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Revisiting the Logistic Growth with Random Disturbances

Abstract We reconsider a one-dimensional probabilistic model of a fire-induced tree-grass coexistence in savannas introduced by D'Odorico, Laio and Ridolfi in [5]. We rewrite it as a logistic growth model with random tree biomass losses caused by fire occurring at random times. We study it by using the stochastic semigroup theory and we give new sufficient conditions for the existence and stability of a unique stationary density of woody biomass.

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Key words and phrases: population dynamics, logistic growth, ecological modeling, savanna, savanna question, stationary density, piecewise deterministic Markov processes.

1. Introduction Population dynamics models in ecology use mathematical tools to study changes of parameters such as population size or age distribution. During over 100 years of population ecology history, theoretical ecologists/biologists and mathematicians developed many different approaches to the problem. Nowadays, modeling approaches are based on variations of the basic ones like the Lotka–Volterra model or the logistic population model. The latter, despite being one of the first and simple, is extremely useful and has been used recently [5] to help address the so-called *savanna question*[11].

Savannas cover roughly 20% of the Earth's land surface and are mixed woodland-grassland ecosystems characterized by open canopy of woody vegetation. There are many environmental disturbances that are said to be responsible for such tree-grass coexistence, including: seasonal rainfalls, grazing and browsing of animals, human activity, and especially fires. Regular fires are characteristic for tropical savannas. The main sources of ignitions are lightnings and human activity (e.g. [13]). Similarly to [7] we work with a model where tree-grass coexistence is induced by fire-vegetation feedbacks emphasizing significant role of fires in stabilizing savannas [6]. Existing in literature disturbance-driven savanna models including fires differ in applied mathematical methods, e.g. [3] they use the loop analysis for graphs while the model presented in [15] is based on impulsive differential equations.

In this paper we put the probabilistic model of [5] on a firm mathematical ground. We propose a logistic growth model of the biomass of trees with random disturbances that exhibits the same type of behaviour. We assume that a random fraction of the biomass survives random occurrences of fires leading to an appropriate piecewise deterministic Markov process (PDMP) [4]. In our previous work (jointly with M. Tyran-Kamińska) [7] we assumed that always the same fraction of trees survives each fire. We study the existence of a unique stationary density of the trees biomass. We also show its stability when it exists by using the results of [8]. Asymptotic properties of randomly disturbed population growth models have been studied recently in [9], where it was assumed that the time of occurrence of disturbances is modelled as a Poisson process with constant intensity λ. In our model the intensity depends on the current amount of the biomass which is the extension of results from [9, Section 5] to non-constant λ.

2. Logistic tree biomass model of mesic savanna We give a brief description of a minimalistic model of tree-grass coexistence in fire-prone semi-arid ecosystems given in [5]. The authors considered the case of mesic savannas where the tree-grass coexistence cannot appear without disturbances, and interspecies competition just slows down the growth of dominating woody vegetation. Fires damage both, trees and grasses, but much slower growth of woody vegetation enables grasses to occupy space left available by trees [12, 14]. Between the fires trees reclaim the space form grasses by outcompeting them since no niche separation is assumed. Without fires it is a simple 1-dimensional model with a state variable reflecting the total woody biomass (a classical logistic growth). The authors assumed that the ecosystem carrying capacity is constant so the state variable can be normalized to be a given fraction of it. Namely, the tree biomass is denoted by $v \in [0, 1]$ in the logistic equation of the form:

$$\frac{dv}{dt} = \alpha v(1 - v) - vF(t, v), \tag{1}$$

where $F(t, v)$ is a noise reflecting the random occurrences of fire and α is the tree growth rate. The grass biomass is assumed to be proportional to the resources left available by trees. Equation (1) is interpreted in [5] as a stochastic differential equation with multiplicative noise. This model supports the "disequilibrium" theories of tree-grass coexistence in savannas via fire-vegetation feedbacks (e.g. [1]).

We consider a similar logistic model with tree biomass losses being due to random fires and rewrite it as an appropriate piecewise deterministic Markov process (PDMP). Using the tools of linear semigroup theory we provide a more careful analysis of the model.

We begin the description of the model with some modeling assumptions: again a state variable $v \in [0, 1]$ denotes the tree biomass, the grass biomass is assumed to be proportional to $1 - v$ (remaining resources that are being reclaimed by trees in periods between fires), and fires are discrete in time events resulting with the woody biomass losses. In the absence of fires the tree biomass is modeled by a classical logistic equation:

$$\frac{dv}{dt} = \alpha v(1 - v) \tag{2}$$

with some growth rate constant $\alpha > 0$. So, the stable stationary point $v = 0$ reflects the landscape dominated by grasses while for $v > 0$ we have a system describing a logistic growth of the biomass of trees leading to a maximal woody vegetation amount for a given area (in reality in such a situation there would still be grass in the space between the trees so the biomass of grasses we refer to is actually the fraction of it occupying the space left available by trees and not the total biomass). Let $\pi_t(w) = v(t)$ be the solution of (2) with initial condition $v(0) = w$. We have

$$\pi_t(w) = \frac{w}{w + e^{-\alpha t}(1 - w)}, \quad w \in [0, 1].$$

Now we add fires into the model by introducing the random disturbances of a woody biomass growth at random times $(t_n)_{n \geqslant 1}$. Let $t_0 = 0$ and denote by $\xi(t_0) = w$ some initial tree biomass amount (an arbitrary value from $(0, 1]$). The system evolves according to equation (2) in periods $t \in (t_{n-1}, t_n), n = 1, 2, \ldots,$ between the consecutive fire occurrences, so that we have $\xi(t) = \pi_{t-t_{n-1}}(\xi(t_{n-1}))$. For each $n \in \mathbb{N}$ the biomass loss is given by:

$$\xi(t_n) = (1 - \theta_n)\xi(t_n^-), \tag{3}$$

where $(\theta_n)_{n \geqslant 1}$ is a sequence of independent random variables taking values from the interval $(0, 1)$ with some density h and we use the short notation for left limits $\xi(t_n^-) = \lim_{s \to t_n^-} \xi(s)$. We characterize occurrences of fire by introducing a sequence of random variables $(\sigma_n)_{n \geqslant 1}$ such that:

$$\begin{cases} t_n = t_{n-1} + \sigma_n \text{ for } n \geqslant 1, \\ \Pr\big(\sigma_n > t \mid \xi(t_{n-1}) = w\big) = e^{-\int_0^t \lambda(\pi_s(w))ds}, \end{cases} \tag{4}$$

where $\lambda \colon [0, 1] \to \mathbb{R}_+$ with $\lambda(0) > 0$ is a bounded continuous function reflecting the fire intensity. Note that this model is a more general case of a continuous time model considered in [9, p. 501, eq. 9] where the authors considered the situation with λ being a constant. Here the fire intensity depends on the current amount of biomass, so more real factors can be taken into account, e.g. the fuel load for fires is provided mainly by the biomass of grasses and after the main result of this paper we consider λ from [5] as an example taking this into account. In the next section we provide sufficient conditions for the existence of the unique stationary density of the tree biomass actually reflecting the savanna specific tree-grass codominance.

Observe that if $\xi(0)=0$, then $\xi(t)=0$ for all t. Thus, we restrict our analysis to $(0,1]$.

3. Results for the model

The process $\xi(t), t \geqslant 0$, is an example of PDMP with state space $(0,1]$. Denote by D the subset of the space $L^1 = L^1(0,1]$ which contains all densities, i.e.

$$D = \{f \in L^1 : f \geqslant 0, \int_0^1 |f(v)|dv = 1\}.$$

Let $p(t,v)$ be the probability density of $\xi(t)$, namely $p(t,\cdot) \in D$ and satisfies

$$\Pr(\xi(t) \in B) = \int_B p(t,v)dv$$

for any Borel subset of $(0,1]$. Then, p is a solution of the following Fokker-Planck type equation

$$\frac{\partial p(t,v)}{\partial t} + \frac{\partial}{\partial v}\big(\alpha v(1-v)p(t,v)\big) = -\lambda(v)p(t,v) + \int_v^1 h\left(1-\frac{v}{w}\right)\frac{\lambda(w)}{w}p(t,w)dw, \quad (5)$$

where h is the probability density of the random variables θ_n. This equation is supplemented with the initial condition

$$p(0,v) = f(v), \quad f \in D, \quad (6)$$

(f is the probability density of $v(0)$).

We assume that the function λ is continuous and a strictly positive function on $[0,1]$. We consider two conditions:

$$\alpha + \lambda(0)\int_0^1 \ln(1-z)h(z)dz > 0 \quad (7)$$

and

$$\alpha\bar{\lambda} + \underline{\lambda}^2 \int_0^1 \ln(1-z)h(z)dz < 0, \quad (8)$$

where $\bar{\lambda} = \sup\{\lambda(v) : v \in [0,1]\}$ and $\underline{\lambda} = \inf\{\lambda(v) : v \in [0,1]\}$. Observe that

$$\alpha + \lambda(0)\int_0^1 \ln(1-z)h(z)dz \leqslant \alpha\frac{\bar{\lambda}}{\underline{\lambda}} + \underline{\lambda}\int_0^1 \ln(1-z)h(z)dz$$

and equality holds when λ is a constant function. We have the following result that extends [9, Theorem 5.1] to non-constant λ:

Theorem 3.1 *If condition (7) holds true, then there exists a unique density $p_*(v)$ which is a stationary solution of (5) and every solution of (5)–(6) converges to it, i.e.*

$$\lim_{t\to\infty}\int_0^1 \big|p(t,v)-p_*(v)\big|dv=0.$$

If condition (8) holds true, then (5)–(6) has no stationary solutions.

Remark 3.2 Consider as in [5] $\lambda(v)=\lambda_0+bv$ with $b\leqslant 0$ and $b>-\lambda_0$. Suppose that θ_n are uniformly distributed random variables on $(0,1)$. Then $h(z)=1$ for $z\in(0,1)$ and $\int_0^1\ln(1-z)dz=-1$. Thus, condition (7) holds if and only if $\alpha>\lambda_0$. In this case, the invariant density is the beta distribution of the same form as in [5, Equation (6)] with $\omega_0=1$.

Before we give the proof let us introduce some notions. We say that a linear mapping $P\colon L^1\to L^1$ is a stochastic (or Markov) operator if $P(D)\subset D$. A density f_* is said to be invarinat for the operator P if $Pf_*=f_*$. Recall that a stochastic semigroup is a family $\{P(t)\}_{t\geqslant 0}$ of stochastic operators satisfying the conditions:

(a) $P(0)=\mathrm{id}$ and $P(t+s)=P(t)P(s)$ for $s,t\geqslant 0$,

(b) the function $t\mapsto P(t)f$ is continuous for each $f\in L^1$.

We say that a density is invariant for the semigroup $\{P(t)\}_{t\geqslant 0}$ if it is invariant for each operator $P(t)$.

From [10, Section 4.2.4] it follows that the process $\xi(t)$, $t\geqslant 0$, induces a stochastic semigroup $\{P(t)\}_{t\geqslant 0}$ on $L^1(0,1]$, so that the solution of (5)–(6) is given by $p(t,v)=P(t)f(v)$, $t\geqslant 0$, $v\in(0,1]$. To show that this semigroup has an invariant density we look at the process at times $(t_n)_{n\geqslant 1}$. Since $\xi(t_n^-)=\pi_{t_n-t_{n-1}}(\xi(t_{n-1}))$ and $\sigma_n=t_n-t_{n-1}$, equation (3) can be rewritten as

$$\xi(t_n)=(1-\theta_n)\pi_{\sigma_n}(\xi(t_{n-1})),\quad n\geqslant 1.$$

We find the density of the random variable $\xi(t_n)$ if $\xi(t_{n-1})=w$. For any bounded measurable function V we have

$$\mathbb{E}(V(\xi(t_n)))=\int_0^1\int_0^\infty V((1-\theta)\pi_t(w))h(\theta)\lambda(\pi_t(w))e^{-\int_0^t\lambda(\pi_s(w))ds}dtd\theta. \quad (9)$$

Substituting $\pi_t(w)=z$ and $(1-\theta)z=v$ we see that

$$\mathbb{E}(V(\xi(t_n)))=\int_0^1 V(v)k(v,w)dv,$$

where

$$k(v,w) = \int_{\max\{v,w\}}^{1} h\left(1-\frac{v}{z}\right)\frac{q(z)}{z}e^{-\int_w^z q(y)dy}dz, \quad q(y) = \frac{\lambda(y)}{\alpha y(1-y)}.$$

Thus, $k(v,w)$ is the density of $\xi(t_n)$ given $\xi(t_{n-1}) = w$. Consequently, if $\xi(t_{n-1})$ has a density f_{n-1}, then $\xi(t_n)$ has a density $f_n = Kf_{n-1}$ where the operator K is of the form

$$Kf(v) = \int_0^1 k(v,w)f(w)dw, \quad f \in L^1. \tag{10}$$

Using $0 < \underline{\lambda} \leq \bar{\lambda} < \infty$ we obtain from [2, Section 3] the following result:

Proposition 1 *The operator K has an invariant density, if and only if the semigroup $\{P(t)\}_{t\geq 0}$ has an invariant density.* □

We also have the following, e.g. by [2, Corrolary 4.4].

Proposition 2 *The operator K is either sweeping with respect to compact subsets of $(0,1]$, i.e. for any compact set $F \subset (0,1]$ we have*

$$\lim_{n\to\infty}\int_F K^n f(v)dv = 0, \quad f \in L^1,$$

or the operator K has a unique invariant density f_*. In the latter case, this density is strictly positive almost everywhere. □

Proof (of Theorem 3.1) We first show that condition (7) implies that the operator K is not sweeping from compact subsets of $(0,1]$, by using [2, Proposition 2.3]. To this end we take an unbounded Lyapunov-type function $V(w) = -\ln w$ for $w \in (0,1]$ and we check that the function

$$w \mapsto \mathbb{E}_w\big(V(\xi(t_1)) - V(\xi(t_0))\big)$$

is bounded on compact subsets of $(0,1]$ and has a negative supremum in the neighbourhood of 0, where $\mathbb{E}_w$ is the expectation conditioned on $\xi(t_0) = w$. For $\xi(t_0) = w$ with $t_0 = 0$ we have $\sigma_1 = t_1$, and

$$V(\xi(t_1)) - V(\xi(t_0)) = -\ln(1-\theta_1) + \ln(w + e^{-\alpha t_1}(1-w)).$$

Fatou's lemma and condition (7) give

$$\limsup_{w\to 0}\mathbb{E}_w\left(V(\xi(t_1)) - V(\xi(t_0))\right) \leqslant -\mathbb{E}(1-\theta_1) + \int_0^\infty \ln(e^{-\alpha s})\lambda(\pi_s(0))e^{-\int_0^t \lambda(\pi_r(0))dr}ds < 0.$$

Thus the operator is not sweeping. Now, Proposition 2 together with [8, Theorem 6 and Remark 2] implies that the semigroup $\{P(t)\}_{t\geqslant 0}$ is asymptotically stable.

Next, assume condition (8). Suppose that $\{P(t)\}_{t\geqslant 0}$ has an invariant density. Then, Proposition 1 implies that the operator K has an invariant density f_*. Take any $\beta > 0$ and consider the function $V(w) = w^\beta$, $w \in (0,1)$. Since V is bounded, we have

$$\int_0^1 V(v) f_*(v)dx = \int_0^1 V(v) K f_*(v)dx = \int_0^1 \mathbb{E}_w(V(\xi(t_1)) f_*(w)dw. \qquad (11)$$

Recall that if ζ is a random variable, then

$$\lim_{\beta\to 0} \left(\mathbb{E}(|\zeta|^\beta)\right)^{1/\beta} = e^{\mathbb{E}(\ln|\zeta|)}.$$

Since $\pi_s(w) \leqslant we^{\alpha s}$ for all w and s, we see that

$$V(\xi(t_1)) = \left((1-\theta_1)\pi_{t_1}(w)\right)^\beta \leqslant w^\beta (1-\theta_1)^\beta e^{\alpha\beta t_1}$$

and for $\zeta = (1-\theta_1)e^{\alpha t_1}$ we have $\mathbb{E}_w \ln\zeta = \mathbb{E}(1-\theta_1) + \alpha\mathbb{E}_w(t_1)$, where

$$\mathbb{E}_w(t_1) = \int_0^\infty s\lambda(\pi_s(w)) e^{-\int_0^s \lambda(\pi_r(w))dr} ds \leqslant \frac{\bar{\lambda}}{(\underline{\lambda})^2}.$$

Condition (8) implies that $\mathbb{E}_w \ln\zeta < 0$ and shows that equality (11) is impossible, leading to a contradiction. ∎

Remark 3.3 Using the more sophisticated methods from [10] one can prove that if there is no invariant density, then the semigroup is sweeping.

4. Summary We proved Theorem 3.1 specifying when the presented model can describe a stable tree-grass coexistence reflecting a savanna. Namely, when condition (7) holds true, then there exists a unique absolutely continuous stationary distribution for positive amount of woody biomass while in the situation (8) such a distribution does not exist. The condition (7) takes a much simpler form for a specified case, in Remark 3.2 we show as an example the situation for a model analogical to the one presented in [5].

The whole analysis in the paper is performed in 1D but it can be straightforwardly taken to higher dimensions, e.g. it can be applied for the author's and M. Tyran-Kamińska's previous paper on the topic with 2D model [7].

One can revisit the logistic model more by taking into consideration putting the term $1-f\big(v(t_n^-)\big)$ (where f is a function depending on the biomass of trees before fire loss) instead of $1-\theta_n$ in equation (3). It would be another interesting generalization of [9, p. 501, eq. 9] and we leave it for future work.

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Ponowna analiza modelu logistycznego z losowymi skokami

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Streszczenie Modele populacyjne oparte o równanie logistyczne wciąż są popularne w modelowaniu ekosytemów i pozwalają lepiej zrozumieć różne zjawiska. W tym artykule rozważamy prosty 1-wymiarowy model sawanny zaproponowany przez D'Odorico, Laio i Ridolfi'ego w pracy [5], który jest modelem współistnienia traw i drzew na sawannach indukowanego losowymi pożarami. Jednak zamiast wprowadzać ubytki biomasy spowodowane występowaniem pożarów bezpośrednio do równań modelu, definiujemy odpowiedni proces stochastyczny. Następnie badamy go z wykorzystaniem teorii półgrup stochastycznych. Zasadniczym wynikiem jest twierdzenie 3.1 określające, kiedy przedstawiony model może opisywać stabilne współistnienie traw i drzew charakterystyczne dla sawann. Mianowicie przy spełnionym warunku (7) istnieje jedyny absolutnie ciągły rozkład stacjonarny biomasy drzew, do którego cały układ będzie dążył, natomiast w sytuacji (8) taki rozkład nie istnieje. Powyższy wynik można łatwo przenieść na wyższe wymiary i zastosować np. w dwuwymiarowym modelu podanym w poprzedniej pracy (na ten temat) autora i Marty Tyran-Kamińskiej [7].

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Słowa kluczowe: dynamika populacyjna, równanie logistyczne, modelowanie ekosystemów, sawanna, gęstość stacjonarna, kawałkami deterministyczne procesy Markova.

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