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Food web complexity analysis: effects of ecosystem changes

B.I. Camara

Abstract In this paper, we use a food web model to investigate the effects of habitat loss and species diversity on ecosystem spatial structure and its elasticity. Our model incorporates functional responses based on the Holling-type-II and the modified Lesie–Gower schemes. Criteria for local stability, global stability of the nonnegative equilibria are obtained. The permanent coexistence of the three species is also discussed. Finally, by computer simulations, we find that far-from equilibria, environmental quality is positively correlated patterns complexity communities. Knowledge of the distribution shape of interacting communities will allow us to make better predictions of environmental quality.

Keywords Tritrophic system · Stability · Habitat loss · Pattern complexity · Bifurcation analysis

1 Introduction

The investigation of relationships between organisms and their biotic and abiotic environments is central in describing and understanding ecological and biological processes. The issues raised require more and more

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a solicitation of tools from complex science theories [7, 8, 16, 38]. In particular, the issue of population interactions is to understand mechanisms impacting the dynamics of trophic food chain.

It is known that ecological communities generally display complex structures that are challenging to integrate into a realistic model [1, 20, 21, 25, 28, 40]. This problem has been considered from the theoretical point of view by Lotka [22–24], followed by Volterra [37]. Lotka has introduced the first model able to elucidate the main features of species interactions and populational cycles in predator–prey systems. However, to gain some more realistic and fundamental understanding of biodiversity conservation or ecosystem loss processes, it is important to take into account spatial degrees of freedom.

Ecosystem loss refers to the disappearance of an ecosystem, or an assemblage of organisms and the physical environment in which they exchange energy and matter. Many studies show the interactions between the effects of disturbances and habitat destruction [15, 30]. Although natural systems are heterogeneous, the direct influence of spatial heterogeneity on most ecological variables is unknown [17, 29, 45]. The lack of spatially explicit, large-scale field studies is identified as a major obstacle to the understanding of fundamental ecological processes. Moreover, the conditions of correlation between the spatial pattern shape and the degree of ecosystem quality are not yet well known.

Turing [35] showed how the coupling of reaction and diffusion can induce pattern formation. Since then, the mechanism responsible for the spontaneous generation of spatial patterns through biological or chemical interactions has been called diffusion instability. The classical Lotka–Volterra type systems are very important in the models of population dynamics. The governing equations for the population densities are described by a system of reaction-diffusion equations, for example, in food webs. A food web can be characterized by a model of complex network, in which a node represents a species Wang et al. [41–44] proposed a class of three-species Lotka–Volterra mutualism models with diffusion, time-varying delay, and linear coupling, which are described by systems of linear parabolic partial differential equations. Ryu and Ahn [31] studied the dynamics of predator–prey interaction systems between two species with ratio-dependent functional responses.

In this paper, we consider a system of reaction-diffusion equations to model the spatiotemporal dynamics of three species linked by a trophic food chain. Our model is based on a modified version of the Leslie–Gower scheme [18, 19]. Modified Leslie and Gower versions was studied by changing the functional response or by adding a third species in the trophic chain [6, 12, 36], also by incorporation a periodic impulsive perturbations [11]. We examine first the mathematical model analysis in Sect. 3 in which we explore the stability of the positive homogeneous equilibrium. Then by numerical simulation in Sect. 4, we focus on complex issues related to patterns of ecosystem loss. Through the analysis of bifurcations, pattern complexity is explored by determining the critical parameter values, which lead to ecosystem changes in a bottom-up scenario of control. We expect that understanding such effects, provide essential tools for the response prediction of communities to global changes or for ecosystem loss.

2 Materials and methods

2.1 Mathematical model

Originally, Leslie and Gower [18] have developed a temporal trophic model without incorporating the spatial dimension. Author in [12] analyzed in detail the nonspatial modified version, which uses the equations below:

$$\begin{cases} \dfrac{dE_1}{dT} = \left(a_0 - b_0 E_1 - \dfrac{v_0 E_2}{E_1 + d_0}\right) E_1 \\ \dfrac{dE_2}{dT} = \left(-a_1 + \dfrac{v_1 E_1}{E_1 + d_0} - \dfrac{v_2 E_3}{E_2 + d_2}\right) E_2, \\ \dfrac{dE_3}{dT} = \left(c_3 - \dfrac{v_3 E_3}{E_2 + d_3}\right) E_3, \end{cases} \quad (1)$$

with $E_1(0) \geq 0$, $E_2(0) \geq 0$, and $E_3(0) \geq 0$ are initial population densities.

E_1 represents the density of prey at time T. E_2 is the density of medium predator at time T and eating E_1. E_3 is the density of top predator at time T and eating E_2. $a_0, b_0, v_0, d_0, a_1, v_1, v_2, d_2, c_3, v_3$, and d_3 are model parameters assuming only positive values.

a_0, (respectively c_3) is the growth rate of prey E_1, (respectively top predator E_3). b_0 measures the strength of competition among individuals of species E_1. v_0 is the maximum value of the per capita reduction rate of E_1 due to E_2. v_1 is the maximum value of the per capita growth rate achieved by E_2. v_2 is the maximum value of the per capita reduction rate of E_2 due to E_3. v_3 is the maximum value that the decay rate that top predator E_3 can reach. d_0 measures the extent to which environment provides protection to prey E_1 and middle predator E_2. a_1 is the natural mortality rate of middle predator E_2. d_3 represents the residual loss, caused by high predation of E_2 top predator E_3.

In order to incorporate into (1) the spatial complexity of interactions, we naturally consider this associated reaction-diffusion system of equations,

$$\begin{cases} \dfrac{\partial U_1}{\partial T} = \left(a_0 - b_0 U_1 - \dfrac{v_0 U_2}{U_1 + d_0}\right) U_1 + \delta_1 \Delta U_1, \\ \qquad T > 0, \\ \dfrac{\partial U_2}{\partial T} = \left(-a_1 + \dfrac{v_1 U_1}{U_1 + d_0} - \dfrac{v_2 U_3}{U_2 + d_2}\right) U_2 + \delta_2 \Delta U_2, \\ \qquad T > 0, \\ \dfrac{\partial U_3}{\partial T} = \left(c_3 - \dfrac{v_3 U_3}{U_2 + d_3}\right) U_3 + \delta_3 \Delta U_3, \quad T > 0 \end{cases}$$

$$(2)$$

where δ_i is the diffusion rate of population i, ($i = 1, 2, 3$) and Δ represent Laplacian operator in a bounded domain Ω_0 of $\mathbb{R}^n$ ($n = 1, 2, 3$). To investi-

gate problem (2), we introduce the following scaling transformations:

$$t = a_0 T, \qquad W_1 = \frac{b_0}{a_0} U_1, \qquad W_2 = \frac{b_0 v_0}{a_0^2} U_2,$$

$$W_3 = \frac{b_0 v_0 v_2}{a_0^3} U_3,$$

$$x = \left(\frac{b_0}{\delta_1}\right)^{\frac{1}{2}} X, \qquad y = \left(\frac{b_0}{\delta_1}\right)^{\frac{1}{2}} Y, \qquad a = \frac{b_0 d_0}{a_0},$$

$$b = \frac{a_1}{a_0}, \qquad c = \frac{v_1}{v_0},$$

$$d = \frac{b_1 v_0}{a_0^2}, \qquad p = \frac{c_3}{a_0}, \qquad q = \frac{v_3}{v_2},$$

$$r = \frac{b_1 v_0 d_3}{a_0^2}, \qquad \varepsilon_1 = 1, \qquad \varepsilon_2 = \frac{a_0 \delta_2}{v_0 \delta_1} \quad \text{and}$$

$$\varepsilon_3 = \frac{a_0 \delta_3}{v_0 v_2 \delta_1}.$$

We obtain the following equations:

$$\begin{cases} \dfrac{\partial W_1}{\partial t} = W_1(1 - W_1) - \dfrac{W_1 W_2}{W_1 + a} + \varepsilon_1 \Delta W_1, \\ \qquad t > 0, \ x \in \Omega \\ \dfrac{\partial W_2}{\partial t} = \dfrac{c W_1 W_2}{W_1 + a} - b W_2 - \dfrac{W_2 W_3}{W_2 + d} + \varepsilon_2 \Delta W_2, \\ \qquad t > 0, \ x \in \Omega \\ \dfrac{\partial W_3}{\partial t} = p W_3 - \dfrac{q W_3^2}{W_2 + r} + \varepsilon_3 \Delta W_3, \\ \qquad t > 0, \ x \in \Omega \end{cases} \tag{3}$$

$-\ \frac{\partial W_1}{\partial \nu} = \frac{\partial W_2}{\partial \nu} = \frac{\partial W_3}{\partial \nu} = 0$ on $\partial \Omega \ t > 0$
$-\ W_1(x, 0) = W_{01}(x), \qquad W_2(x, 0) = W_{02}(x),$
$\quad W_3(x, 0) = W_{03}(x) \ x \in \Omega$

where Ω is a bounded domain in $\mathbb{R}^n$, $n = 1, 2, 3$, with smooth boundary $\partial \Omega$ and Δ is Laplacian operator. ε_1, ε_2, and ε_3 are respectively the diffusion rate of prey, medium predator, and top predator. $\frac{\partial}{\partial \nu} |_{\partial \Omega}$ is the outward normal of $\partial \Omega$. Therefore, the three boundary conditions imply that the region is insular.

$W_1(., t)$, $W_2(., t)$, and $W_3(., t)$ are all densities, so only nonnegative solutions will make sense. In fact, this can be proved by using the comparison principle as long as the initial functions are nonnegative,

[9, 33]. In order to simplify computations let us recall that without diffusion, the scaling system is written as follows:

$$\begin{cases} \dfrac{dE_1}{dt} = E_1(1 - E_1) - \dfrac{E_1 E_2}{E_1 + a}, \\ \dfrac{dE_2}{dt} = \dfrac{c E_1 E_2}{E_1 + a} - b E_2 - \dfrac{E_2 E_3}{E_2 + d}, \\ \dfrac{dE_3}{dt} = p E_3 - \dfrac{q E_3^2}{E_2 + r}. \end{cases} \tag{4}$$

In the mathematical analysis section, we first study the permanence and persistence of solutions of systems (3), then we analyze the stability of the positive homogeneous equilibrium.

2.2 Numerical study

In the section numerical study section, we consider the equation system (2) with positive values of $U_1(x, 0)$, $U_2(x, 0)$, and $U_3(x, 0)$ in domain $\Omega = [0\ 100] \times [0\ 100]$. We set Neumann boundary conditions and fix the following parameter values: $a_0 = 0.7$, $b_0 = 0.25$, $v_0 = 0.3$, $a_1 = 0.4$, $v_1 = 0.8$, $v_2 = 0.4$, $d_2 = 0.4$, $c_3 = 0.2$, $v_3 = 0.6$, $\delta_1 = 0.04$, $\delta_2 = 0.04$, $\delta_3 = 0.002$.

Note that in system (2) environmental prey carrying capacity K equals $\frac{a_0}{b_0}$ and d_0 is its environmental protection. Thus, we define the percentage of protection (pp) by the following ratio: $pp = \frac{d_0}{K} * 100$. This index pp will be used as a measure of the environment quality in a bottom-up control. For a given value of pp, we can determine d_0 and have all the values system (2) parameters.

With the software Matlab R2009b, we solve the system (2) by implementing the combined finite differences method and the method Runge–Kutta 4. In our algorithm, we divide our domain $\Omega = [0\ 100] \times [0\ 100]$ into 500^2 small cells ω_{ij}, $i, j = 1, 2, \dots, 500$. At each time t, we compute the density $U_l^{ij}(t)$ of each species $l = 1, 2, 3$ in the cell ω_{ij}. Thus, we can quantify at time t, the spatial complexity $sc(t)$ of each species distribution using the renormalized Shannon index [32]. For prey population, the spatial complexity $sc(t)$ of the distribution at time t is

$$sc(t) = -\frac{\sum_{i,j=1}^{500} \left(\frac{U_1^{ij}(t)}{K} \ln\left(\frac{U_1^{ij}(t)}{K}\right)\right)}{500^2 + 1}$$

The spatial complexity $sc(t)$ ranges from 0 to 1. In fact, when $sc(t) = 0$ is the completely ordered case equivalent to a uniform spatial distribution in all cells ω_{ij}. $sc(t) = 1$ is the most complex case corresponding to the equal frequency of cells with densities varying from 0 to K.

For a given index value pp, we determine the evolution of the spatial complexity $sc(t)$ over a period between 0 and $T_{max} = 4500$. Then we calculate the mean and standard deviation of the spatial complexity produced by this index pp on this observation period.

3 Mathematical results

3.1 Permanence and persistence of solutions

By standard existence theory, [2–4], it is not difficult to establish the local existence of the unique solution $(W_1(.,t), W_2(.,t), W_3(.,t))$ of (3) for $0 = t < T_{max}$, where T_{max} is determined by $W_{01}(x)$, $W_{02}(x)$, and $W_{03}(x)$. Now we establish the global existence by proving that for any finite time T, $\|W_1(.,t)\|_{L^\infty}$, $\|W_2(.,t)\|_{L^\infty}$, $\|W_3(.,t)\|_{L^\infty}$ are bounded for $0 \leq t < T$.

Theorem 1 *For any smooth nonnegative functions $W_{01}(x) \leq 1$, and $W_{02}(x)$, and $W_{03}(x)$, (3) has a unique smooth global solution for $t > 0$.*

Proof First, it is easily seen that $W_1(x,t) \geq 0$, $W_2(x,t) \geq 0$, and $W_3(x,t) \geq 0$, since 0 is a subsolution of each equation of (3). We have

$$\begin{cases} \dfrac{\partial W_1}{\partial t} \leq W_1(1 - W_1) + \varepsilon_1 \Delta W_1 \\[2mm] \dfrac{\partial W_1}{\partial \nu} = 0, \quad t > 0, \\[2mm] W_1(x,0) = W_{01}(x) \leq \overline{W_{01}} \equiv \max_{\bar{\Omega}} W_{01}(x), \quad x \in \Omega. \end{cases}$$

(5)

By the comparison principle, we have $W_1(x,t) \leq W(t) \leq 1$, where $W(t) = e^t \dfrac{\overline{W_{01}}}{1 - \overline{W_{01}} + e^t}$ is the solution of

the initial value problem:

$$\begin{cases} \dfrac{dW}{dt} = W(1 - W), \\[2mm] W(0) = \overline{W_{01}} \leq 1, \end{cases}$$

(6)

$$\frac{\partial W_2}{\partial t} = \frac{cW_1 W_2}{W_1 + a} - bW_2 - \frac{W_2 W_3}{W_2 + d} + \varepsilon_2 \Delta W_2.$$

By the comparison principle, we deduce that

$$\frac{1}{c}\frac{\partial W_2}{\partial t} \leq \frac{1}{c}\frac{dE_2}{dt}$$

where E_2 is solution of system (4) with initial value $E_2(0) = \max_{\bar{\Omega}} W_{02}(x)$. Thus, from [5, 13],

$$\frac{1}{c}\frac{\partial W_2}{\partial t} \leq \frac{1}{c}\frac{dE_2}{dt} + \frac{dE_1}{dt}.$$

Let us denote by $\sigma = \frac{1}{c}E_2 + E_1$,

$$\frac{1}{c}\frac{\partial W_2}{\partial t} \leq \frac{d\sigma}{dt}$$

$$\leq \frac{1}{4} + b - b\sigma.$$

So,

$$W_2(x,t) \leq c + \frac{c}{4b}, \quad \text{for } 0 \leq t < T.$$

From the third equation of system (3), we have

$$\alpha \frac{\partial W_3}{\partial t} = \alpha p W_3 - \frac{\alpha q W_3^2}{W_2 + r} + \alpha \varepsilon_3 \Delta W_3,$$

with $\alpha = \dfrac{4b}{(b + p)^2(4bc + c + 4br)}.$

By the comparison principle, we deduce that

$$\alpha \frac{\partial W_3}{\partial t} \leq \alpha \frac{dE_3}{dt}$$

where E_3 is solution of system (4) with initial value $E_3(0) = \max_{\bar{\Omega}} W_{03}(x)$.

Thus,

$$\alpha \frac{\partial W_3}{\partial t} \leq \alpha \frac{dE_3}{dt} + \frac{1}{c}\frac{dE_2}{dt} + \frac{dE_1}{dt}$$

$$\leq E_1(1 - E_1) - \frac{b}{c}E_2 - \frac{1}{c}\frac{E_2 E_3}{E_2 + d}$$

$$+ \alpha \left(p - \frac{qE_3}{E_2 + r} \right) E_3$$

$$\leq \frac{1}{4} + b - \alpha b W_3 + \alpha b E_3$$

$$+ \alpha \left(p - \frac{qE_3}{E_2 + r} \right) E_3.$$

So,

$$\alpha \frac{\partial W_3}{\partial t} + \alpha b W_3 \leq \frac{1}{4} + b + M$$

where $M = \frac{1}{4q}$.

Finally,

$$W_3(x, t) \leq \frac{1}{\alpha} + \frac{1}{4\alpha b} + \frac{M}{\alpha b} \quad \text{for } 0 \leq t < T. \qquad \square$$

Theorem 2 *The domain*

$$A \equiv [0, 1] \times \left[0, c + \frac{c}{4b} \right] \times \left[0, \frac{1}{\alpha} + \frac{1}{4\alpha b} + \frac{M}{\alpha b} \right],$$

where

$$\alpha = \frac{4b}{(b + p)^2 (4bc + c + 4br)},$$

is a positively invariant region for the global solutions of system (3).

Proof As we can see before,

$$W_1 \leq E_1, \qquad W_2 \leq E_2, \qquad W_3 \leq E_3,$$

and from [5, 13] we have

$$\overline{\lim}_{t \to +\infty} E_1(t) \leq 1,$$

$$\overline{\lim}_{t \to +\infty} \left(E_1(t) + \frac{1}{c} E_2(t) \right) \leq 1 + \frac{1}{4b},$$

$$\overline{\lim}_{t \to +\infty} \left(E_1(t) + \frac{1}{c} E_2(t) + \alpha E_3 \right) \leq 1 + \frac{1}{4b} + \frac{M}{\alpha b}.$$
$$\qquad \square$$

3.2 Local stability of the positive steady-state solutions

To investigate the stability of positive equilibria, we consider the solutions $W_s(x)$ of system (3),

$$W_s(x) = \left(W_{1s}(x), W_{2s}(x), W_{3s}(x) \right),$$

satisfying $\left(\frac{\partial W_1}{\partial t}, \frac{\partial W_2}{\partial t}, \frac{\partial W_3}{\partial t} \right) = (0, 0, 0)$. Let us consider a solution $W(x, t)$ of system (3) having the following form:

$$\begin{aligned} W(x, t) &= \left(W_1(x, t), W_2(x, t), W_3(x, t) \right) \\ &= W_s(x) + Z(x, t) \\ &= W_s + \left(Z_1(x, t), Z_2(x, t), Z_3(x, t) \right). \end{aligned} \quad (7)$$

Let us substitute $W(x, t)$ with the form (7) into system (3) and then pick up all the terms which are linear in Z:

$$\frac{\partial Z}{\partial t} = D \Delta Z + L(W_s) Z, \qquad (8)$$

where

$$D = \text{diag}(\varepsilon_1, \varepsilon_2, \varepsilon_3),$$

$$L(W_s) = \begin{pmatrix} F_{W_1} & F_{W_2} & F_{W_3} \\ G_{W_1} & G_{W_2} & G_{W_3} \\ H_{W_1} & H_{W_2} & H_{W_3} \end{pmatrix} \qquad (9)$$

with

$$F_{W_1} = 1 - 2W_1 - \frac{aW_2}{(W_1 + a)^2},$$

$$F_{W_2} = -\frac{W_1}{W_1 + a},$$

$$F_{W_3} = 0,$$

$$G_{W_1} = \frac{acW_2}{(W_1 + a)^2},$$

$$G_{W_2} = \frac{cW_1}{W_1 + a} - b - \frac{dW_3}{(W_2 + d)^2},$$

$$G_{W_2} = -\frac{W_2}{W_2 + d},$$

$$H_{W_1} = 0,$$

$$H_{W_2} = \frac{qW_3^2}{(W_2 + d)^2},$$

$$H_{W_3} = p - \frac{2qW_3}{W_2 + d}.$$

Theorem 3 *A necessary condition for W_s to be locally stable is, at W_s,*

$$F_{W_1} + G_{W_2} + H_{W_3} < 0,$$

$$F_{W_1} G_{W_2} + F_{W_1} H_{W_3} + G_{W_2} H_{W_3} - F_{W_2} G_{W_1}$$

$$- F_{W_3} H_{W_1} - G_{W_3} H_{W_2} > 0,$$

$$F_{W_1} G_{W_3} H_{W_2} + F_{W_2} G_{W_1} H_{W_3} + F_{W_3} G_{W_2} H_{W_1}$$
$$- F_{W_1} G_{W_2} H_{W_3} - F_{W_2} G_{W_3} H_{W_1} - F_{W_3} G_{W_1} H_{W_2}$$
$$> 0.$$

Proof Let ϕ_j denote the jth eigenfunction of $-\Delta$ on Ω with homogeneous Neumann boundary condition. That is,

$$\begin{cases} -\Delta \phi_j = \lambda_j \phi_j, & \text{in } \Omega \\ \left. \dfrac{\partial \phi_j}{\partial \nu} \right|_{\partial \Omega} = 0 \end{cases} \tag{10}$$

for scalar λ_j satisfying $0 = \lambda_0 < \lambda_1 < \lambda_2 < \cdots$.

We expand the solution Z of Eq. (8) via

$$Z = \sum_{j=0}^{\infty} z_j(t) \phi_j(x, y), \tag{11}$$

where each $z_j(t) \in \mathbb{R}^n$. Using the form of Z given in (11) into Eq. (8) and equating the coefficients of each ϕ_j, we have

$$\frac{dz_j}{dt} = C_j z_j,$$

where C_j is the matrix

$$C_j = L(W_s) - \lambda_j D.$$

Now the solution W_s is stable if and only if each $z_j(t)$ decays to zero. This is equivalent to the condition that each C_j has three eigenvalues with negative real parts. The eigenvalues ρ_k, $k = 1, 2, 3$, of C_j are determined by

$$\rho^3 + a\rho^2 + b\rho + c = 0,$$

where

$$a = \lambda_j(\varepsilon_1 + \varepsilon_2 + \varepsilon_3) - (F_{W_1} + G_{W_2} + H_{W_3}),$$

$$b = \lambda_j^2(\varepsilon_1\varepsilon_2 + \varepsilon_1\varepsilon_3 + \varepsilon_2\varepsilon_3) - \lambda_j(\varepsilon_1 G_{W_2} + \varepsilon_1 H_{W_3}$$
$$+ \varepsilon_2 F_{W_1} + \varepsilon_2 H_{W_3} + \varepsilon_3 F_{W_1} + \varepsilon_3 G_{W_2})$$
$$+ F_{W_1} G_{W_2} + F_{W_1} H_{W_3} + G_{W_2} H_{W_3} - F_{W_2} G_{W_1}$$
$$- F_{W_3} H_{W_1} + G_{W_3} H_{W_2},$$

$$c = \lambda_j^3 \varepsilon_1\varepsilon_2\varepsilon_3 - \lambda_j^2(\varepsilon_1\varepsilon_2 H_{W_3} + \varepsilon_1\varepsilon_3 G_{W_2} + \varepsilon_2\varepsilon_3 F_{W_1})$$

$$+ \lambda_j(\varepsilon_1 G_{W_2} H_{W_3} + \varepsilon_2 F_{W_1} H_{W_3} + \varepsilon_3 F_{W_1} G_{W_2}$$
$$- \varepsilon_1 G_{W_3} H_{W_2} - \varepsilon_2 F_{W_3} H_{W_1} - \varepsilon_3 F_{W_2} G_{W_1})$$
$$+ F_{W_1} G_{W_3} H_{W_2} + F_{W_2} G_{W_1} H_{W_3} + F_{W_3} G_{W_2} H_{W_1}$$
$$- F_{W_1} G_{W_2} H_{W_3} - F_{W_2} G_{W_3} H_{W_1} - F_{W_3} G_{W_1} H_{W_2}. \tag{12}$$

Now the three eigenvalues all have negative real part implies that

$$F_{W_1} + G_{W_2} + H_{W_3} - \lambda_j(\varepsilon_1 + \varepsilon_2 + \varepsilon_3) < 0, \tag{13}$$

$$F_{W_1} G_{W_2} + F_{W_1} H_{W_3} + G_{W_2} H_{W_3} - F_{W_2} G_{W_1}$$
$$- F_{W_3} H_{W_1} + G_{W_3} H_{W_2} - \lambda_j(\varepsilon_1 G_{W_2}$$
$$+ \varepsilon_1 H_{W_3} + \varepsilon_2 F_{W_1} + \varepsilon_2 H_{W_3} + \varepsilon_3 F_{W_1} + \varepsilon_3 G_{W_2})$$
$$+ \lambda_j^2(\varepsilon_1\varepsilon_2 + \varepsilon_1\varepsilon_3 + \varepsilon_2\varepsilon_3) > 0, \tag{14}$$

$$F_{W_1} G_{W_3} H_{W_2} + F_{W_2} G_{W_1} H_{W_3} + F_{W_3} G_{W_2} H_{W_1}$$
$$- F_{W_1} G_{W_2} H_{W_3} - F_{W_2} G_{W_3} H_{W_1} - F_{W_3} G_{W_1} H_{W_2}$$
$$+ \lambda_j(\varepsilon_1 G_{W_2} H_{W_3} + \varepsilon_2 F_{W_1} H_{W_3} + \varepsilon_3 F_{W_1} G_{W_2}$$
$$- \varepsilon_1 G_{W_3} H_{W_2} - \varepsilon_2 F_{W_3} H_{W_1} - \varepsilon_3 F_{W_2} G_{W_1})$$
$$- \lambda_j^2(\varepsilon_1\varepsilon_2 H_{W_3} + \varepsilon_1\varepsilon_3 G_{W_2} + \varepsilon_2\varepsilon_3 F_{W_1})$$
$$+ \lambda_j^3 \varepsilon_1\varepsilon_2\varepsilon_3 > 0. \tag{15}$$

In particular, these three inequalities should hold for $j = 0$.

For $j = 0$, they are reduced to

$$F_{W_1} + G_{W_2} + H_{W_3} < 0, \tag{16}$$

$$F_{W_1} G_{W_2} + F_{W_1} H_{W_3} + G_{W_2} H_{W_3} - F_{W_2} G_{W_1}$$
$$- F_{W_3} H_{W_1} + G_{W_3} H_{W_2} > 0, \tag{17}$$

$$F_{W_1} G_{W_3} H_{W_2} + F_{W_2} G_{W_1} H_{W_3} + F_{W_3} G_{W_2} H_{W_1}$$
$$- F_{W_1} G_{W_2} H_{W_3} - F_{W_2} G_{W_3} H_{W_1}$$
$$- F_{W_3} G_{W_1} H_{W_2} > 0. \tag{18}$$

$\square$

Recall the assumptions that guarantee the existence of positive steady states are

$$F_{W_2} \le 0, \qquad F_{W_3} \le 0, \qquad G_{W_1} \ge 0, \qquad G_{W_3} \le 0,$$
$$H_{W_1} \ge 0, \qquad H_{W_2} \ge 0.$$

Under these conditions, by using the Routh–Hurwitz criteria (see [14]), we can obtain sufficient conditions

for the stability of the positive steady state solutions. But it is too complicated for the general situation. If the positive steady state is constant, denoted by (W_1^*, W_2^*, W_3^*), we can prove the following theorem about the sufficient conditions.

Theorem 4 *Let us assume that*

$$p < 2, \quad b > \frac{c}{a} \quad and \quad a \in \,]7 - 4\sqrt{3}, 7 + 4\sqrt{3}[.$$

The homogeneous positive steady state solution $W_s = (W_1^*, W_2^*, W_3^*)$ is locally stable.

Proof From the proof of Theorem 3, we know that we need only to prove that the solutions of

$$\rho^3 + a\rho^2 + b\rho + c = 0,$$

have negative real parts, where a, b, c are given by (12). From the Routh–Hurwitz criteria, we know that it is true if

$$a > 0, \qquad ab - c > 0, \qquad abc - c^2 > 0.$$

To have this, we need only have $a > 0$, $ab > c > 0$.

From condition (12), we need, for all $j \geq 0$,

$$\left\{ \lambda_j(\varepsilon_1 + \varepsilon_2 + \varepsilon_3) - (F_{W_1} + G_{W_2} + H_{W_3}) > 0 \quad (19) \right.$$

$$\left\{ \begin{aligned}
& \lambda_j^3 \left(2\varepsilon_1\varepsilon_2\varepsilon_3 + \varepsilon_1^2\varepsilon_2 + \varepsilon_1^2\varepsilon_3 + \varepsilon_1\varepsilon_2^2 + \varepsilon_1\varepsilon_3^2 + \varepsilon_3\varepsilon_2^2 \right. \\
& \left. + \varepsilon_2\varepsilon_3^2 \right) - \lambda_j^2 \left(\varepsilon_1^2 G_{W_2} + \varepsilon_1^2 H_{W_3} + \varepsilon_2^2 F_{W_1} \right. \\
& \left. + \varepsilon_2^2 H_{W_3} + \varepsilon_3^2 F_{W_1} + \varepsilon_3^2 G_{W_2} + 2\varepsilon_1\varepsilon_2 F_{W_1} \right) \\
& - \lambda_j^2 (2\varepsilon_1\varepsilon_2 H_{W_3} + 2\varepsilon_1\varepsilon_3 F_{W_1} + 2\varepsilon_1\varepsilon_3 G_{W_2} \\
& + 2\varepsilon_1\varepsilon_2 G_{W_2}) - \lambda_j^2 (2\varepsilon_1\varepsilon_3 H_{W_3} + 2\varepsilon_2\varepsilon_3 F_{W_1} \\
& + 2\varepsilon_2\varepsilon_3 G_{W_2} + 2\varepsilon_2\varepsilon_3 H_{W_3}) + \lambda_j \left(\varepsilon_1 G_{W_2}^2 \right. \\
& + \varepsilon_1 H_{W_3}^2 + \varepsilon_2 F_{W_1}^2 + \varepsilon_2 H_{W_3}^2 + \varepsilon_3 F_{W_1}^2 \\
& + \varepsilon_3 G_{W_2}^2 + 2\varepsilon_1 F_{W_1} G_{W_2} + 2\varepsilon_1 F_{W_1} H_{W_3} \\
& + 2\varepsilon_1 G_{W_2} H_{W_3} - \varepsilon_1 F_{W_2} G_{W_1} - \varepsilon_1 F_{W_3} H_{W_1} \\
& + 2\varepsilon_2 F_{W_1} G_{W_2} + 2\varepsilon_2 F_{W_1} H_{W_3} + 2\varepsilon_2 G_{W_2} H_{W_3} \\
& - \varepsilon_2 F_{W_2} G_{W_1} - \varepsilon_3 G_{W_3} H_{W_2} + 2\varepsilon_3 F_{W_2} u G_{W_2} v \\
& + 2\varepsilon_3 F_{W_1} H_{W_3} w + 2\varepsilon_3 G_{W_2} H_{W_3} - \varepsilon_3 F_{W_3} H_{W_1} \\
& \left. - \varepsilon_3 G_{W_3} H_{W_2} \right) - F_{W_1}^2 G_{W_2} - F_{W_1}^2 H_{W_3} \\
& - 2 F_{W_1} G_{W_2} H_{W_3} + F_{W_1} F_{W_2} G_{W_1} + F_{W_1} F_{W_3} H_{W_1} \\
& - F_{W_1} G_{W_2}^2 - G_{W_2}^2 H_{W_3} + F_{W_2} G_{W_1} G_{W_2} \\
& + G_{W_2} G_{W_3} H_{W_2} + F_{W_2} G_{W_3} H_{W_1} + F_{W_3} G_{W_1} H_{W_2} \\
& - F_{W_1} H_{W_3}^2 - G_{W_2} H_{W_3}^2 + F_{W_3} H_{W_1} H_{W_3} \\
& + G_{W_3} H_{W_2} H_{W_3} > 0,
\end{aligned} \right.$$

$$\left\{ \begin{aligned}
& \lambda_j^3 \varepsilon_1\varepsilon_2\varepsilon_3 - \lambda_j^2 (\varepsilon_1\varepsilon_2 H_{W_3} + \varepsilon_1\varepsilon_3 G_{W_2} + \varepsilon_2\varepsilon_3 F_{W_1}) \\
& + \lambda_j (\varepsilon_1 G_{W_2} H_{W_3} + \varepsilon_2 F_{W_1} H_{W_3} + \varepsilon_3 F_{W_1} G_{W_2} \\
& - \varepsilon_1 G_{W_3} H_{W_2} - \varepsilon_3 F_{W_2} G_{W_1} - \varepsilon_2 F_{W_3} H_{W_1}) \\
& + F_{W_1} G_{W_3} H_{W_2} + F_{W_2} G_{W_1} H_{W_3} + F_{W_3} G_{W_2} H_{W_1} \\
& - F_{W_1} G_{W_2} H_{W_3} - F_{W_2} G_{W_3} H_{W_1} \\
& - F_{W_3} G_{W_1} H_{W_2} > 0.
\end{aligned} \right.$$

Observing that $\lambda_j \geq 0$, we need only

$$\left\{ F_{W_1} + G_{W_2} + H_{W_3} < 0, \right. \qquad (20)$$

$$\left\{ \begin{aligned}
& \lambda_j^2 \left(\varepsilon_1^2 G_{W_2} + \varepsilon_1^2 H_{W_3} + \varepsilon_2^2 F_{W_1} + \varepsilon_2^2 H_{W_3} + \varepsilon_3^2 F_{W_1} \right. \\
& \left. + \varepsilon_3^2 G_{W_2} + 2\varepsilon_1\varepsilon_2 F_{W_1} + 2\varepsilon_1\varepsilon_2 H_{W_3} + 2\varepsilon_1\varepsilon_3 F_{W_1} \right. \\
& + 2\varepsilon_1\varepsilon_3 G_{W_2} + 2\varepsilon_1\varepsilon_2 G_{W_2} \\
& + 2\varepsilon_1\varepsilon_3 H_{W_3} + 2\varepsilon_2\varepsilon_3 F_{W_1} + 2\varepsilon_2\varepsilon_3 G_{W_2} \\
& \left. + 2\varepsilon_2\varepsilon_3 H_{W_3} \right) - \lambda_j \left(\varepsilon_1 G_{W_2}^2 + \varepsilon_1 H_{W_3}^2 + \varepsilon_2 F_{W_1}^2 \right. \\
& + \varepsilon_2 H_{W_3}^2 + \varepsilon_3 F_{W_1}^2 + \varepsilon_3 G_{W_2}^2 + 2\varepsilon_1 F_{W_1} G_{W_2} \\
& + 2\varepsilon_1 F_{W_1} H_{W_3} + 2\varepsilon_1 G_{W_2} H_{W_3} - \varepsilon_1 F_{W_2} G_{W_1} \\
& - \varepsilon_1 F_{W_3} H_{W_1} + 2\varepsilon_2 F_{W_1} G_{W_2} + 2\varepsilon_2 F_{W_1} H_{W_3} \\
& + 2\varepsilon_2 G_{W_2} H_{W_3} - \varepsilon_2 F_{W_2} G_{W_1} - \varepsilon_3 G_{W_3} H_{W_2} \\
& + 2\varepsilon_3 F_{W_2} u G_{W_2} v + 2\varepsilon_3 F_{W_1} H_{W_3} w \\
& + 2\varepsilon_3 G_{W_2} H_{W_3} - \varepsilon_3 F_{W_3} H_{W_1} \\
& \left. - \varepsilon_3 G_{W_3} H_{W_2} \right) + F_{W_1}^2 G_{W_2} - F_{W_1}^2 H_{W_3} \\
& - 2 F_{W_1} G_{W_2} H_{W_3} + F_{W_1} F_{W_2} G_{W_1} + F_{W_1} F_{W_3} H_{W_1} \\
& - F_{W_1} G_{W_2}^2 - G_{W_2}^2 H_{W_3} + F_{W_2} G_{W_1} G_{W_2} \\
& + G_{W_2} G_{W_3} H_{W_2} + F_{W_2} G_{W_3} H_{W_1} + F_{W_3} G_{W_1} H_{W_2} \\
& - F_{W_1} H_{W_3}^2 - G_{W_2} H_{W_3}^2 + F_{W_3} H_{W_1} H_{W_3} \\
& + G_{W_3} H_{W_2} H_{W_3} < 0,
\end{aligned} \right.$$

$$\qquad (21)$$

$$\left\{ \begin{aligned}
& \lambda_j^2 (\varepsilon_1\varepsilon_2 H_{W_3} + \varepsilon_1\varepsilon_3 G_{W_2} + \varepsilon_2\varepsilon_3 F_{W_1}) \\
& - \lambda_j (\varepsilon_1 G_{W_2} H_{W_3} + \varepsilon_2 F_{W_1} H_{W_3} + \varepsilon_3 F_{W_1} G_{W_2} \\
& - \varepsilon_1 G_{W_3} H_{W_2} - \varepsilon_3 F_{W_2} G_{W_1} - \varepsilon_2 F_{W_3} H_{W_1}) \\
& - F_{W_1} G_{W_3} H_{W_2} - F_{W_2} G_{W_1} H_{W_3} - F_{W_3} G_{W_2} H_{W_1} \\
& + F_{W_1} G_{W_2} H_{W_3} + F_{W_2} G_{W_3} H_{W_1} \\
& + F_{W_3} G_{W_1} H_{W_2} < 0.
\end{aligned} \right.$$

$$\qquad (22)$$

At

$$W_1^* = \frac{a(bq + p)}{qc - bq - p},$$
$$W_2^* = (1 - W_1^*)(W_1^* + a),$$
$$W_3^* = \frac{p(W_2^* + r)}{q},$$

and thanks to the hypothesis of the theorem,

$$H_{W_3} = p - 2 < 0,$$
$$G_{W_2} = c\frac{W_1^*}{W_1^* + a} - b - \frac{d}{W_2^* + d}$$
$$= \frac{(c - b)W_1^* - ab}{W_1^* + a} - \frac{d}{W_2^* + d} < 0,$$

and,

$$F_{W_1} = 1 - 2W_1^* - \frac{a(1 - W_1^*)}{W_1^* + a}$$
$$= \frac{-2(W_1^*)^2 + (a + 1)W_1^* - 2a}{W_1^* + a} < 0.$$

The second and third inequalities (21) and (22) hold because we have, $F_{W_1} < 0$, $F_{W_2} < 0$, $F_{W_3} = 0$, $G_{W_1} \geq 1$, $G_{W_2} < 0$, $G_{W_3} < 0$, $H_{W_1} = 0$, $H_{W_2} > 0$, $H_{W_3} < 0$.

This completes the proof of the theorem. □

3.3 Global stability of the positive steady-state solutions

Theorem 5 *Let us assume that*

$$b < c, \quad 1 - a < W_1^* < \frac{ab}{c - b}, \quad and \tag{23}$$
$$W_2^* < d(c - b).$$

Then, the homogeneous positive steady state solution (W_1^*, W_2^*, W_3^*) is globally asymptotically stable.

Proof Let us denote by

$$\phi(W_1, W_2, W_3)$$
$$= \int_{W_1^*}^{W_1} \frac{\eta - W_1^*}{\eta} \, d\eta + \int_{W_2^*}^{W_2} \frac{(\eta - W_2^*)(\eta + d)}{\eta} \, d\eta$$
$$+ \int_{W_3^*}^{W_3} \frac{\eta - W_3^*}{\eta} \, d\eta, \tag{24}$$

$$\Phi(W_1, W_2, W_3) = \int_\Omega \phi(W_1, W_2, W_3) \, dx. \tag{25}$$

We need to prove that Φ is a Lyapunov function, so we have to show that $\frac{d\Phi}{dt} < 0$.

$$\frac{d\Phi}{dt} = \int_\Omega \frac{d\phi(W_1, W_2, W_3)}{dt} \, dx$$
$$= I_1 + I_2. \tag{26}$$

We have

$$I_1 = \int_\Omega \left[\frac{W_1 - W_1^*}{W_1} \left(W_1(1 - W_1) - \frac{W_1 W_2}{W_1 + a} \right) \right.$$
$$+ \frac{(W_2 - W_2^*)(W_2 + d)}{W_2} \left(\frac{cW_1 W_2}{W_1 + a} - bW_2 \right.$$
$$\left. - \frac{W_2 W_3}{W_2 + d} \right) + \frac{W_3 - W_3^*}{W_3} \left(pW_3 - \frac{q W_3^2}{W_2 + r} \right) \right] dx$$
$$= \int_\Omega \left[\frac{W_1 - W_1^*}{W_1 + a} ((1 - W_1)(W_1 + a) - W_2 + W_2^* \right.$$
$$- (1 - W_1^*)(W_1^* + a)) + \frac{(W_2 - W_2^*)(W_2 + d)}{W_2}$$
$$(cW_1(W_2 + d) - b(W_1 + a)(W_2 + d)$$
$$- W_3(W_1 + a) - cW_1^*(W_2^* + d)$$
$$- b(W_1^* + a)(W_2^* + d) - W_3^*(W_1^* + a))$$
$$\left. + (W_2 - W_2^*) \left(\frac{q W_3^*}{W_2^* + r} - \frac{q W_3}{W_2 + r} \right) \right] dx$$
$$= -\int_\Omega (W_1 - W_1^*, W_2 - W_2^*, W_3 - W_3^*)$$
$$\times B(W_1 - W_1^*, W_2 - W_2^*, W_3 - W_3^*)^T \, dx, \tag{27}$$

where

$$\begin{pmatrix} \frac{W_1 + W_1^* + a - 1}{W_1 + a} & \frac{W_3^* - (c - b)(W_2^* + d)}{W_1 + a} & 0 \\ \frac{1}{W_1 + a} & \frac{ab - (c - b)W_1^*}{W_1 + a} & -\frac{p}{W_2 + r} \\ 0 & 1 & \frac{q}{W_2 + r} \cdot \end{pmatrix}. \tag{28}$$

From hypothesis (23), the matrix B is positive, and consequently $I_1 < 0$.

On the other hand, we have

$$I_2 = \int_\Omega \left[\varepsilon_1 \frac{W_1 - W_1^*}{W_1} \Delta W_1 \right.$$
$$+ \varepsilon_2 \frac{(W_2 - W_2^*)(W_2 + d)}{W_2} \Delta W_2$$
$$\left. + \varepsilon_3 \frac{W_3 - W_3^*}{W_3} \Delta W_3 \right] dx$$

$$= -\varepsilon_1 \int_\Omega |\nabla W_1|^2 \frac{W_1^*}{W_1} \, dx \qquad\qquad -\varepsilon_3 \int_\Omega |\nabla W_3|^2 \frac{W_3^*}{W_3} \, dx < 0. \tag{29}$$

$$-\varepsilon_2 \int_\Omega |\nabla W_2|^2 \frac{W_2 + dW_2^*}{W_2} \, dx \qquad\qquad \text{This completes the proof.} \qquad\qquad \square$$
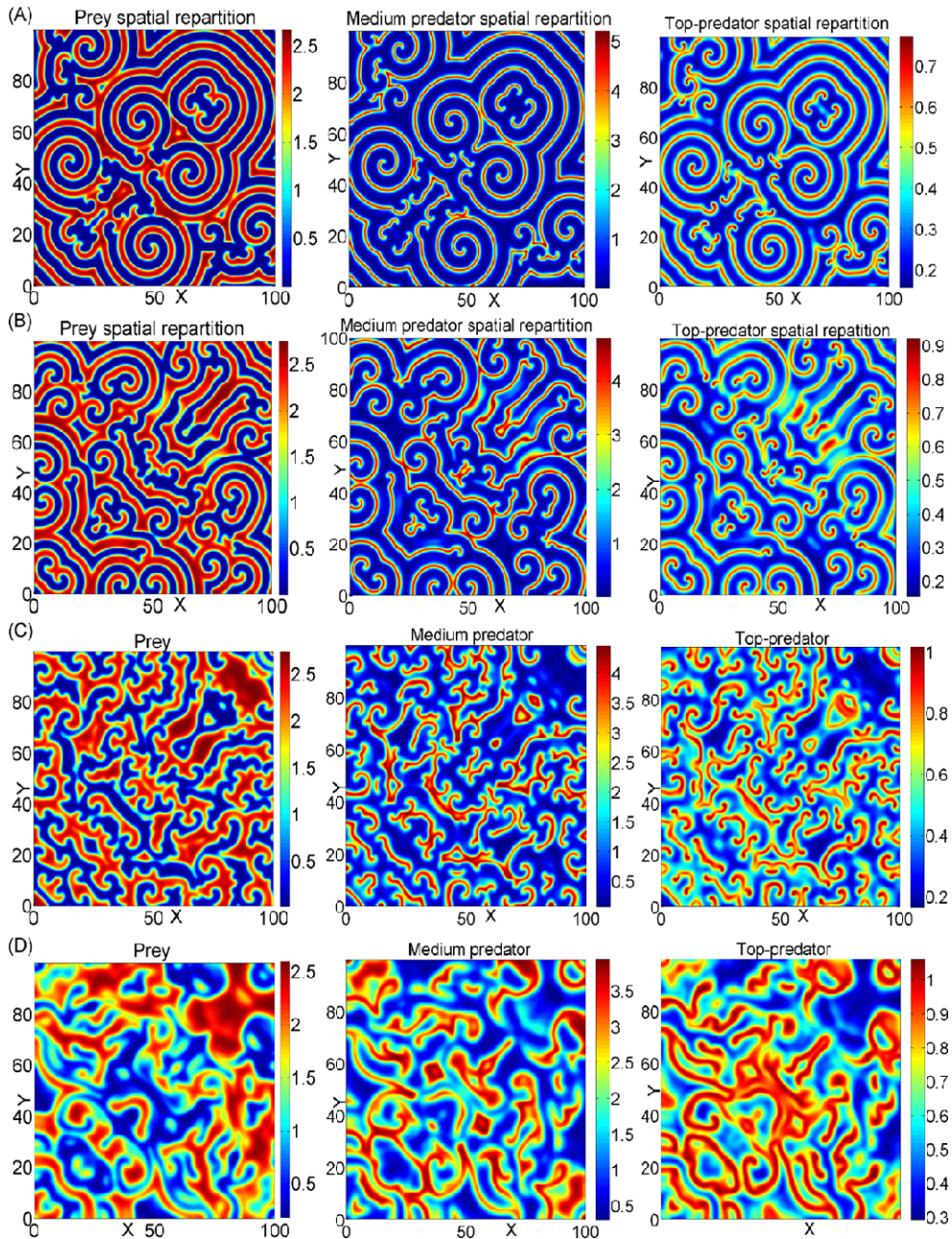

Fig. 1 Spatial distribution of communities of prey, medium predator, and top predator at time $t = 4500$, for different index values of environmental quality, in (**A**) $pp = 5$, in (**B**) $pp = 10$, in (**C**) $pp = 15$, in (**D**) $pp = 20$
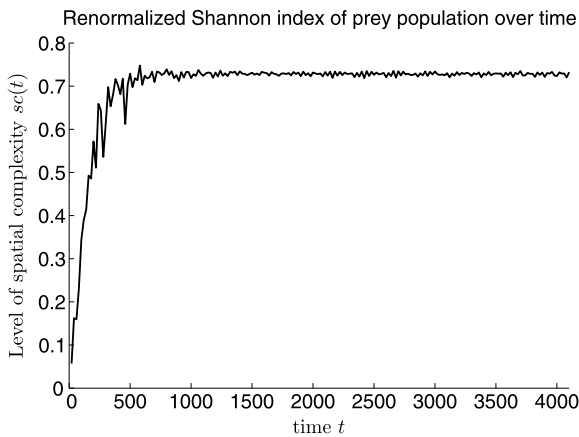
Fig. 2 Dynamics of prey spatial complexity sc(t), for a given proportion of protection $pp = 10$

Fig. 3 Mean and standard deviation of spatial complexity of prey pattern over environment quality

4 Numerical results of far-from equilibrium dynamics

Figure 1(A) corresponding to a percentage of protection $pp = 5$, shows the distribution of communities of prey, medium predator, and top predator in the domain Ω at time $T_{\max}$. Thus the system is far-from-equilibrium. Figures 1(B), (C), and (D) are obtained for $pp = 10$, $pp = 15$, and $pp = 20$. Thus, variations in the percentage of protection pp impact significantly on the qualitative aspects of the pattern of different communities. The pattern structures are more ordered for lower values of pp than for higher values.

For a given percentage of protection pp, the pattern structure produced by each community is not static (see Fig. 2). It varies in time with a strong increase in the spatial complexity sc(t) at the beginning of observations and with small oscillation amplitudes beyond $t = 500$ (see Fig. 2). In practice, several measures are therefore necessary for a better approximation of sc(t).

Qualitative differences of patterns (Fig. 1) induced by the change in pp are quantified in Fig. 3. Thus, the average value of the spatial complexity sc(t) is an increasing function of the proportion of protection index pp, with $pp \in [1, 20]$. This average value of sc(t) in neighborhoods of equilibria decreases, before to vanish.

5 Conclusions and discussions

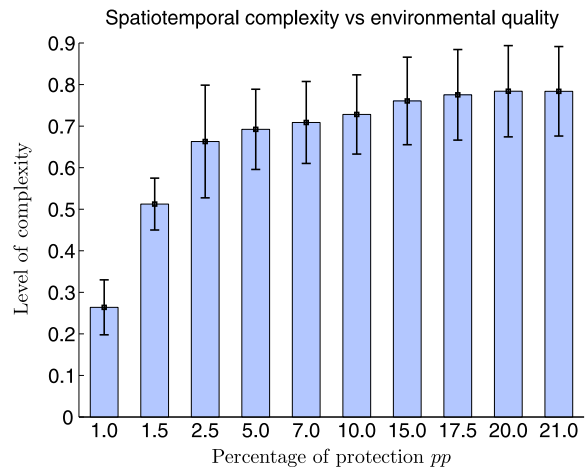In this study, we first perform the local stability analysis of the positive equilibrium homogeneous of our spatiotemporal system modeling three species interaction dynamics. Then we established the conditions for global stability of this positive equilibrium homogeneous by constructing a Lyapunov function. We show numerically that a low prey environmental protection produces light pressure on species leading to the extinction of prey population and medium predator population. This means the system converges to the homogeneous equilibrium $(0, 0, \frac{c_3 d_3}{v_3})$. However, a high prey environmental protection makes the population of medium predator vulnerable and increases the risk of extinction. Therefore, the system converges to the homogeneous equilibrium $(K, 0, \frac{c_3 d_3}{v_3})$. Through direct habitat changing, bottom-up effects lead to a cascade of fluctuations only for far-from equilibrium ecosystems. This helps to capture and quantify the differences between order and disorder. Moreover, this helps to establish the conditions of positive correlation between the spatial distribution complexity and the degree of environmental protection for species. However, the attractors of ecosystem equilibria alter the correlation between environmental quality and the spatial pattern of species. However, although our model is composed of three species, diversity is low and interspecies competition is not considered. These factors can be considered in the future.

Obviously, the measurement of pattern complexity is critical for understanding and preventing the ling bursting risk from environmental quality changes. This confirms the importance of the spatial dimension [10, 26, 27, 34, 39] in the study of ecosystem conservation and supports the work of dos Santos et al. [30],

which state that predictions of the impacts of changing disturbance rates on biodiversity depend on community structure and cannot be made without knowledge of concurrent permanent habitat destruction. A detailed evaluation of ecosystem loss before restoration and a precise understanding of the factors structuring assemblages in the systems to be restored appear to be prerequisites [17]. Furthermore, these measurements can provide precision characterization and quantification for the spatial characteristics in biomonitoring approaches.

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