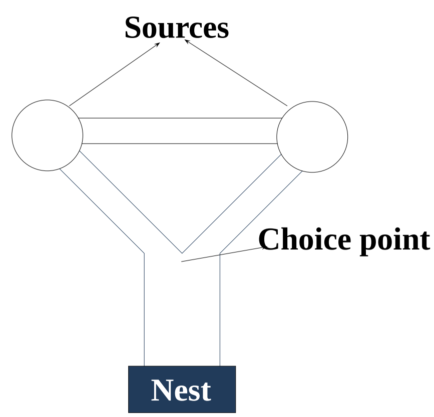

Figure 3: Experimental setup with communicating sources

A model, which is in eq. (4) can be extend with linear traffic term and written as[24]

$$\frac{dc_i}{dt} = \phi q \frac{(1+c_i)^2}{\sum_{j=1}^{s}(1+c_j)^2} - \nu c_i + \sum_{i \neq j} J_{ij}$$

The last (positive) term is the traffic of individuals between source i and the sources $j(1, 2, ..., i-1, i+1, , s)$ as expected to arise in realistic situatons. The mathematical expression of the traffic term is not welll established. The idea is that traffic between sources reflects primarily (i), individual-level randomness; (ii), the exploration of the environment by individuals having attained the sources and moving subsequently, with some probability, in the part of space outside the trails joining them with the nest: and (iii), crowding effects in the sense that if the density of individuals (and hence of pheromone) around a particular source is very high, individuals will have a tendency to move away from it and explore other possibilities. So we can write

$$\sum_{i \neq j} J_{ij} = D_{ij}(c_j - c_i)$$

Here D_{ij} is the transfer coefficients depend on the length and texture of the channel through which sources i and j communicate and are assumed to define a symmetric, positive definate matrix. So we have

$$\frac{dc_i}{dt} = \phi q \frac{(1+c_i)^2}{\sum_{j=1}^{s}(1+c_j)^2} - \nu c_i + \sum_{i \neq j} D(c_j - c_i) \tag{10}$$

The solutions of eq. (10) depend on the parameters ϕq , ν , D and s.

3.1.1 Analysis

When two identical and equidistant food sources ($s = 2$), eq. (10) can be written as

$$\begin{cases} \dfrac{dc_1}{dt} = \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2 + (1+c_2)^2} - \nu c_1 + D(c_2 - c_1) \\ \dfrac{dc_2}{dt} = \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2 + (1+c_2)^2} - \nu c_2 + D(c_1 - c_2) \end{cases}$$

For steady states:

$$\frac{dc_1}{dt} = \frac{dc_2}{dt} = 0.$$

$$\begin{cases} \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2 + (1+c_2)^2} - \nu c_1 + D(c_2 - c_1) = 0 \\ \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2 + (1+c_2)^2} - \nu c_2 + D(c_1 - c_2) = 0 \end{cases}$$

or

$$\begin{cases} \dfrac{(1+c_1)^2}{(1+c_1)^2+(1+c_2)^2} = \dfrac{\nu}{\phi q}c_1 - \dfrac{D}{\phi q}(c_2-c_1) \\ \dfrac{(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2} = \dfrac{\nu}{\phi q}c_2 - \dfrac{D}{\phi q}(c_1-c_2) \end{cases} \tag{11}$$

Adding and dividing the two eqs. in (11), we get

$$c_1 + c_2 = \frac{\phi q}{\nu} \tag{12}$$

and

$$\frac{(1+c_1)^2}{(1+c_2)^2} = \frac{\nu - D(c_2-c_1)}{\nu - D(c_1-c_2)}. \tag{13}$$

Substituting eq. (12) in eq. (13), we get

$$2(\nu+2D)c_1^3 - 3\phi q(1+\frac{2D}{\nu})c_1^2 + (2\nu + \frac{(\phi q)^2}{\nu} + \frac{4D\phi q}{\nu} + 4D(\frac{\phi q}{\nu})^2 + 4D)c_1 - \frac{D\phi q}{\nu}(2 + \frac{2\phi q}{\nu} + (\frac{\phi q}{\nu})^2) - \phi q = 0$$

After simplification, we get

(i) the homogeneous state

$$c_1 = c_2 = \frac{\phi q}{2\nu} \tag{14}$$

in which all sources are exploited in an identical manner, and

(ii) non-homogeneous state

$$\begin{cases} (\nu+2D)c_1^2 - \dfrac{\phi q}{\nu}(\nu+2D)c_1 + \nu + 2D + \dfrac{D\phi q}{\nu}(2+\dfrac{\phi q}{\nu}) = 0 \\ (\nu+2D)c_2^2 - \dfrac{\phi q}{\nu}(\nu+2D)c_2 + \nu + 2D + \dfrac{D\phi q}{\nu}(2+\dfrac{\phi q}{\nu}) = 0 \end{cases} \tag{15}$$

So, we have three steady states, which are

$$S_1 = \begin{bmatrix} \frac{\phi q}{2\nu} \\ \frac{\phi q}{2\nu} \end{bmatrix}$$

$$S_2 = \begin{bmatrix} \frac{\phi q/\nu(\nu+2D)+\sqrt{(\phi q/\nu(\nu+2D))^2-4(\nu+2D)(\nu+2D+D\phi q/\nu(2+\phi q/\nu))}}{2(\nu+2D)} \\ \frac{\phi q/\nu(\nu+2D)-\sqrt{(\phi q/\nu(\nu+2D))^2-4(\nu+2D)(\nu+2D+D\phi q/\nu(2+\phi q/\nu))}}{2(\nu+2D)} \end{bmatrix}$$

$$S_3 = \begin{bmatrix} \frac{\phi q/\nu(\nu+2D)-\sqrt{(\phi q/\nu(\nu+2D))^2-4(\nu+2D)(\nu+2D+D\phi q/\nu(2+\phi q/\nu))}}{2(\nu+2D)} \\ \frac{\phi q/\nu(\nu+2D)+\sqrt{(\phi q/\nu(\nu+2D))^2-4(\nu+2D)(\nu+2D+D\phi q/\nu(2+\phi q/\nu))}}{2(\nu+2D)} \end{bmatrix}$$

Stability is determined at the steady state S_1, S_2 and S_3 as a function of ϕ. At S_1, the state is stable if $\phi \leq 0.2$ and unstable if $\phi > 0.2$. It has found that the homogeneous state loses its stability at the bifurcation point and dividing the solutions into two inhomogeneous states, which are stable as shown in Fig. 4a. By increasing the values of the parameter D, the range of homogeneous state is gradually increasing, as shown in Fig. 4. The bifurcation diagram representing c_2 against ϕ is identical.

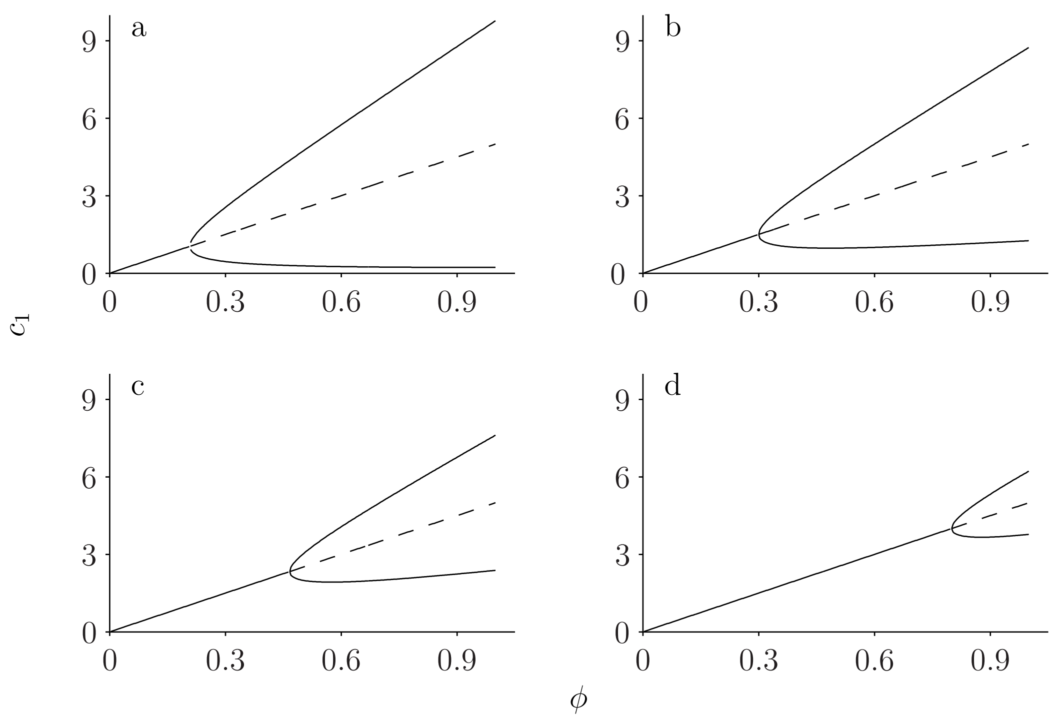

Figure 4: Bifurcation diagrams of the steady states solutions of eq. (10) in the case of $s = 2$, $D = 0.001$ (a), $D = 0.01$ (b), $D = 0.02$ (c) and $D = 0.03$ (d). Other parameter values as in Figure 2.

Turning next to the case of three identical and equidistant sources ($s = 3$) in (10), the traffic term is now J_{ik} is $\sum_{k\neq i} J_{ik} = D(c_{i+1} + c_{i-1} - 2c_i)$, where all indexes are taken mod 3, than the model equations will be of the form

$$\begin{cases} \dfrac{dc_1}{dt} = \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_1 + D(c_2+c_3-2c_1) \\ \dfrac{dc_2}{dt} = \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_2 + D(c_3+c_1-2c_2) \\ \dfrac{dc_3}{dt} = \phi q \dfrac{(1+c_3)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_3 + D(c_1+c_2-2c_3) \end{cases}$$

For steady states:

$$\frac{dc_1}{dt} = \frac{dc_2}{dt} = \frac{dc_3}{dt} = 0$$

$$\begin{cases} \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_1 + D(c_2+c_3-2c_1) = 0 \\ \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_2 + D(c_3+c_1-2c_2) = 0 \\ \phi q \dfrac{(1+c_3)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_3 + D(c_1+c_2-2c_3) = 0 \end{cases}$$

or

$$\begin{cases} \dfrac{(1+c_1)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} = \dfrac{\nu}{\phi q} c_1 - \dfrac{D}{\phi q}(c_2+c_3-2c_1) \\ \dfrac{(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} = \dfrac{\nu}{\phi q} c_2 - \dfrac{D}{\phi q}(c_3+c_1-2c_2) \\ \dfrac{(1+c_3)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} = \dfrac{\nu}{\phi q} c_3 - \dfrac{D}{\phi q}(c_1+c_2-2c_3) \end{cases} \tag{16}$$

Adding the eqs. in (16) yields

$$c_1 + c_2 + c_3 = \frac{\phi q}{\nu} \tag{17}$$

Dividing the first two eqs. in (16) yields

$$\frac{(1+c_1)^2}{(1+c_2)^2} = \frac{\nu c_1 - D(c_2+c_3-2c_1)}{\nu c_2 - D(c_3+c_1-2c_2)}$$

or

$$(1+c_1)^2(\frac{\nu}{\phi q}c_2 - \frac{D}{\nu} + 3\frac{D}{\phi q}c_2) = (1+c_2)^2(\frac{\nu}{\phi q}c_1 - \frac{D}{\nu} + 3\frac{D}{\phi q}c_1)$$

or

$$\begin{cases} c_2 = c_1 = \bar{c} \\ c_2 = \dfrac{\nu + 3D + 2D\phi q/\nu + (D\phi q/\nu)c_1}{\nu c_1 - D\phi q/\nu + 3Dc_1} \end{cases} \tag{18}$$

Similarly, dividing first and third eq. in (16), we get

$$\frac{(1+c_1)^2}{(1+c_3)^2} = \frac{\nu c_1 - D(c_2 + c_3 - 2c_1)}{\nu c_3 - D(c_1 + c_2 - 2c_3)}$$

or

$$(1+c_1)^2(\frac{\nu}{\phi q}c_3 - \frac{D}{\nu} + 3\frac{D}{\phi q}c_3) = (1+c_3)^2(\frac{\nu}{\phi q}c_1 - \frac{D}{\nu} + 3\frac{D}{\phi q}c_1)$$

or

$$\begin{cases} c_3 = c_1 = \bar{c} \\ c_3 = \dfrac{\nu + 3D + 2D\phi q/\nu + (D\phi q/\nu)c_1}{\nu c_1 - D\phi q/\nu + 3Dc_1} \end{cases} \tag{19}$$

Using eqs. (18) and (19) in eq. (17). we get

(i) the homogeneous state

$$c_1 = c_2 = c_3 = \frac{\phi q}{3\nu} \tag{20}$$

in which all sources exploited in an identical manner, and

(ii) non-homogeneous state

$$c_1 = \frac{\phi q/2\nu(\nu+2D) \pm \sqrt{(\phi q/2\nu(\nu+3D))^2 - 2(\nu+3D)(\nu+3D+D\phi q/\nu(2+\phi q/2\nu))}}{\nu+3D} \tag{21}$$

and

$$\bar{c} = \frac{1}{2}(\frac{\phi q}{\nu} - c_1) \tag{22}$$

The homogeneous state loses its stability at the bifurcation point. The limit points are dividing the solutions into four semi-inhomogeneous states, two of which are stable and two are unstable. By increasing the value of the parameter D, it has analyzed that (i), the range of homogeneous state is increasing; and (ii), the range of coexistance between homogeneous and semi-inhomogeneous states is also increasing, as shown in Fig. 5, The bifurcation diagrams representing c_2 against ϕ and c_3 against ϕ are identical.

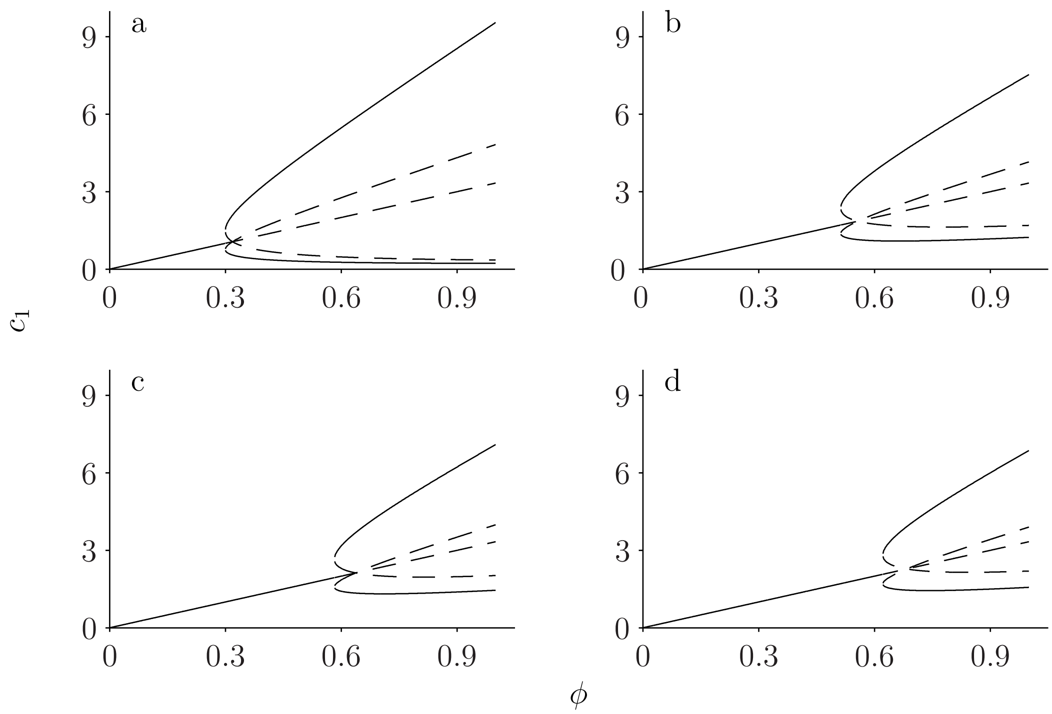

Figure 5: Same as figure 4 but for $s = 3$, $D = 0.001$ (a), $D = 0.01$ (b), $D = 0.012$ (c) and $D = 0.014$ (d).

3.2 Nonlinear traffic term

A minimal model with nonlinear traffic term is

$$\frac{dc_i}{dt} = \phi q \frac{(1+c_i)^2}{\sum_{j=1}^{s}(1+c_j)^2} - \nu c_i + \sum_{i \neq j} D(c_j - c_i)^3 \tag{23}$$

where the third term is a nonlinear term, which describes the traffic between the sources. The solutions of eq. (23) depend on the parameters ϕq , ν , D and s.

3.2.1 Analysis

When two identical and equidistant sources ($s = 2$), eq. (23), can be written as

$$\begin{cases} \dfrac{dc_1}{dt} = \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2+(1+c_2)^2} - \nu c_1 + D(c_2 - c_1)^3 \\ \dfrac{dc_2}{dt} = \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2} - \nu c_2 + D(c_1 - c_2)^3 \end{cases}$$

For steady states:

$$\frac{dc_1}{dt} = \frac{dc_2}{dt} = 0.$$

$$\begin{cases} \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2+(1+c_2)^2} - \nu c_1 + D(c_2 - c_1)^3 = 0 \\ \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2} - \nu c_2 + D(c_1 - c_2)^3 = 0 \end{cases}$$

or

$$\begin{cases} \dfrac{(1+c_1)^2}{(1+c_1)^2+(1+c_2)^2} = \dfrac{\nu}{\phi q} c_1 - \dfrac{D}{\phi q}(c_2 - c_1)^3 \\ \dfrac{(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2} = \dfrac{\nu}{\phi q} c_2 - \dfrac{D}{\phi q}(c_1 - c_2)^3 \end{cases} \tag{24}$$

Adding and subtracting the two eqs. in (24), we get

$$c_1 + c_2 = \frac{\phi q}{\nu} \tag{25}$$

and

$$\frac{(1+c_1)^2-(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2}=\frac{\nu}{\phi q}(c_1-c_2)+2\frac{D}{\phi q}(c_1-c_2)^3$$

Setting $z=c_1-c_2$, and after simplification, we get

$$\frac{(\phi q/\nu)z+2z}{2+2\phi q/\nu+1/2((\phi q/\nu)^2+z^2)}=(\nu/\phi q)z+(2D/\phi q)z^2 \tag{26}$$

(i) the homogeneous state

$$z=0 \tag{27}$$

corresponding to the symmetric exploitation of the two sources.

(ii) non-homogeneous state

$$\frac{D}{\phi q}z^4+(\frac{\nu}{2\phi q}+4\frac{D}{\phi q}+4\frac{D}{\nu}+\frac{D\phi q}{\nu^2})z^2-\frac{\phi q}{2\nu}+2\frac{\nu}{\phi q}=0 \tag{28}$$

For $D=0$, the solutions of eq. (28) reduce to the result of eq. (4). The homogeneous state loses its stability and dividing the solutions into two inhomogeneous states. By increasing the value of the parameter D, it has been observed that the inhomogeneous states are bending towards the central state, it mean that difference between the exploitation is not so big, as shown in Fig. 6.

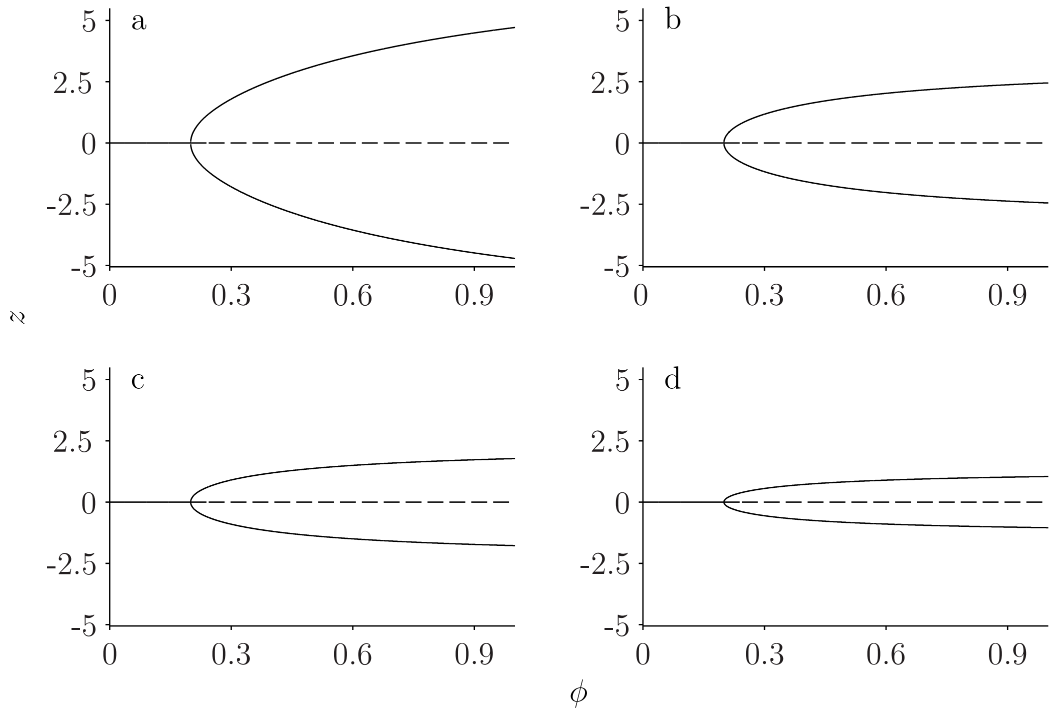

Figure 6: Same as figure 4 but for eq. (23), $D = 0.001$ (a), $D = 0.005$ (b), $D = 0.01$ (c) and $D = 0.03$ (d).

When three identical and equidistant sources ($s = 3$). in eq. (23), the traffic term is now J_{ik} is $\sum_{k\neq i} J_{ik} = D(c_{i+1} + c_{i-1} - 2c_i)^3$, where all indexes are taken mod 3, than the model equations will be of the form

$$\begin{cases} \dfrac{dc_1}{dt} = \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2 + (1+c_2)^2 + (1+c_3)^2} - \nu c_1 + D(c_2 + c_3 - 2c_1)^3 \\ \dfrac{dc_2}{dt} = \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2 + (1+c_2)^2 + (1+c_3)^2} - \nu c_2 + D(c_3 + c_1 - 2c_2)^3 \\ \dfrac{dc_3}{dt} = \phi q \dfrac{(1+c_3)^2}{(1+c_1)^2 + (1+c_2)^2 + (1+c_3)^2} - \nu c_3 + D(c_1 + c_2 - 2c_3)^3 \end{cases} \tag{29}$$

For $D = 0$, the solutions of eq. (29) reduce to the result of eq. (4). By solving the system of eqs. (29) numerically, only stable states have shown in the results. By increasing the value of the parameter D, it has been analysed that (i), the range of homogeneous state is increasing; (ii), the semi inhomogeneous stable states are bending towards the central state; and (iii), there is a coexistance between the homogeneous and semi-inhomogeneous states, as shown in Fig. 7.

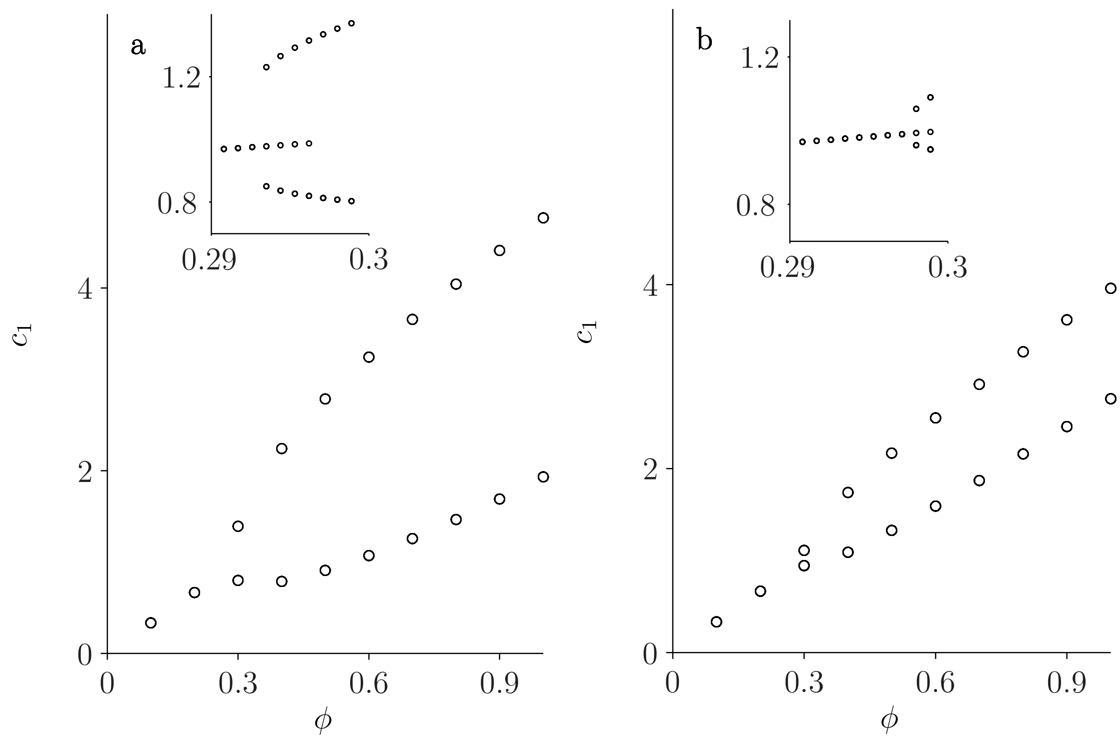

Figure 7: Bifurcation diagram in the case of $s = 3$ as computed numerically by integrating eq. (23) for 15 random initial conditions until the system reaches the steady state ($t = 30000$) in the case of $D = 0.001$ (a) and $D = 0.005$ (b). Other parameter values as in Figure 2.

3.3 Linear and nonlinear traffic term

A model with linear and nonlinear traffic terms will be

$$\frac{dc_i}{dt} = \phi q \frac{(1+c_i)^2}{\sum_{j=1}^{s}(1+c_j)^2} - \nu c_i + \sum_{i\neq j} D_0(c_j - c_i) + \sum_{i\neq j} D(c_j - c_i)^3 \tag{30}$$

where the third and fourth terms are linear and nonlinear traffic terms with coefficients D_0 and D respectivly, which describes the traffic between the sources. The solutions of eq. (30) depend on the parameters ϕq , ν , D_0 , D and s.

3.3.1 Analysis

When two identical and equidistant sources ($s = 2$), in (30)

$$\begin{cases} \dfrac{dc_1}{dt} = \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2 + (1+c_2)^2} - \nu c_1 + D_0(c_2 - c_1) + D(c_2 - c_1)^3 \\ \dfrac{dc_2}{dt} = \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2 + (1+c_2)^2} - \nu c_2 + D_0(c_1 - c_2) + D(c_1 - c_2)^3 \end{cases}$$

For steady states:

$$\frac{dc_1}{dt} = \frac{dc_2}{dt} = 0.$$

$$\begin{cases} \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2 + (1+c_2)^2} - \nu c_1 + D_0(c_2 - c_1) + D(c_2 - c_1)^3 = 0 \\ \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2 + (1+c_2)^2} - \nu c_2 + D_0(c_1 - c_2) + D(c_1 - c_2)^3 = 0 \end{cases}$$

or

$$\begin{cases} \dfrac{(1+c_1)^2}{(1+c_1)^2 + (1+c_2)^2} = \dfrac{\nu}{\phi q} c_1 - \dfrac{D_0}{\phi q}(c_2 - c_1) - \dfrac{D}{\phi q}(c_2 - c_1)^3 \\ \dfrac{(1+c_2)^2}{(1+c_1)^2 + (1+c_2)^2} = \dfrac{\nu}{\phi q} c_2 - \dfrac{D_0}{\phi q}(c_1 - c_2) - \dfrac{D}{\phi q}(c_1 - c_2)^3 \end{cases} \tag{31}$$

Adding and subtracting the two eqs. in (31), we get

$$c_1 + c_2 = \frac{\phi q}{\nu} \tag{32}$$

and

$$\frac{(1+c_1)^2-(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2}=\frac{\nu}{\phi q}(c_1-c_2)+2\frac{D_O}{\phi q}(c_1-c_2)+2\frac{D}{\phi q}(c_1-c_2)^3$$

Setting $z=c_1-c_2$, and after simplification, we get

$$\frac{(\phi q/\nu)z+2z}{2+2\phi q/\nu+1/2((\phi q/\nu)^2+z^2)}=(\nu/\phi q)z+(2D_0/\phi q)z+(2D/\phi q)z^3$$

(i) the homogeneous state

$$z=0 \tag{33}$$

corresponding to the symmetric exploitation of the two sources.

(ii) non-homogeneous state

$$\frac{D}{\phi q}z^4+(\frac{\nu}{2\phi q}+\frac{D_0}{\phi q}+4\frac{D}{\phi q}+4\frac{D}{\nu}+\frac{D\phi q}{\nu^2})z^2+4\frac{D_0}{\phi q}+4\frac{D_0}{\nu}+\frac{D_0\phi q}{\nu^2}-\frac{\phi q}{2\nu}+2\frac{\nu}{\phi q}=0 \tag{34}$$

For $D_0=D=0$, the solution of eq. (34) reduce to the result of eq. (4). By taking the different values of the parameters D and D_0, it has been observed that (i), when D is fixed and D_0 is increasing, the homogeneous state is rapidly increasing, as shown in Fig. 8 (a-d); (ii), on the other hand, when D_0 is fixed and D is increasing, the inhomogeneous states are bending towards the central state, as shown in Fig. 8 (e-h).

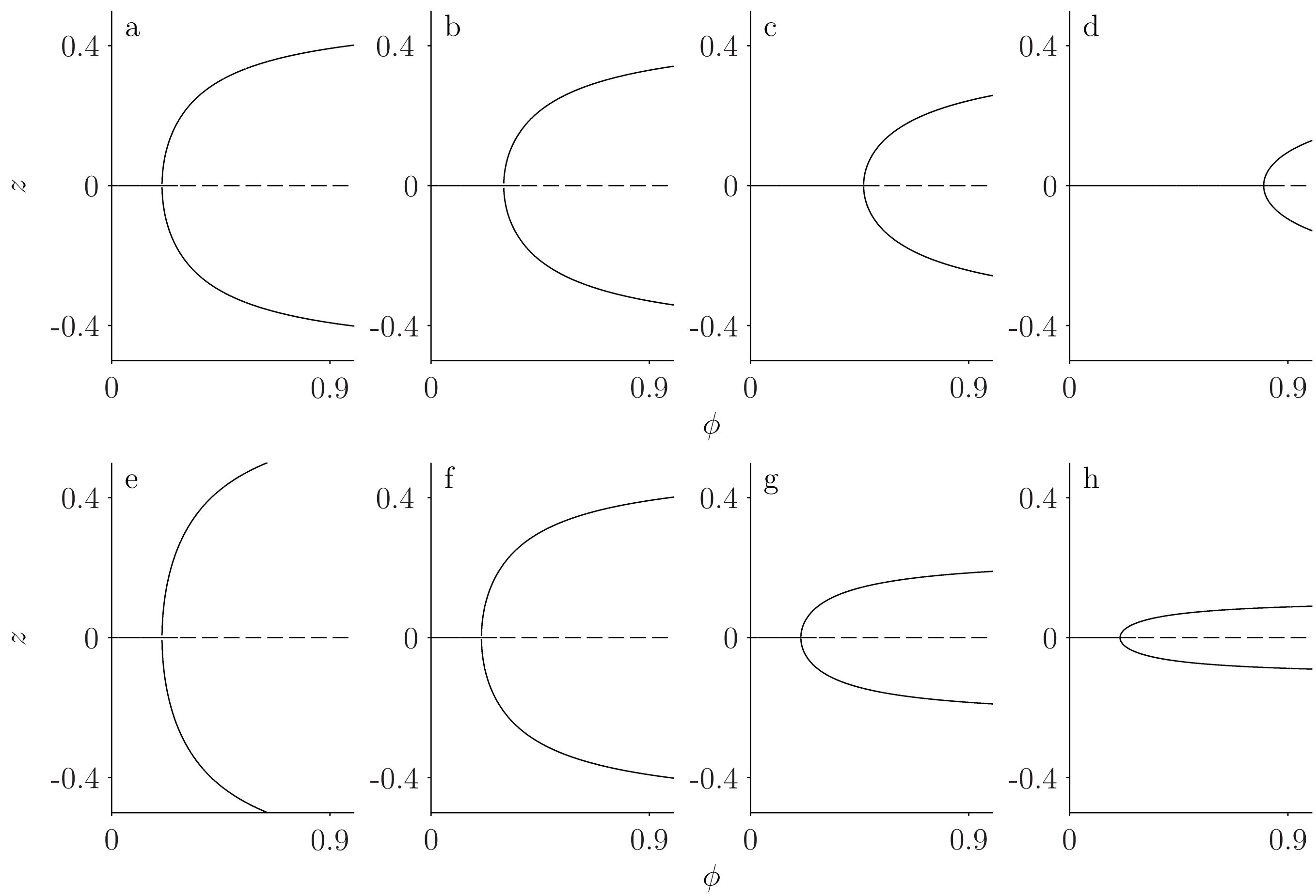

Figure 8: Same as figure 6 but for eq. (30), D=0.2, D_0=0.001 (a), D_0=0.01 (b), D_0=0.02 (c), D_0=0.03 (d) and D_0=0.001, D=0.1 (e), D=0.2 (f), D=0.9 (g), D=4 (h).

When three identical and equidistant sources ($s = 3$), eq. (30) yields

$$\begin{cases} \dfrac{dc_1}{dt} = \phi q \dfrac{(1+c_1)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_1 + +D_0(c_2+c_3-2c_1) + D(c_2+c_3-2c_1)^3 \\ \dfrac{dc_2}{dt} = \phi q \dfrac{(1+c_2)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_2 + +D_0(c_3+c_1-2c_2) + D(c_3+c_1-2c_2)^3 \\ \dfrac{dc_3}{dt} = \phi q \dfrac{(1+c_3)^2}{(1+c_1)^2+(1+c_2)^2+(1+c_3)^2} - \nu c_3 + +D_0(c_1+c_2-2c_3) + D(c_1+c_2-2c_3)^3 \end{cases} \tag{35}$$

Again, for $D_0 = D = 0$, the solution of eq. (35) reduce to the result of eq. (4). By solving system of eqs. (35) numerically, only stable states have been shown in the results. By taking the different values of the parameters D and D_0, we have the following observations (i), there is a coexistance between the stable states and semi inhomogeneous states are bending towards the central state as shown in Fig. 9 (a-b); and (ii), the range of homogeneous state is rapidly increasing, there is coexistance between the stable states and the semi inhomogeneous states are bending towards the central state, as shown in Fig. 9 (c-d).

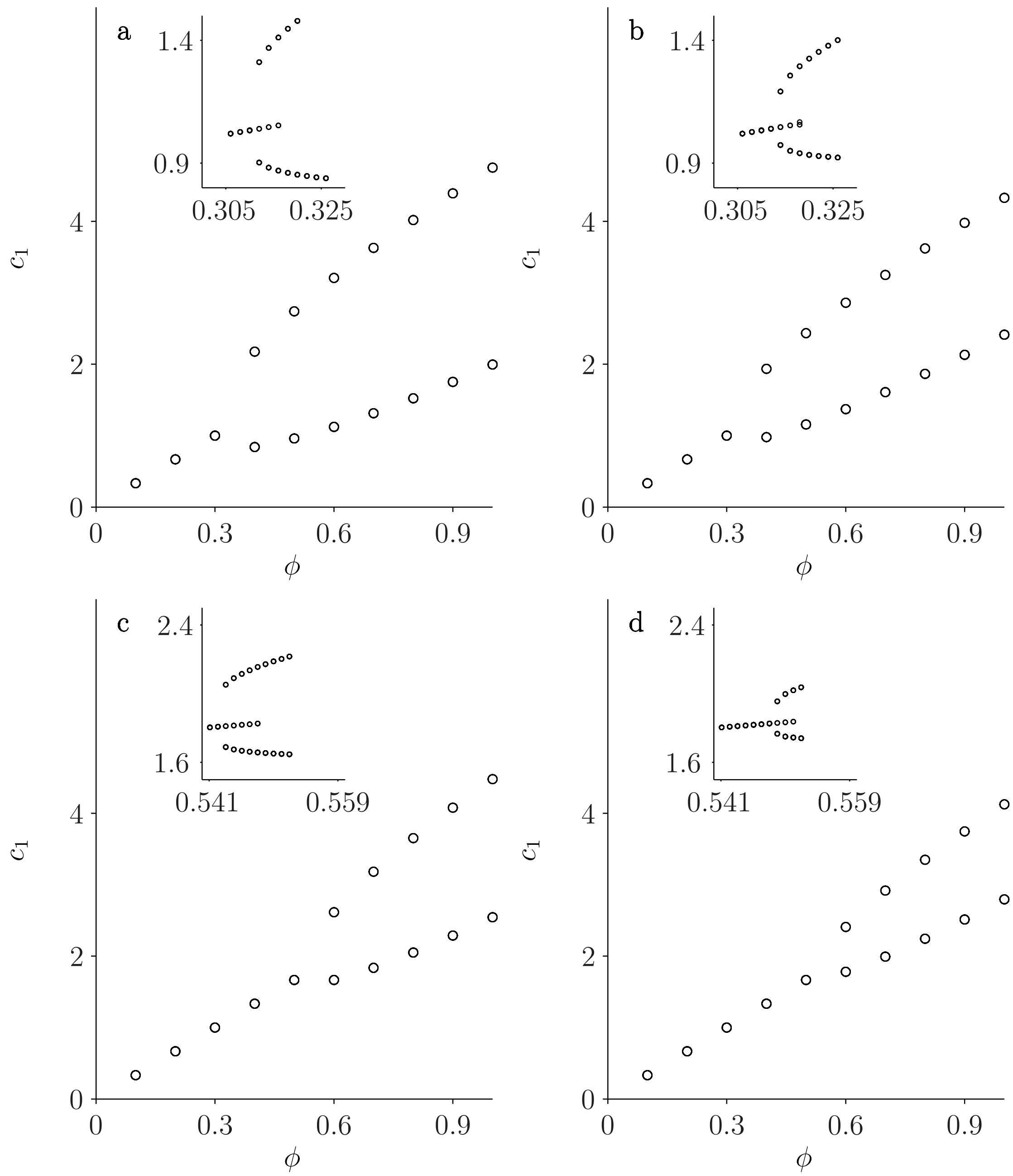

Figure 9: Same as figure 7 but for eq. (30), D_0=0.001 and D=0.001 (a),D_0=0.001 and D=0.002 (b), D_0=0.01 and D=0.001 (c) D_0=0.01 and D =0.002 (d).

4 Conclusions

A mathematical model with three types of traffic terms: linear , non linear and the combination of both in relation with two and three food sources have been analyzed in this work. In all cases the food sources were considered to be identical and equidistant. For this, two parameters played an important role: the flux (ϕ), providing a measure of the size of the colony and the number of food sources (s) visited by the individuals. The bifurcation phenomena emerged when the two chemical trail leading to the food sources, in which one of the trail became more attractive for most of the individuals and clearly prevail over the other as summarized in Fig. 2a; has taken as a reference in section 2. In the presence of the three food sources, the homogeneous state has lost its stability at the bifurcation point. There was also coexistence between stable states when ϕ lies between the limit points and the point of lose of stability of homogeneous state which means mixed exploitation occurred as shown in Fig. 2b. A model have been extended by taking linear traffic term with new parameter D. This parameter played a key role in the results. In case of two sources, we have observed that the range of homogeneous state was increasing as shown in Fig. 4. Similarly in case of three sources. It has been noticed that the range of homogeneous state was increasing as have been seen in case of two sources. The domain of coexistance between the stable states was also increasing, and this was a distinguish feature that have not been noticed in the model without traffic term, in other word there was mixed exploitation as shown in Fig. 5. Now a model with nonlinear traffic term with the same parameter D. In case of two sources the results showed that stable state were bending towards the homogeneous state, means difference between the exploitation was not big as shown in Fig. 6. Similarly, in case of the three sources, it was difficult to solve equation analytically, so we have solved it numerically by integrating the equation untill the system reaches at steady state and having the results; the range of homogeneous state is increasing, it was also expected in case of two sources but was not observed. The stable states were bending towards the central state as shown in Fig. 7. Now a model with both the linear and the nonlinear traffic terms have been taken together, it has been analyzed that the same type of results has been observed as in the linear and nonlinear traffic term as shown in Figs. 8 and 9.

After observing the above results we have concluded (i), enhancement of stability of the homogeneous state; (ii), enhancement of range of coexistance of homogeneous and semi-inhomogeneous states; and (iii), semi-inhomogeneous states are gradually bending towards the central state.

The above derived results also arise in real world situations, where individuals can freely circulate around and between the sources.

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