A Minimalistic model of spatial structuration of humid savanna vegetation

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ABSTRACT. In this work, we propose a spatio-temporal tree-grass interactions model, allowing to account for a possibly periodic spatial structuring sometimes observes in humid savanna zone. The proposed model relies on an integro-differential reaction-diffusion system, involving kernels of intra and inter-specific interactions. From a linear stability analysis performed in the vicinity of a homogeneous stationary state that denotes tree-grass coexistence, we succeed first to find a condition for the appearance of periodic solutions in space with predictable wavelength and second, to illustrate it numerically.

RÉSUMÉ. Dans ce travail, nous proposons un modèle spatio-temporel d'interactions arbres-herbes, permettant de rendre compte d'une structuration spatiale éventuellement périodique parfois observée en zone de savane humide. Le modèle proposé repose sur un système de réaction-diffusion intégro-différentiel, impliquant des noyaux d'interactions spatiales intra et inter spécifique. A partir d'une analyse de stabilité linéaire realisée au voisinage d'un état stationnaire de coexistence, nous réussissons premièrement, à trouver une condition pour l'apparition de solutions périodiques en espace avec une longueur d'onde prévisible et deuxièmement, nous illustrons cette condition numériquement.

KEYWORDS : Tree, Grass, Non local interaction, fire, Turing Bifurcation.

MOTS-CLÉS : Arbre, Herbe, Interactions non locales, feu, Bifurcation de Turing.

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1. Introduction

Savannas are complex ecosystems where, trees and grasses coexist permanently without one species excluding the other. In Africa, savannas occupy 50% of the land area, or 15.1 million km^2 [5]. Being able to predict, the spatial structuring of vegetation mainly in humid zones, is therefore part of maintaining bio-diversity in the face of recurring climatic changes in Africa. The mechanisms that allow this tree-grass coexistence, have been the subject of several researches in ecology known as savanna problem:"how tree and grass coexists over a wide climatic, edaphic and historical condition?"[3]. The essential factors for maintaining this coexistence, encountered in the literature include: fire, herbivory, rains, nutriments, soil texture. In fact, several research groups have produced results using modeling with Ordinary Differential Equations (ODE), Impulsive Differential Equations (IDE) or Partial Differential Equations (PDE). The most of works done using PDE was carried out in arid or semi-arid environmental context, using a reaction-diffusion-advection system (emphasizing the dynamics of vegetation and water) or, using an integro-differential equation, where kernel model interactions between plants. In humid environment, mathematical models that tackle the issue of vegetation patterns in humid savannas are very scarce. However, some authors proposed: first, CA models to explain, formation of vegetation patterns in arid and semi-arid savannas and how trees can invade the grass stratum in humid savannas despite repeated fires [1]. Second, IDE models to predict the physiognomies of the vegetation along the gradient of precipitation highlighting the effect of fires on tree-grass coexistence ([6, 8]).

Our objective is therefore to build a mathematical tractable spatio-temporal model allowing, to illustrate the spatial structuration of vegetation in wet savanna zone and specifically in Cameroon. This model will highlight the fire resistance strategies of trees.

2. Model construction

Our model follow the IDE model of Tchuinté et al. [7] and the ODE version of Yatat et al. [9]. We consider two state variables, $G(t)$ and $T(t)$ that stand for the the grassy biomass and the woody biomass at time t respectively. In [7, 9], the following hypotheses are done:

– Tree and grass biomasses have a logistic growth.

– Mortality at the level of herbs is related to external factors (grazing, termites,...), interactions with trees and fire.

– Tree mortality results from external factor (browsers,...) or is fire-induced.

– Fires occur impulsively at each moment t_n.

Neglecting the pulse effect of fires, we have incorporated a spatial component on the state variables. Hence, $G(x,t)$ and $T(x,t)$ denote the normalized densities of the respective biomass of grass and tree populations at a spatial point x and at a time t. We put the following assumptions:

• Trees and grasses populations, have a logistic growth but with an intra-specific competition which takes place in a non-local way, thanks to the respective root systems of the two species. In fact, trees (respectively grasses) located at a point x, can consume re-

sources (water, nutriment) at point y where, another trees (respectively grasses) is located. Then,

$$T(x,t) \int_{-\infty}^{+\infty} \phi_{M_2}(x-y)T(y,t)dy \text{ and } G(x,t) \int_{-\infty}^{+\infty} \phi_{M_1}(x-y)G(y,t)dy \quad (1)$$

describes this non-local intra specific competition where, for $i = 1, 2$, the kernel $\phi_{M_i}(x-y)$ represents, the efficiency of consumption of resources in the area $[-M_i; M_i]$ of the space domain.

• trees exert competition on grasses in a non-local way. The consequence here is to reduce the grass continuum on the ground, which will reduce the spread of fire. Indeed a tree located at a point y can, either by its root system or by the shade created by its crown, reduces the density of grasses located at a point x by reducing the resources in x. Then,

$$G(x,t) \int_{-\infty}^{+\infty} \phi_{M_2}(x-y)T(y,t)dy \quad (2)$$

describes this non-local inter-specific competition.

• The function describing the intensity of fires, $\omega(G)$, is a non linear and increasing function of the grass density, that we take under the form of a Holling Type III function (see also [7, 9])

$$\omega(G) = \frac{G^2}{G^2 + g_0^2}, \quad (3)$$

where g_0^2 is the grass biomass at which fires reach its half maximal intensity.

• We insert a probability of fire induced-tree mortality at a space point x. If trees are numerous, less the fire harm. Then, tree mortality will be reduced. This probability is therefore, a decreasing function of tree density. Referring to the work of [4], this probability in a point x of the space is:

$$\mathcal{V}_T(x) = \exp\left(-p\int_{-\infty}^{+\infty} \phi_{M_2}(x-y)T(y,t)dy\right). \quad (4)$$

• Moreover, according to [2], trees facilitate the germination and the recruitment of new trees by improving the conditions under the canopy. Then, we assume that there is a factor of cooperation $\Omega \in [0;1]$ between trees promoting regrowth and growth of young trees and allowing it to reach a threshold of non-vulnerability.

• We suggest, according to [9], that grass biomass and tree biomass, experience local isotropic biomass propagation in space with the coefficient D_G and D_T respectively.

All this leads to the following model:

$$\begin{cases} \dfrac{\partial G}{\partial t} &= D_G \dfrac{\partial^2 G}{\partial x^2} + \gamma_G G\left(1 - \int_{-\infty}^{+\infty} \phi_{M_1}(x-y)G(y,t)dy\right) - \delta_G G - \\ & \quad \gamma_{TG}G\left(\int_{-\infty}^{+\infty} \phi_{M_2}(x-y)T(y,t)dy\right) - \lambda_{fG}fG, \\ \dfrac{\partial T}{\partial t} &= D_T \dfrac{\partial^2 T}{\partial x^2} + \gamma_T T(1+\Omega T)\left(1 - \int_{-\infty}^{+\infty} \phi_{M_2}(x-y)T(y,t)dy\right) - \delta_T T - \\ & \quad \lambda_{fT}f\omega(G)\exp\left(-p\int_{-\infty}^{+\infty} \phi_{M_2}(x-y)T(y,t)dy\right)T, \end{cases}$$

$$(5)$$

where $x \in [-L; L]$ and $t > 0$, with non negative and sufficiently smooth initial data. In addition, we also consider homogeneous Newman boundary condition at $-L$ and L. For $0 \leq M_i \leq L$, we consider the kernels:

$$\phi_{M_i}(x) = \begin{cases} \dfrac{1}{2M_i} & , \quad |x| \leq M_i \\ 0 & , \quad |x| > M_i \end{cases} \quad i = 1, 2;$$

with ϕ_0 a dirac function and $\int_{-\infty}^{+\infty} \phi_{M_i}(y) dy = 1$.

Symbols	Definition	Units
γ_G	Intrinsic growth of grass	$t.ha^{-1}$
δ_G	Grass biomass loss due to human activities and herbivory	$t.ha^{-1}$
λ_{fG}	Grass biomass loss due to fire	
γ_{TG}	Tree grass interaction parameters	$ha.t^{-1}.yr^{-1}$
γ_T	Intrinsic growth of trees	yr^{-1}
δ_T	Tree biomass loss due to human activities and herbivory	yr^{-1}
λ_{fT}	Tree biomass loss due to fire	
p	proportionnal to the inverse of biomass suffering and intermediate level of mortality	$t^{-1}.ha$
Ω	Cooperation factor	
f	fire frequency	
D_G	Grass biomass diffusion rate	$ha^2.yr^{-1}$
D_T	Tree biomass diffusion rate	$ha^2.yr^{-1}$

Table 1: Definition of parameters used in model (5)

3. Linear stability analysis

3.1. Linear stability analysis in the local case $(M_1 = M_2 = 0)$

In this part, we are interested in the behavior of homogeneous stationary solutions, notably in the characterization of savanna equilibrium (i.e. an equilibrium where $T > 0$ and $G > 0$) stability properties. Homogeneous stationary solutions of (5) are solutions of system (6):

$$\begin{cases} \gamma_G G(1 - G) - \delta_G G - \gamma_{TG} TG - \lambda_{fG} fG & = 0, \\ \gamma_T T(1 + \Omega T)(1 - T) - \delta_T T - \lambda_{fT} f\omega(G) \exp(-pT)T & = 0. \end{cases} \quad (6)$$

It is assumed that (see also [7, 9]):

$$\gamma_T - \delta_T > 0 \text{ and } \gamma_G - \delta_G > 0. \quad (7)$$

Conditions in (7) means that, desert cannot be stable (see for instance [7, 9]). Set:

$$\mathcal{R}_G = \frac{\gamma_G}{\delta_G + f\lambda_{fG}} \text{ and } \mathcal{R}_F = \frac{\gamma_G}{\delta_G + \lambda_{fG}f + \gamma_{TG}T_i}.$$

The following result is valid.

Proposition 3.1. *(Trivial equilibrium and semi trivial equilibrium)*

1) *If $\mathcal{R}_G \leq 1$, then system* (5) *admits two homogeneous stationary solutions:*

    a) desert equilibrium $E_0 = (0; 0)$.

    b) forest equilibrium:

        $*$ *if $\Omega = 0$, then $E_{T_1} = \left(0; \dfrac{\gamma_T - \delta_T}{\gamma_T} \right)$ is the forest equilibrium in case of no*

    tree-tree facilitation.

        $*$ *if $\Omega > 0$, then $E_{T_2} = \left(0; \dfrac{\sqrt{(1-\Omega)^2 + 4\Omega\left(1 - \frac{\delta_T}{\gamma_T}\right)} - (1-\Omega)}{2\Omega} \right)$ is the*

    forest equilibrium with tree-tree facilitation.

2) *If $\mathcal{R}_G > 1$ then we have the desert equilibrium E_0, the forest equilibrium E_{T_i}, $(i = 1, 2)$ and a grassland equilibrium:*

$$E_{G_e} = (G_e; 0) = \left((1 - \frac{\delta_G + f\lambda_{fG}}{\gamma_G}); 0 \right) = \left(1 - \frac{1}{\mathcal{R}_G}; 0 \right).$$

We are now interested in the coexistence equilibrium (savanna equilibrium). Set:

$$a = -\frac{\lambda_{fG}f + \delta_G}{\gamma_{TG}}, \quad b = \frac{\gamma_G}{\gamma_{TG}}, \quad \theta = 2(a+b)b\Omega\gamma_T + \gamma_T(1-\Omega)b$$

$$\alpha = \Omega\gamma_T b^2, \quad q = (\gamma_T - \delta_T) + \gamma_T(\Omega-1)(a+b) - \Omega\gamma_T(a+b)^2, \quad m = \lambda_{fT}f\exp\left(-p(a+b)\right)$$

$$\theta^* = \frac{24\alpha + mpb\left((pb)^2 + 6(pb) + 6\right)\exp(pb)}{6}.$$

Straightfoward computations lead the following result.

Proposition 3.2. *(Savanna equilibrium)*

- $f = 0$. *If $\mathcal{R}_{F,f=0} > 1$, then we have the unique savanna equilibrium $E_s = (G^*, T^*)$ such that*

$$G^* = 1 - \frac{1}{\mathcal{R}_{F,f=0}} \quad \text{and} \quad T^* = T_i, i = 1, 2. \tag{8}$$

- $f > 0$. *If $\mathcal{R}_G > 1$, then a savanna equilibrium $E_s = (G^*, T^*)$ musth satisfy these two relations:*

$$-\alpha(G^*)^4 + \theta(G^*)^3 - m\exp(pbG^*)(G^*)^2 + (q - \alpha g_0^2)(G^*)^2 + \theta g_0^2 G^* + q g_0^2 = 0, \tag{9}$$

and

$$T^* = (a+b) - bG^*. \tag{10}$$

Moreover G^* must satisfy the inequality

$$\max\left\{ G_e - \frac{\gamma_{TG}}{\gamma_G}; 0 \right\} < G^* < G_e. \tag{11}$$

We can therefore summarize the maximum number of savanna equilibrium according to the following case:

• **Case 1**: $\theta < mpb$

Condition	$q < m + \alpha g_0^2$	$q > m + \alpha g_0^2$
Maximal number of savanna equilibria	2	3

Table 2: Maximal number of savanna equilibria of (5) with $\theta < mpb$

• **Case 2**: $\theta > mpb$,

Condition	$\theta < \theta^*$	$\theta > \theta^*$
Maximal number on savanna equilibria	4	3

Table 3: Maximal number of savanna equilibria of (5) with $\theta > mpb$

Let us look now at the conditions of stability of a savanna equilibrium when it exists. Considering the space-implicit system related to system (5), we obtain that the Jacobian matrix at savanna equilibrium has the entries $(a_{i,j})_{1 \leq i,j \leq 2}$ where:

$$
\begin{aligned}
a_{11} &= -\gamma_G G^*, \\
a_{12} &= -\gamma_{TG} G^*, \\
a_{21} &= -\lambda_{fT} f \omega'(G^*) \exp(-pT^*) T^*, \\
a_{22} &= -\gamma_T \left[(1-\Omega)T^* + 2\Omega(T^*)^2\right] + p\lambda_{fT} f \omega(G^*) \exp(-pT^*) T^*.
\end{aligned}
$$

The savanna equilibrium is locally asymptotically stable when:

$$ a_{11} + a_{22} < 0 \quad \text{and} \quad a_{11}a_{22} - a_{21}a_{12} > 0. \tag{12} $$

From (12), we define the following thresholds:

$$ \mathcal{R}_1^* = \frac{\gamma_T \left[(1-\Omega) + 2\Omega T^*\right]}{p\lambda_{fT} f \omega(G^*) \exp(-pT^*)} \quad \text{and} \quad \mathcal{R}_2^* = \frac{\gamma_{TG}\omega'(G^*)}{p\gamma_G\omega(G^*)}, \tag{13} $$

and then, we have this proposition.

Proposition 3.3. *(Stability Condition of a savanna equilibrium)*
The stability condition of a coexistence equilibrium when it exists in the absence of non local interactions ($M_1 = M_2 = 0$) is given by:

• *case 1: Assume that $f = 0$, then $E_s = (G^*, T^*)$ is locally asymptotically stable (LAS) without any condition.*

• *case 2: Assume that $f > 0$, then if:*

$$ \mathcal{R}_1^* - \mathcal{R}_2^* > 1 \tag{14} $$

then $E^* = (G^*, T^*)$ is locally asymptotically stable..

Remark 1. *(i) $\mathcal{R}_G = \dfrac{\gamma_G}{\delta_G + f\lambda_{fG}}$ denotes the primary production of grass biomass relative to grass biomass loss due to grazing or human action and additional fire-induced biomass loss.*

(ii) $\mathcal{R}_F = \dfrac{\gamma_G}{\delta_G + f\lambda_{fG} + \gamma_{TG}T_i}$ represents the primary production of grass biomass, relative to grass biomass loss induced by fire, herbivory (grazing) or human action and additional grass suppression due to tree competition, at the closed forest equilibrium.

3.2. Linear analysis stability of savanna equilibruim in the non-local case

Our aim now is to derive a condition on spatial convolution such that the savanna equilibrium $(G^*; T^*)$ is locally stable in the case $M_1 = M_2 = 0$, but unstable for some $M_i > 0$, $i = 1, 2$.

Set $c = \gamma_T \Omega T^*(1 - T^*)$. For $g(x, t) = G(x, t) - G^*$ and $h(x, t) = T(x, t) - T^*$, two perturbations around the savanna equilibrium. The system obtained after linearization is:

$$\begin{cases} \dfrac{\partial g}{\partial t} &= D_G \dfrac{\partial^2 g}{\partial x^2} + a_{11} \displaystyle\int_{-\infty}^{+\infty} \phi_{M_1}(x - y)g(y, t)dy + a_{12} \int_{-\infty}^{+\infty} \phi_{M_2}(x - y)h(y, t)dy, \\ \dfrac{\partial h}{\partial t} &= D_T \dfrac{\partial^2 h}{\partial x^2} + (a_{22} - c)\displaystyle\int_{-\infty}^{+\infty} \phi_{M_2}(x - y)h(y, t)dy + ch + a_{21}g. \end{cases}$$

(15)

Then, by considering the eigenvalue problem of the system (15) where λ is the eigenvalue and taking the Fourier transform of this eigenvalue problem, we obtain the following system:

$$\begin{cases} \lambda\overline{g}(k) &= -D_G k^2 \overline{g}(k) + a_{11}\overline{\phi_{M_1}}(k)\overline{g}(k) + a_{12}\overline{\phi_{M_2}}(k)\overline{h}(k), \\ \lambda\overline{h}(k) &= -D_T k^2 \overline{h}(k) + c\overline{h}(k) + (a_{22} - c)\overline{\phi_{M_2}}(k)\overline{h}(k) + a_{21}\overline{g}(k), \end{cases}$$

(16)

where k is the wavenumber ($k \in \mathbb{R}$) with $\overline{\phi_{M_i}}(k) = \dfrac{\sin kM_i}{kM_i}$, $i = 1, 2$ where, $\overline{g}(k)$, $\overline{h}(k)$ and $\overline{\phi_{M_i}}(k)$ are the Fourier transforms of the functions $g(x, t)$, $p(x, t)$, $\phi_{M_i}(x)$.

Proposition 3.4. *(Characteristic equation)*
The characteristic equation of system (16) *is:*

$$\lambda^2 - Tr(k, M_1, M_2)\lambda + Det(k, M_1, M_2) = 0,$$

(17)

where:

$$Tr(k, M_1, M_2) = -(D_G + D_T)k^2 + a_{11}\overline{\phi_{M_1}}(k) + a_{22}\overline{\phi_{M_2}}(k) + (1 - \overline{\phi_{M_2}}(k))c$$

and

$$\begin{aligned} Det(k, M_1, M_2) &= D_G D_T k^4 - \left[a_{22}D_G\overline{\phi_{M_2}}(k) + a_{11}D_T\overline{\phi_{M_1}}(k) + cD_G(1 - \overline{\phi_{M_2}}(k))\right]k^2 + \\ &\quad a_{11}(a_{22} - c)\overline{\phi_{M_1}}(k)\overline{\phi_{M_2}}(k) + ca_{11}\overline{\phi_{M_1}}(k) - a_{12}a_{21}\overline{\phi_{M_2}}(k). \end{aligned}$$

From the characteristic equation (17), we can write the stability conditions of the savanna equilibrium (G^*, T^*) as follows:

$$Tr(k, M_1, M_2) < 0,$$

(18)

and

$$Det(k, M_1, M_2) > 0.$$

(19)

If (18) holds and (19) is not satisfied, then there is a real eigenvalue crossing the origin. Initially ($k = M_1 = M_2 = 0$), (18) and (19) hold. So, we find the thresholds k^T, M_1^T and M_2^T, so that (19) is not satisfied (it is call Turing Bifurcation). Then, this threshold satisfies:

$$Det(k, M_1, M_2) = 0, \quad \frac{\partial Det(k, M_1, M_2)}{\partial M_1} = 0, \quad \frac{\partial Det(k, M_1, M_2)}{\partial M_2} = 0, \quad \frac{\partial Det(k, M_1, M_2)}{\partial k} = 0.$$

(20)

With the given conditions in (20) we have:

Proposition 3.5. *(Stationary pattern condition)*
Consider z_1 and z_2 two positive solutions of the equation $\tan(z) = z$ $(z_1 < z_2)$ such that: $\mu_j = \dfrac{\sin z_j}{z_j} < 0, \;\; j = 1, 2.$ Then, suppose that:

$$\frac{a_{11}(c - a_{22})\mu_1\mu_2}{ca_{11}\mu_1 - a_{12}a_{21}\mu_2} < 1. \tag{21}$$

If:

$$M_j > M_j^T = z_j \left(\frac{D_G D_T}{(a_{11}a_{22} - ca_{11})\,\mu_1\mu_2 + ca_{11}\mu_1 - a_{12}a_{21}\mu_2} \right)^{1/4}, \;\; j = 1, 2 \tag{22}$$

and

$$k > k^T = \left(\frac{(a_{11}a_{22} - ca_{11})\,\mu_1\mu_2 + ca_{11}\mu_1 - a_{12}a_{21}\mu_2}{D_G D_T} \right)^{1/4}, \tag{23}$$

then we have the appearance of periodic solutions in space in the neighborhood of savanna equilibrium.

Because of the difficulty of interpretation of condition (21), we find a sufficient condition to the previous one. Note that if $c - a_{22} > 0$ then (21) is verified. Then, set:

$$\mathcal{R}_3^* = \frac{\gamma_T(1 + \Omega T^*)}{p\lambda_{fT} f\omega(G^*)\exp(-pT^*)}.$$

Remark 2. – *If $\mathcal{R}_3^* > 1$, then we have all results in the Proposition 3.5.*

– *$\mathcal{R}_3^*$ is the primary production of tree biomass and additional production of tree biomass due to tree-tree facilitation relative to fire induced tree biomass loss.*

– *The period σ of the spatial structures at the stability boundary is:*

$$\sigma = \frac{2n\pi}{k^T} = 2n\pi \left(\frac{D_G D_T}{(a_{11}a_{22} - ca_{11})\,\mu_1\mu_2 + ca_{11}\mu_1 - a_{12}a_{21}\mu_2} \right)^{1/4}, \;\; n \in \mathbb{N}^*.$$

– *Condition (22) give the rank beyond which the non-local interactions are necessary for the coexistence of both tree and grass species in the same domain.*

4. Numerical illustration

To illustrate the condition in the Proposition 3.5, we consider the value in Table 4 as parameters of our model (5). With this choice of parameters, we find that the savanna

Parameters	D_G	D_T	γ_G	δ_G	γ_T	δ_T	f	λ_{fG}	λ_{fT}	p	γ_{TG}	g_0	Ω
Values	1	1	3.1	0.1	1.5	0.015	0.6	0.5	0.7	0.15	0.04	2	0.8

Table 4: Parameter values for simulation

equilibrium $E^* = (0.03; 0.99)$ is locally asymptotically stable in absence of non-local interactions.

Then, the minimal positive value solution of the equation $\tan(z) = z$ is $z_1 = 4.49$. We take $z_2 = 10.9$ also solution of $\tan(z) = z$.

From these two values we find $\mu_1 = -0.22$, $\mu_2 = -0.09$ and we get the Turing bifurcation condition: $M_1 > 7.12m$ and $M_2 > 17.28m$.

Numerical simulations of model (5) are carried out in the interval $[-150; 150]$. We consider the initial data as a random perturbation around the savanna equilibrium (G^*, T^*), then

$$G(x,0) = G^* + \epsilon_1, \ \ T(x,0) = T^* + \epsilon_2 \ \text{ with } \ 0 \leq \epsilon_i \leq 1 \times 10^{-3}.$$

We observe from Figure 1 that, the solutions of system (5) converge toward a space inhomogeneous tree-grass coexistence solution thanks, to a Turing bifurcation.
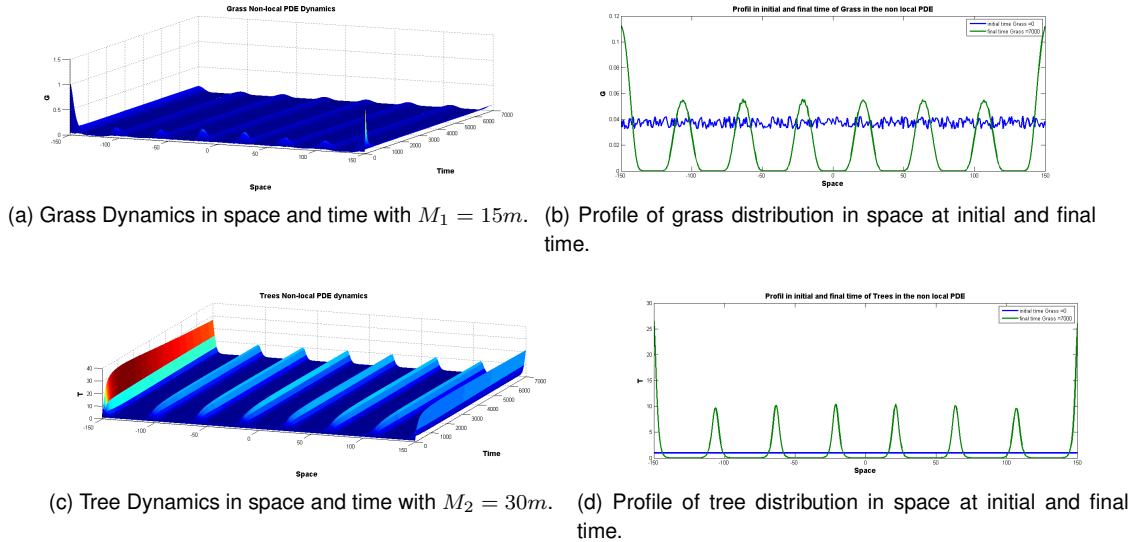

(a) Grass Dynamics in space and time with $M_1 = 15m$. (b) Profile of grass distribution in space at initial and final time.

(c) Tree Dynamics in space and time with $M_2 = 30m$. (d) Profile of tree distribution in space at initial and final time.

Figure 1: Illustration of Grass and Tree distribution and their profile in space at initial and final times.

5. Conclusion

In this paper, we developed a spatio-temporal model able to illustrate the spatial structuring of the vegetation in wet savanna zone. We find, thanks to linear stability analysis, a necessary condition about the ranks of non-local interactions for the coexistence of trees and grasses in the same space domain.

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7. Appendix: Proof of Proposition 3.6

Suppose that $\dfrac{a_{11}(c - a_{22})\mu_1\mu_2}{ca_{11}\mu_1 - a_{12}a_{21}\mu_2} < 1$, we have:

$$
\begin{aligned}
Det(k, M_1, M_2) = {} & D_G D_T k^4 - \left[a_{22} D_G \overline{\phi_{M_2}}(k) + a_{11} D_T \overline{\phi_{M_1}}(k) + c D_G (1 - \overline{\phi_{M_2}}(k)) \right] k^2 + \\
& a_{11}(a_{22} - c)\overline{\phi_{M_1}}(k)\overline{\phi_{M_2}}(k) + ca_{11}\overline{\phi_{M_1}}(k) - a_{12}a_{21}\overline{\phi_{M_2}}(k)
\end{aligned}
$$

and

$$
\overline{\phi_{M_i}}(k) = \frac{\sin(kM_i)}{kM_i}, \quad i = 1, 2.
$$

We are interested by the determination of thresholds k^T, M_1^T and M_2^T so that:

$$
Det(k^T, M_1^T, M_2^T) = 0.
$$

These thresholds are solution of the equations:

$$
Det(k, M_1, M_2) = 0, \quad \frac{\partial Det(k, M_1, M_2)}{\partial M_1} = 0, \quad \frac{\partial Det(k, M_1, M_2)}{\partial M_2} = 0 \quad \frac{\partial Det(k, M_1, M_2)}{\partial k} = 0 \tag{24}
$$

Differentiating $Det(k, M_1, M_2)$ with respect to M_1 and M_2 and use the fact that: $\dfrac{\partial Det(k, M_1, M_2)}{\partial M_1} = 0$ and $\dfrac{\partial Det(k, M_1, M_2)}{\partial M_2} = 0$ we obtain:

$$
(a_{11}a_{22} - ca_{11})\left(\phi_{M_2}(k) + \frac{ca_{11} - a_{11}D_T k^2}{a_{11}a_{22} - ca_{11}} \right)\frac{\partial \overline{\phi_{M_1}}}{\partial M_1} = 0,
$$

and:

$$(a_{11}a_{22} - ca_{11})\left(\phi_{M_1}(k) - \frac{D_G(a_{22} - c)k^2 + a_{12}a_{21}}{a_{11}a_{22} - ca_{11}}\right)\frac{\partial\overline{\phi_{M_2}}}{\partial M_2} = 0.$$

We suppose that:

$$\overline{\phi_{M_1}}(k) \neq \frac{D_G(a_{22} - c)k^2 + a_{12}a_{21}}{a_{11}a_{22} - ca_{11}} \text{ and } \overline{\phi_{M_2}}(k) \neq \frac{-ca_{11} + a_{11}D_Tk^2}{a_{11}a_{22} - ca_{11}}$$

then:

$$\frac{\partial\overline{\phi_{M_1}}}{\partial M_1} = 0 \text{ and } \frac{\partial\overline{\phi_{M_2}}}{\partial M_2} = 0$$

and we obtain

$$\tan(kM_1) = kM_1 \text{ and } \tan(kM_2) = kM_2.$$

Set $z_1 = kM_1$ and $z_2 = kM_2$, then z_1 and z_2 are solution of :

$$\tan(z) = z. \tag{25}$$

Set:

$$\mu_1 = \frac{\sin(z_1)}{z_1} \text{ and } \mu_2 = \frac{\sin(z_2)}{z_2}$$

$Det(k, M_1, M_2) = 0$ give that:

$$(k^T)^2 = \frac{D_G a_{22}\mu_2 + a_{11}D_T\mu_1 + cD_G(1 - \mu_2) + \sqrt{\Sigma}}{2D_G D_T} \tag{26}$$

with

$$\Sigma = (D_G a_{22}\mu_2 + a_{11}D_T\mu_1 + cD_G(1 - \mu_2))^2 - 4D_G D_T\left((a_{11}a_{22} - ca_{11})\mu_1\mu_2 - a_{12}a_{21}\mu_2 + ca_{11}\mu_1\right)$$

and use the fact that $\dfrac{\partial Det(k, M_1, M_2)}{\partial k} = 0$, we obtain:

$$(D_G a_{22}\mu_2 + a_{11}D_T\mu_1 + cD_G(1 - \mu_2))^2 = 4D_G D_T\left((a_{11}a_{22} - ca_{11})\mu_1\mu_2 - a_{12}a_{21}\mu_2 + ca_{11}\mu_1\right) \tag{27}$$

$(a_{11}a_{22} - ca_{11})\mu_1\mu_2 - a_{12}a_{21}\mu_2 + ca_{11}\mu_1 > 0$ because of assumption in (21) then, the relation in (27) is well defined and therefore:

$$(k^T)^2 = \sqrt{\frac{(a_{11}a_{22} - ca_{11})\mu_1\mu_2 - a_{12}a_{21}\mu_2 + ca_{11}\mu_1}{D_G D_T}} \tag{28}$$

and the values of M_1 and M_2 associated are

$$M_1^T = z_1\left(\frac{D_G D_T}{(a_{11}a_{22} - ca_{11})\mu_1\mu_2 + ca_{11}\mu_1 - a_{12}a_{21}\mu_2}\right)^{1/4}, \tag{29}$$

and

$$M_2^T = z_2\left(\frac{D_G D_T}{(a_{11}a_{22} - ca_{11})\mu_1\mu_2 + ca_{11}\mu_1 - a_{12}a_{21}\mu_2}\right)^{1/4}. \tag{30}$$