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Stochastic Processes in Ecological Modelling

DOCTORAL DISSERTATION

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Abstract

This dissertation consists of the following series of four publications on the application of piecewise deterministic Markov processes (PDMPs) in modelling population dynamics:

[I] P. Klimasara. Revisiting the logistic growth with random disturbances. *Math. Appl. (Warsaw)*, 47(2):177–186, 2019.

[II] P. Klimasara and M. Tyran-Kamińska. A model for random fire induced tree-grass coexistence in savannas. *Math. Appl. (Warsaw)*, 46(1):87–96, 2018.

[III] P. Klimasara and M. Tyran-Kamińska. A model of seasonal savanna dynamics. *SIAM J. Appl. Math.*, 83(1):122–143, 2023.

[IV] P. Klimasara, M. C. Mackey, A. Tomski, and M. Tyran-Kamińska. *Randomly switching evolution equations. Nonlinear Anal. Hybrid Syst.*, 39:Paper No. 100948, 15, 2021.

The research problem, thematically linking the articles that constitute this dissertation, is the analysis of the impact of different types of perturbations on population dynamics models based on PDMPs and the development of formal methods to analyze such models.

After a concise presentation of key concepts – and short mathematical preliminaries – the main part of the dissertation is divided into three sections.

In the first, we present two population models of antagonistic plant groups – grasses and trees – in the savanna. It is conjectured that the lack of transition to another biome, in which one of them dominates, is due to the frequent occurrence of environmental disturbances that cause losses in the biomass of both vegetation types. Among the most important such factors are fires. Most existing mathematical models do not directly account for the random nature of fires – either by assuming their periodic recurrence, or by introducing expressions corresponding to continuous biomass losses into the equations (deterministic models). Furthermore, they often lack analytical results, and are limited to numerical simulations and bifurcation analysis. In paper [I], we study a one-dimensional model in which the logistic growth of tree biomass (assuming that grasses would maximally fill all remaining space) is perturbed at random times – denoting fire outbreaks – by the discrete loss of a random fraction of the accumulated biomass. On the other hand, in paper [II] we analyze a two-dimensional model that considers also grass biomass and its growth rate, but takes the amount of plant biomass loss due to fire as a fixed fraction of the biomass accumulated so far (value at the time of fire outbreak). In both articles, we use PDMPs to describe the model and – by examining *stochastic semigroups* induced

by these processes – we justify mathematically that random fires allow the possibility of (typical for savannas) long-time tree-grass coexistence.

In the next part of the thesis we extend the models from [I] and [II] with additional variables – introducing the populations of herbivores and taking into account the impact of their occurrence on grass and tree biomasses. Moreover, we propose an approach that allows us to take into account a periodic "environmental disturbance" – seasonality (in the case of savanna: switching between dry season and wet season). Its occurrence is very important for many different ecosystems, but unfortunately the inclusion of seasons in mathematical models poses many technical difficulties in their study. In the paper [III], we approach the subject in a new (for this problem) way – by using PDMPs with two types of switching: jumps in phase space (fire-induced losses) at random times and with random severity (biomass damage), and discrete changes in the model dynamics at fixed intervals (i.e. during the change of seasons). In the proposed PDMPs, the periodicity of the additional time variable (counting the time since the last season change) prevents us from examining the convergence of the distributions to a stationary distribution and we instead examine the convergence of time averages for such processes. In particular, we provide conditions for which stationary distributions for grass and tree biomasses (as well as populations of additionally introduced herbivores) exist. These methods can be used also for such processes when more seasons than two are present.

The final part of the thesis – based on the publication [IV] – deals with models in which random environmental disturbances affect all individuals simultaneously. Conducting considerations from a population perspective – in contrary to so-called individual perspective – leads us to models with an infinite-dimensional state space (where states are represented by population density). The study of the corresponding evolution equations poses many formal difficulties – the only results in the literature are determination of moment equations for diffusion processes in randomly switching environment. We extend these results for a broader class of processes – described by *randomly switching stochastic semigroups* – and we study *the mean of such processes at large time.*

Procesy stochastyczne w modelowaniu ekosystemów

Streszczenie

Niniejszą rozprawę doktorską stanowi poniższy cykl czterech publikacji poświęconych zastosowaniu *kawałkami deterministycznych procesów Markowa* (PDMPs) w modelowaniu dynamiki liczebności populacji:

[I] P. Klimasara. Revisiting the logistic growth with random disturbances. *Math. Appl. (Warsaw)*, 47(2):177–186, 2019.

[II] P. Klimasara and M. Tyran-Kamińska. A model for random fire induced tree-grass coexistence in savannas. *Math. Appl. (Warsaw)*, 46(1):87–96, 2018.

[III] P. Klimasara and M. Tyran-Kamińska. A model of seasonal savanna dynamics. *SIAM J. Appl. Math.*, 83(1):122–143, 2023.

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Zasadniczym problemem badawczym, łączącym tematycznie artykuły składające się na tę rozprawę, jest analiza wpływu różnego typu zaburzeń na modele dynamiki populacyjnej oparte o PDMPs oraz rozwój metod matematycznych badania takich modeli.

Po opisowym nakreśleniu rozważanych zagadnień we wstępie i zwięzłym przedstawieniu najważniejszych pojęć, merytoryczna część rozprawy została podzielona na trzy części.

W pierwszej z nich prezentujemy dwa modele populacyjne antagonistycznych grup roślin – traw i drzew – na sawannie. Przypuszcza się, że brak przejścia do innego biomu, w którym dominuje jedna z nich, spowodowany jest częstym występowaniem zaburzeń środowiskowych powodujących straty w biomasie obu typów roślinności. Wśród najważniejszych tego typu czynników wymienia się pożary. Większość istniejących modeli matematycznych nie uwzględnia bezpośrednio losowej natury pożarów, zakładając ich okresową powtarzalność lub wprowadzając do równań wyrazy odpowiadające ciągłym stratom (opis deterministyczny). Ponadto najczęściej nie są dla nich dowodzone wyniki analityczne – badacze ograniczają się do przeprowadzenia symulacji numerycznych i analizy odpowiednich bifurkacji. W pracy [I] badamy jednowymiarowy model, w którym logistyczny wzrost biomasy drzew (przy założeniu, że trawy wypełnią całą pozostałą im przestrzeń) zaburzany jest w losowych momentach – oznaczających wybuchy pożarów – przez utratę losowej części zgromadzonej biomasy. Z kolei w pracy [II] badamy model dwuwymiarowy,

uwzględniający bezpośrednio również biomasę traw i jej tempo wzrostu, ale przyjmujący wielkość strat w biomasie roślin jako ustaloną część dotychczas zgromadzonej (wartości w momencie wystąpienia pożaru). W obu artykułach do opisu modelu wykorzystujemy PDMPs i – badając indukowane przez nie *półgrupy stochastyczne* – uzasadniamy matematycznie wpływ losowych pożarów na możliwość (typowej dla sawanny) długotrwałej koegzystencji tych grup roślin.

W kolejnej części rozprawy rozbudowujemy modele z [I] i [II] o dodatkowe zmienne, wprowadzając do nich obecność roślinożerców i uwzględniając wpływ ich występowania na biomasy traw i drzew. Dodatkowo proponujemy podejście umożliwiające uwzględnienie „zaburzenia środowiskowego" o stałej zmienności (okresowego) – sezonowości (w przypadku sawanny: pory suchej oraz mokrej). Jej występowanie jest bardzo ważne dla wielu różnych ekosystemów, niestety uwzględnienie sezonów w modelach matematycznych przysparza wielu trudności technicznych w ich badaniu. W pracy [III] podejmujemy temat w nowy dla tego problemu sposób – poprzez zastosowanie PDMPs z dwoma rodzajami przełączeń: skoków w przestrzeni fazowej (straty wywołane pożarami) w losowych momentach i o losowej sile zniszczeń oraz dyskretne zmiany dynamiki modelu w ustalonych odstępach czasu, to jest podczas zmiany sezonów. W zaproponowanych PDMPs, okresowość dodatkowej zmiennej czasowej (liczącej upływ czasu od ostatniej zmiany sezonu) uniemożliwia nam badanie zbieżności rozkładów do rozkładu stacjonarnego i zamiast tego badamy zbieżność średnich z rozkładów dla takich procesów. W szczególności podajemy warunki, dla których dowodzimy istnienia rozkładów stacjonarnych dla biomas traw i drzew (a także populacji wprowadzonych dodatkowo roślinożerców). Wykorzystane metody umożliwiają zastosowanie analogicznego podejścia dla tego typu procesów przy występowaniu większej liczby sezonów.

Ostatnia część rozprawy – oparta o publikację [IV] – dotyczy modeli, w których losowo występujące zaburzenia środowiskowe wpływają równocześnie na wszystkie osobniki. Prowadzenie rozważań z perspektywy całej populacji prowadzi nas do badań na nieskończenie wymiarowej przestrzeni stanów (reprezentujących gęstość populacji). Badanie odpowiednich równań na ewolucję gęstości przysparza wielu formalnych trudności – w literaturze (dotyczącej fizyki statystycznej) pojawiają się wyniki pod postacią wyznaczenia równań na momenty dla losowo zaburzanych procesów dyfuzji. Rozszerzamy te wyniki dla szerszej klasy procesów – opisywanych *półgrupami stochastycznymi z losowymi przełączeniami* – oraz badamy dla nich zachowanie *średniej procesu w długim czasie*.

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Autoreferat

1 Wstęp i motywacja

Modelowanie matematyczne zjawisk przyrodniczych wykorzystuje szeroką i zróżnicowaną gamę dostępnych teorii matematycznych. W niniejszej rozprawie rozważamy modele stochastyczne, które wykorzystują *kawałkami deterministyczne procesy Markowa* (dla spójności z zamieszczonymi pracami i większością literatury, będziemy stosowali skrót PDMP - od angielskiego zapisu *piecewise deterministic Markov process*. Podobnie dla liczby mnogiej, tzn. wielu takich procesów, użyjemy zapisu PDMPs). Jest to szczególny rodzaj procesu Markowa z czasem ciągłym, który powiązany jest z rosnącym ciągiem losowych wartości czasu – zwanych momentami skoku. Pomiędzy takimi skokami dysponujemy deterministycznym opisem trajektorii procesu – najczęściej przy pomocy równań różniczkowych zwyczajnych. Moment skoku jest dyskretnym wydarzeniem zmieniającym dynamikę układu lub dosłownie skokiem - natychmiastowym przeniesieniem do innego punktu w przestrzeni fazowej. W naukach przyrodniczych modele oparte o PDMPs okazują się dość uniwersalnym narzędziem, reprezentując bardzo szeroki wachlarz zastosowań [23].

W zaprezentowanych pracach rozwijamy metody wykorzystania PDMPs do modelowania zaburzeń środowiskowych wpływających bezpośrednio i pośrednio na liczebność populacji. W szczególności wykorzystujemy je do opisu oraz przewidywania wpływu zjawisk zmieniających znacząco i w krótkim czasie liczebność populacji (takich jak pożary), a także takich, które wpływając na jakościowe cechy całego układu, mają znaczący wpływ na jego dynamikę (na przykład wpływ występowania pór roku na tempo wzrostu roślin). Wspólnym problemem badawczym, łączącym tematycznie publikacje składające się na tę rozprawę, jest analiza wpływu różnego typu zaburzeń na modele dynamiki populacyjnej oparte o PDMPs oraz rozwój metod badania takich modeli.

W pierwszej części przeglądu najważniejszych wyników opisujemy nasz kluczowy przykład po stronie zastosowań w ekologii – tak zwany „problem sawanny" (w literaturze ekologicznej pojawiają się nazwy *savanna problem* oraz *savanna question*), który – kilkadziesiąt lat od pierwszego opisania – wciąż pozostaje nie do końca zrozumiany i bez referencyjnego modelu teoretycznego [10]. Immanentną cechą typowej sawanny (szeroko występującego biomu) jest relatywnie stabilne współistnienie – konkurujących o przestrzeń życiową, wodę oraz składniki mineralne – roślin trawiastych i drzewiastych, które utrzymuje się długotrwale – mimo że zazwyczaj w analogicznych sytuacjach kończy się to dominacją jednej z grup roślin (przemiana biomu w odpowiedni typ lasu lub stepu/łąki). Badania prowadzone przez ekologów wskazują na szczególne znaczenie w utrzymaniu takiej sytuacji przeróżnych zjawisk: nierównomierność występowania surowców i różne dostosowanie grup organizmów do ich pozyskania z różnych źródeł, tzw. *nisze ekologiczne* [13], straty powodowane wybuchami pożarów (zobacz np. [25]), wpływ populacji roślinożerców pożywiających się konkretnym typem roślin (np. [24], [31]), czy występowanie pory mokrej i suchej (np. [8], [12]). W literaturze fachowej odnajdziemy wiele różnych pomysłów na próby modelowania wpływu tych czynników na populacje traw i drzew na sawannie (często z powodów praktycznych wyrażone nie jako „liczba osobników", ale jako ilość biomasy danego typu roślin). Jednak dostępne modele – z powodu trudnej analizy – często nie uwzględnieniają bezpośrednio losowości zjawisk takich jak występowanie pożarów, korzystając z opisów deterministycznych. Formalnie wykorzystano nawet modelowanie za pomocą sieci (grafu skierowanego z ważonymi krawędziami) [4], ale najczęściej pożary są uwzględniane przez zastosowanie układów impulsowych: zwyczajnych równań różniczkowych (np. [30], [11]) lub – wprowadzając zależności przestrzenne – równań reakcji–dyfuzji (np. [1],[26]).

W pierwszych dwóch pracach [I, II] rozważamy jedno- oraz dwuwymiarowy model koegzystencji na sawannie, oparty o zwyczajne równania różniczkowe, i uwzględniamy stochastyczną naturę pożarów – definiując odpowiedni proces stochastyczny (PDMP). Korzystając z metod teorii liniowych półgrup stochastycznych, dowodzimy istnienia rozkładów stacjonarnych biomas traw i drzew (oraz ich asymptotycznej stabilności).

W kolejnej części rozprawy rozbudowujemy nasze modele poprzez uwzględnienie bardzo ważnego z punktu widzenia ekologii, ale niemal nietkniętego w jej typowych modelach matematycznych [29], czynnika – występowania sezonów (w wypadku sawanny: pory suchej oraz pory mokrej). Dany sezon wpływa nie tylko bezpośrednio na dynamikę populacji (np. tempo wzrostu roślin, znacząco je hamując w porze suchej poprzez skąpe opady), ale również pośrednio – wpływając na prawdopodobieństwo występowania i siłę niektórych zaburzeń środowiskowych (np. wybuchanie pożarów i rozległość dokonanych przez nie zniszczeń). Praca [III] jako główny przykład zastosowania wciąż odnosi się do współistnienia populacji antagonistycznych roślin na sawannie, ale uzyskane wyniki są ogólne i dotyczą całej klasy tego typu modeli populacyjnych – opartych na PDMPs z losowymi zaburzeniami środowiskowymi (spadki liczebności populacji w momentach skoków danego PDMP), w których dodatkowo występuje sezonowość (skokowe zmiany dynamiki, ale w stałych odstępach czasu, odpowiadających typowemu czasowi trwania danych sezonów).

Ostatnia część przeglądu najważniejszych wyników dotyczy losowych zaburzeń modeli opisanych przez PDMP z perspektywy całej populacji – w odróżnieniu od częstszego podejścia osobniczego. Matematycznie sprowadzi to sytuację do analizy procesów określonych na nieskończenie wymiarowej przestrzeni stanów. W artykule [IV] proponujemy wprowadzenie *półgrup stochastycznych z losowymi przełączeniami* i badamy rodzinę stochastycznych równań ewolucji na przestrzeni gęstości (L_1). W odniesieniu do procesów dyfuzji P. C. Bessloff utożsamił [5] średnią takiego procesu w długim czasie z pewnymi rozwiązaniami równania na ewolucję gęstości (*stochastycznej wersji równania Liouville'a*) i podał równania na momenty rozważanego procesu. Uogólniamy i uzasadniamy analitycznie te wyniki dla szerszej klasy modeli (wspomnianych półgrup stochastycznych z losowymi przełączeniami). Ponadto badamy szczegółowo drugie momenty ewolucyjnych równań stochastycznych i opisujemy jak przez analogię przenieść nasze rozumowanie na wyższe momenty.

Zanim przejdziemy do bardziej szczegółowej prezentacji zasadniczych wyników publikacji składających się na rozprawę, w kolejnej preliminaryjnej części przytoczymy krótko najważniejsze definicje i fakty dotyczące PDMPs oraz ich związków z teorią półgrup stochastycznych. Odniesienia do nich umożliwią nam w bardziej zwięzły i klarowny sposób uzasadnienie niektórych twierdzeń oraz lepszą prezentację i powiązanie z nimi modeli z sezonowością oraz półgrup stochastycznych z losowymi przełączaniami.

2 PDMPs i półgrupy stochastyczne

PDMPs zostały wprowadzone przez M.H.A. Davis'a w pracy [6]. Mówimy, że proces stochastyczny z czasem ciągłym $\{\xi(t)\}_{t\geq 0}$ jest kawałkami deterministyczny, gdy istnieje rosnący ciąg losowych wartości czasu $(t_n)_{n\geq 1}$ (nazywanych momentami skoków), taki że pomiędzy dwoma kolejnymi momentami proces jest deterministyczny (na przykład opisywany przez autonomiczne układy równań różniczkowych zwyczajnych). Wartości tego procesu w momentach skoków $\xi(t_1),\ \xi(t_2),\ \xi(t_3),\ \ldots$ wybierane są z zadanego rozkładu prawdopodobieństwa zależnego od stanu procesu bezpośrednio przed skokiem, natomiast intensywność występowania skoków zależy od bieżącej wartości procesu.

Formalnie PDMP jest określony przez trzy lokalne charakterystyki $(\pi, q, \mathcal{P})$, gdzie π jest semi-układem dynamicznym opisującym deterministyczne części procesu, $q(x)$ jest funkcją intensywności skoku z x, a $\mathcal{P}(x,\cdot)$ jest rozkładem stanu osiągniętego przez ten skok. Zakładamy, że zbiór X – *przestrzeń stanów* – jest przestrzenią borelowską. Odwzorowanie $\pi\colon \mathbb{R}_+ \times X \to X$, $(t,x) \mapsto \pi_t x$ nazywamy *semi-układem dynamicznym* na X, gdy ([14, Section 7.2]):

a) $\pi_0 x = x$,

b) $\pi_{t+s}x = \pi_t(\pi_s x)$ dla $x \in X$ oraz $s, t \in \mathbb{R}_+$,

c) odwzorowanie $(t, x) \mapsto \pi_t x$ jest ciągłe.

Nakładamy istotny warunek – aby $\pi_t(X) \subseteq X$ dla każdego $t \geq 0$. Dla *funkcji intensywności skoku* $q\colon X \to [0, \infty)$ przyjmujemy, że jest borelowska, wymagamy aby odwzorowanie $s \mapsto q(\pi_s x)$ było całkowalne na każdym przedziale $[0, t)$ dla $t > 0$ oraz zakładamy, że:

$$\lim_{t\to\infty} \int_0^t q(\pi_s x)ds = +\infty, \quad x \in X.$$

Natomiast dla funkcji przejścia $\mathcal{P}\colon X \times \mathcal{B}(X) \to [0,1]$ zakładamy, że $\mathcal{P}(x, X \setminus \{x\}) = 0$ dla wszystkich $x \in X$. Przypomnijmy, że funkcję $\mathcal{P}\colon X \times \mathcal{B}(X) \to [0,1]$ nazywamy *funkcją przejścia (jądrem)*, jeśli dla każdego $x \in X$ funkcja $\mathcal{P}(x, \cdot)$ jest miarą probabilistyczną (miarą skończoną) i dla wszystkich $B \in \mathcal{B}(X)$ funkcja $\mathcal{P}(\cdot, B)$ jest mierzalna.

Opiszemy teraz krótko konstrukcję PDMP $\{\xi(t)\}_{t\geq 0}$ o charakterystykach $(\pi, q, \mathcal{P})$ ([6, 7]). Zdefiniujmy funkcję

$$F_x(t) = \exp\{-\int_0^t q(\pi_s x)ds\}, \quad t \geq 0,\ x \in X$$

i zauważmy, że założenia dla q implikują, że $1 - F_x$ jest dystrybuantą nieujemnej i skończonej zmiennej losowej dla wszystkich $x \in X$. Weźmy $t_0 = 0$ i niech $\xi(0) = \xi_0$ będzie zmienną losową o wartościach w X. Za n–ty *moment skoku* t_n (dla każdego $n \geq 1$) możemy przyjąć nieujemną zmienną losową, dla której:

$$\Pr(t_n - t_{n-1} > t | \xi_{n-1} = x) = F_x(t), \quad t \geq 0.$$

Określamy

$$\xi(t) = \begin{cases} \pi_{t-t_{n-1}}(\xi_{n-1}) & \text{dla } t_{n-1} \leq t < t_n, \\ \xi_n & \text{dla } t = t_n, \end{cases}$$

gdzie n-te *położenie po skoku* ξ_n jest taką zmienną losową o wartościach w zbiorze X, że $\Pr(\xi_n \in B | \xi(t_n-) = x) = \mathcal{P}(x, B)$ oraz $\xi(t_n-) = \lim_{t\uparrow t_n} \xi(t) = \pi_{t_n - t_{n-1}}(\xi_{n-1})$. Wtedy trajektoria procesu jest zdefiniowana dla wszystkich $t < t_\infty := \lim_{n\to\infty} t_n$. Rozszerzamy definicję na dowolny czas t przyjmując $\xi(t) = \Delta$ dla $t \geq t_\infty$, gdzie $\Delta \notin X$ oznacza pewien dodatkowy stan spoza przestrzeni. Proces $\{\xi(t)\}_{t\geq 0}$ nazywamy *minimalnym PDMP* odpowiadającym $(\pi, q, \mathcal{P})$ – i mówimy, że jest *niewybuchający* – jeśli $\mathbb{P}_x(t_\infty = \infty) = 1$ dla wszystkich $x \in X$, gdzie $\mathbb{P}_x$ to rozkład procesu startującego z punktu x. Jeśli q jest funkcją ograniczoną, to proces jest niewybuchający. O mierze probabilistycznej μ mówimy, że jest *niezmiennicza* dla procesu ξ, jeśli dla wszystkich $B \in \mathcal{B}(X)$:

$$\mu(B) = \int_X \mathbb{P}_x(\xi(t) \in B)\mu(dx), \quad t \geq 0.$$

M. H. A. Davis w definicji PDMP z [6] za przestrzeń stanów bierze podzbiór przestrzeni euklidesowej, a zamiast semi-układu dynamicznego rozważa lokalny układ dynamiczny $\pi_t x$ opisujący rozwiązania równania różniczkowego zwyczajnego

$$x'(t) = b(x(t)) \tag{2.1}$$

przy warunku początkowym $x(0) = x$, wybranym ze zbioru otwartego X^0, natomiast $b\colon \mathbb{R}^d \to \mathbb{R}^d$ jest odwzorowaniem (lokalnie) lipschitzowskim. Rozwiązania te mogą wychodzić (w skończonym czasie) z przestrzeni stanów X – która jest podzbiorem domknięcia zbioru X^0. Wobec tego określa się moment pierwszego wyjścia $t_+(x)$ z przestrzeni stanów oraz zbiór $\Gamma = \{x : t_+(x) < \infty\}$. Jeżeli Γ jest niepusty, to nazywamy go *aktywnym brzegiem* i wtedy funkcja przejścia musi być określona również dla punktów z tego brzegu, przy czym uwzględnia się wyłącznie skoki do przestrzeni stanów: $\mathcal{P}(x, X \setminus \{x\}) = 1$ dla $x \in X \cup \Gamma$. Przyjmując definicję

$$F_x(t) = \mathbf{1}_{[0,t_+(x))}(t) \exp\left\{-\int_0^t q(\pi_r x)dr\right\}, \quad t \geq 0,$$

możemy skonstruować proces analogicznie do schematu zastosowanego wcześniej.

W [6, 7] M. H. A. Davis charakteryzuje *rozszerzony generator* $\mathcal{L}$ procesu ξ jako operator liniowy na przestrzeni funkcji borelowskich na X, który dany jest wzorem [7, Proposition 26.14]:

$$\mathcal{L}V(x) = \mathcal{L}_0 V(x) + q(x)\int_X (V(y) - V(x))\mathcal{P}(x, dy), \quad x \in X,$$

a jego dziedzina $\mathcal{D}(\mathcal{L})$ zawiera w szczególności wszystkie mierzalne funkcje ograniczone $V : X \to \mathbb{R}$, dla których:

a) funkcja $t \mapsto V\big(\phi_t(x)\big)$ jest absolutnie ciągła na $[0, t_+(x))$ dla $x \in X$,

b) rozszerzając V na aktywny brzeg, przyjmując $V(x) = \lim_{t\to 0} V(\pi_{-t}x)$ dla $x \in \Gamma$, zachodzi

$$V(x) = \int_X V(y)\mathcal{P}(x, dy), \quad x \in \Gamma,$$

c) $\mathcal{L}_0$ odpowiada układowi π:

$$\mathcal{L}_0 V(x) = \lim_{t\downarrow 0} \frac{V\big(\pi_t(x)\big) - V(x)}{t}.$$

Załóżmy, że m jest σ-skończoną miarą na $\mathcal{B}(X)$, natomiast D niech będzie podzbiorem przestrzeni $L^1 = L^1(X, \mathcal{B}(X), m)$ zawierającym wszystkie gęstości:

$$D = \{f \in L^1 : f \geq 0, \|f\| = 1\}, \quad \text{gdzie } \|f\| = \int_X |f(x)|m(dx).$$

Jeżeli dla operatora liniowego $P\colon L^1 \to L^1$ zachodzi $P(D) \subset D$, to nazywamy go *operatorem stochastycznym*. Z kolei rodzina takich operatorów $\{P(t)\}_{t\geq 0}$ nazywana jest *półgrupą stochastyczną* ([14]), jeśli spełnia ona warunki:

a) $P(0) = \mathrm{Id}$,

b) $P(t+s) = P(t) \circ P(s)$ dla $t, s > 0$,

c) funkcja $t \mapsto P(t)f$ jest ciągła dla każdego $f \in L^1$.

Dla półgrupy $\{P(t)\}_{t\geq 0}$ definiujemy jej *generator infinitezymalny* A przez

$$Af = \lim_{t\downarrow 0} \frac{1}{t}(P(t)f - f), \quad f \in \mathcal{D}(A),$$

gdzie do jego dziedziny $\mathcal{D}(A)$ należą wszystkie funkcje z L^1, dla których ta granica istnieje.

O półgrupie stochastycznej $\{P(t)\}_{t\geq 0}$ mówimy, że jest *asymptotycznie stabilna*, jeśli istnieje takie $f_* \in D$, że dla wszystkich $t \geq 0$ zachodzi $P(t)f_* = f_*$ oraz

$$\lim_{t\to\infty} \|P(t)f - f_*\| = 0, \quad f \in D.$$

Wtedy taka gęstość f_* nazywana jest *niezmienniczą*. Ogólne rezultaty dotyczące asymptotycznej stabilności półgrup stochastycznych należą do R. Rudnickiego [22], a ich uogólnienia do K. Pichór i R. Rudnickiego [19, 20, 21].

Niech $\{\xi(t)\}_{t\geq 0}$ będzie niewybuchającym PDMP o charakterystykach $(\pi, q, \mathcal{P})$, określonym na przestrzeni stanów X bez aktywnego brzegu. Mówimy, że proces ten indukuje *półgrupę stochastyczną* $\{P(t)\}_{t\geq 0}$ na przestrzeni L^1, gdy dla dowolnych $B \in \mathcal{B}(X)$, $t > 0$ oraz gęstości f zachodzi

$$\int_B P(t)f(x)m(dx) = \int_X \mathbb{P}_x(\xi(t) \in B)f(x)m(dx).$$

Czyli jeśli f jest gęstością ξ_0, to $P(t)f$ jest gęstością $\xi(t)$ dla każdego t. Generator infinitezymalny takiej półgrupy jest postaci [23]

$$Af = A_0 f - qf + P(qf),$$

gdzie operator A_0 jest generatorem półgrupy stochastycznej indukowanej przez układ dynamiczny π, a $P\colon L^1 \to L^1$ jest *operatorem przejścia* odpowiadającym funkcji przejścia $\mathcal{P}$, czyli spełniającym:

$$\int_X \mathcal{P}(x, B)f(x)m(dx) = \int_B Pf(x)m(dx), \quad B \in \mathcal{B}(X),\ f \in D.$$

Kiedy układ π opisuje rozwiązania równania (2.1), a funkcja b jest klasy C^1, to dla f będących funkcjami gładkimi zachodzi $A_0 f(x) = -\operatorname{div}(b(x)f(x))$ dla wszystkich $x \in X$.

3 Przegląd najważniejszych wyników

Poniżej, w trzech sekcjach, omawiamy kluczowe rezultaty uzyskane w pracach [I, II, III, IV]. Z oryginałami referowanych artykułów można się zapoznać w kolejnych sekcjach następujących po anglojęzycznej wersji tego autoreferatu (Extended Abstract).

3.1 Modele współistnienia traw i drzew na sawannach

Nasze rozważania rozpoczniemy opisem dwóch modeli współistnienia traw i drzew na sawannach, wprowadzonych w pracach [I] i [II], oraz zwięzłym opisem ustanowionych dla nich wyników.

Wprowadzamy zmienną stanu $v \in [0,1]$ oznaczającą biomasę drzew, gdzie 0 będzie odpowiadało sytuacji z minimalnym występowaniem drzew na danym obszarze, z kolei wartość 1 – maksymalnemu zalesieniu. Za [9] stosujemy następujące uproszczenie: zamiast wprowadzenia dodatkowej zmiennej, opisującej biomasę traw – oraz uwzględnienia bezpośrednio konkurencji międzygatunkowej – przyjmujemy, że trawy rosiewają się po całej dostępnej przestrzeni (pozostałej pomiędzy drzewami) i proporcjonalnie do pozostałych zasobów $(1-v)$. Taką sytuację bez zaburzeń modelujemy klasycznym równaniem logistycznym

$$v'(t) = \alpha v(t)(1-v(t)), \tag{3.1}$$

gdzie $\alpha > 0$ jest stałą wzrostu. Wobec tego, poza sytuacją w której dominują trawy (punkt stabilny $v = 0$), równanie to opisuje wypieranie roślinności trawiastej przez drzewa, aż do ich całkowitej dominacji (wzrost logistyczny do wartości $v = 1$) i możemy łatwo je rozwiązać uzyskując

$$\pi_t(w) = v(t) = \frac{w}{w + e^{-\alpha t}(1-w)},$$

przyjmując warunek początkowy $v(0) = w \in [0,1]$.

Zakładamy, że pożary występują w losowych momentach $(t_n)_{n\geq 1}$. Biomasę drzew będziemy teraz opisywać procesem stochastycznym $\xi(t), t \geq 0$, który pomiędzy pożarami zmienia się zgodnie z równaniem (3.1). Utratę biomasy od pożaru w każdym z momentów t_n wyznacza

$$\xi(t_n) = (1-\theta_n)\xi(t_n^-),$$

gdzie $(\theta_n)_{n\geq 1}$ jest ciągiem niezależnych zmiennych losowych o pewnej gęstości h i przyjmujących wartości z przedziału $(0,1)$. Zauważmy, że przyjęcie $\xi(0) = 0$ pociąga za sobą $\xi(t) = 0$ dla wszystkich t. Wobec tego ograniczamy naszą analizę do przedziału $(0,1]$.

O funkcji intensywności skoków $\lambda\colon [0,1] \to \mathbb{R}_+$ zakładamy, że jest funkcją ciągłą, ograniczoną i dodatnią w zerze. Tak zdefiniowany proces $\xi(t), t \geq 0$ jest przykładem PDMP o charakterystykach $(\pi, \lambda, \mathcal{P})$ na przestrzeni stanów $X = (0,1]$, a funkcja przejścia $\mathcal{P}$ jest postaci

$$\mathcal{P}(v, B) = \Pr((1-\theta_n)v \in B) = \int_0^1 \mathbf{1}_B((1-\theta)v)h(\theta)d\theta, \quad v \in (0,1],\ B \in \mathcal{B}((0,1]),$$

gdzie h jest wprowadzoną wcześniej gęstością prawdopodobieństwa zmiennej losowej θ_n.

W przestrzeni stanów X jako miarę m bierzemy miarę Lebesgue'a i wtedy operator przejścia na L^1 wyraża się wzorem

$$Pf(v) = \int_v^1 h\left(1 - \frac{v}{w}\right)\frac{1}{w}f(w)dw.$$

Proces $\{\xi(t)\}_{t\geq 0}$ indukuje półgrupę stochastyczną $\{P(t)\}_{t\geq 0}$ o generatorze postaci

$$Af(v) = -\frac{\partial}{\partial v}\big(\alpha v(1-v)f(v)\big) - \lambda(v)f(v) + \int_v^1 h\left(1 - \frac{v}{w}\right)\frac{\lambda(w)}{w}f(w)dw.$$

Przy założeniu, że funkcja λ jest ciągła i silnie dodatnia na przedziale $[0,1]$, rozważamy dwa następujące warunki:

$$\alpha + \lambda(0)\int_0^1 \ln(1-z)h(z)dz > 0 \tag{3.2}$$

oraz

$$\alpha\bar{\lambda} + \underline{\lambda}^2\int_0^1 \ln(1-z)h(z)dz < 0, \tag{3.3}$$

gdzie skróciliśmy zapis ograniczeń górnych i dolnych przyjmując $\bar{\lambda} = \sup\{\lambda(v) : v \in [0,1]\}$ oraz $\underline{\lambda} = \inf\{\lambda(v) : v \in [0,1]\}$. Dodatkowo zauważmy, że zachodzi

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

gdzie równość uzyskamy, kiedy λ jest funkcją stałą.

W pracy [I] wykazaliśmy [I, Theorem 2.1], że jeśli warunek (3.2) jest spełniony, to półgrupa $\{P(t)\}_{t\geq 0}$ jest asymptotycznie stabilna. Natomiast jeśli spełniony jest warunek (3.3), to półgrupa ta nie ma gęstości niezmienniczej.

Przechodzimy teraz do opisu dwuwymiarowego modelu przedstawionego w pracy [II], gdzie korzystamy ze zmodyfikowanych równań podanych w [2].

Ponownie opisujemy zmiany ilości biomasy roślinności na sawannie w obecności zaburzeń spowodowanych pożarami, jednak tym razem konkurencję pomiędzy trawami (zmienną w czasie ilością biomasy g – od *grass*) i drzewami (analogicznie, funkcją w czasie ilości biomasy w – od *wood*) uwzględnimy bezpośrednio – wychodząc od modelu deterministycznego opisanego układem:

$$\begin{cases} w'(t) = r_w w(t)\big(1 - w(t)\big), \\ g'(t) = r_g g(t)\big(1 - g(t) - w(t)\big), \end{cases} \tag{3.4}$$

gdzie $r_w,\ r_g$ to odpowiednie stałe wzrostu oraz $w(t),\ g(t) \in [0,1]$. Do tego opisu dodajemy losowe momenty skoku $(t_n)_{n\geq 1}$, w których będą występowały pożary, oraz przyjmujemy $t_0 = 0$ i dowolne wartości początkowe (z przedziału $[0,1]$) dla biomas $w(t_0) = w_0$ oraz $g(t_0) = g_0$. W tym modelu zakładamy, że siła pożaru jest proporcjonalna do nagromadzonej biomasy, która się spala – straty w każdym momencie t_n (dla dowolnego $n \geq 1$) wyrażamy poprzez

$$\begin{cases} w(t_n) = w(t_n^-) - M_w\, w(t_n^-), \\ g(t_n) = g(t_n^-) - M_g\, g(t_n^-), \end{cases}$$

dla stałych $M_w,\ M_g$ o ustalonych wartościach z przedziału $(0,1)$.

Proces stochastyczny $\xi(t)$ wyznaczający biomasy $(w(t), g(t))$ jest PDMP, przy czym dla funkcji intensywności skoku $\lambda\colon [0,1]^2 \to \mathbb{R}_+$ przyjmujemy ponownie, że jest ciągła, nieujemna i ograniczona. Zakładamy dodatkowo:

$$\lambda(w,0) = 0 \quad \text{dla } w \geq 0 \qquad \text{oraz} \qquad \lambda(w,g) > 0 \quad \text{dla } w \geq 0,\ g > 0,$$

gdyż – zgodnie z obserwacjami ekologów – głównym nośnikiem ognia są przesuszone trawy (ilość proporcjonalna do biomasy g). Mianowicie, przyjmując jako wartość początkową $g(0) = 0$ oraz $w(0) > 0$, wartość biomasy trawy pozostanie zerowa w każdym czasie i wtedy – zgodnie z warunkami nałożonymi na funkcję λ – ogień się nie pojawi. W takiej sytuacji biomasa drzew będzie stale rosła, dążąc do „lasu” (granica $w = 1$). Wobec tego miara punktowa $\delta_{\{(1,0)\}}$ jest miarą niezmienniczą dla procesu ξ. Podobnie, gdy wyjdziemy od wartości zerowych dla obu biomas, to pozostaną one zerowe i wtedy miarą niezmienniczą dla procesu ξ będzie $\delta_{\{(0,0)\}}$. Na koniec rozważmy sytuację gdzie wartość początkowa biomasy drzew jest zerowa, natomiast $g(0) > 0$. Wtedy wartość $w(t)$ będzie stale zerowa, ale pożary będą występowały. Proces ten sprowadza się do wcześniej omówionej sytuacji z modelu jednowymiarowego [I], tylko zamiast biomasy drzew v opisuje on biomasę traw $g(t) = 1 - v(t)$, przy czym dodatniości funkcji intensywności w zerze odpowiada ograniczenie górne na λ. Przyjmijmy więc założenie:

$$r_g + \bar{\lambda}_0(1 - M_g) > 0,$$

gdzie $\bar{\lambda}_0 = \sup\{\lambda(0,g) : g \in [0,1]\}$. Wtedy proces ξ ma miarę niezmienniczą będącą miarą produktową $\delta_{\{0\}}$ i absolutnie ciągłej miary o gęstości niezmienniczej z procesu jednowymiarowego.

Skorzystamy tutaj z okazji by sprostować przeoczenie z oryginalnej pracy (tj. [II]). W związku z powyższymi uwagami, jako przestrzeń stanów naszego procesu dwuwymiarowego przyjmujemy $X = (0,1) \times (0,1]$ i dodatkowo zakładamy, że

$$r_w + \bar{\lambda}(1 - M_w) > 0, \tag{3.5}$$

gdzie $\bar{\lambda} = \sup\{\lambda(w,g) : w, g \in [0,1]\}$.

Proces ξ jest PDMP o charakterystykach $(\pi, \lambda, \mathcal{P})$, gdzie odwzorowanie π jest semi-układem dynamicznym wyznaczonym przez (3.4), a funkcja przejścia dana jest wzorem

$$\mathcal{P}((w,g), B) = \mathbf{1}_B(S(w,g)), \quad B \in \mathcal{B}(X),$$

gdzie S jest transformacją liniową opisującą wartości procesu w momentach skoków zgodnie z

$$S(w,g) = ((1 - M_w)w, (1 - M_g)g).$$

W konsekwencji funkcji $\mathcal{P}$ odpowiada operator stochastyczny postaci

$$Pf(w,g) = (1 - M_w)^{-1}(1 - M_g)^{-1} f(S^{-1}(w,g)).$$

Proces $\{\xi(t)\}_{t \geq 0}$ indukuje półgrupę stochastyczną $\{P(t)\}_{t \geq 0}$ z generatorem

$$\begin{aligned} Af(w,g) = &-\frac{\partial\big(r_w w(1-w) f(w,g)\big)}{\partial w} - \frac{\partial\big(r_g g(1-g-w) f(w,g)\big)}{\partial g} \\ &- \lambda(w,g) f(w,g) + \frac{\lambda\big(S^{-1}(w,g)\big) f\big(S^{-1}(w,g)\big)}{(1-M_w)(1-M_g)}. \end{aligned}$$

Zasadniczym wynikiem pracy [II] jest pokazanie, że półgrupa $\{P(t)\}_{t \geq 0}$ jest asymptotycznie stabilna [II, Theorem 2.1]. Dowód w pracy przebiega przy wykorzystaniu wyniku [21, Theorem 2.2] (w wersji z książki [23, Theorem 5.6]). Do sprawdzenia warunku (WT) korzystamy z *funkcji Hasminskiego* V (zobacz [23, Section 5.2.4]) – tzn. takiej mierzalnej funkcji, że dla rozszerzonego generatora $\mathcal{L}$ funkcja $\mathcal{L}V$ jest dobrze określona oraz – dla pewnego zbioru zwartego $F \subset X$ – funkcja $\mathcal{L}V$ jest ograniczona na tym zbiorze, z kolei poza nim jest ujemna i odgraniczona od zera. W artykule [II] rozważamy przestrzeń stanów $X = (0,1]^2$ (wspomniane wcześniej przeoczenie) i wtedy dobrana funkcja

$$V(w,g) = -\ln(w) - \ln(g)$$

nie jest funkcją Hasminskiego. Mianowicie $\mathcal{L}V$ zmierza do zera, gdy wartość w zmierza do jedynki, a g do zera. Zakładając warunek (3.5) i przyjmując $X = (0,1) \times (0,1]$ oraz

$$V(w,g) = \frac{1}{w^{a_w}} + \frac{1}{g^{a_g}} - \ln(1-w),$$

przy odpowiednio dobranych stałych $a_w,\ a_g \in (0,1]$, zasadniczy wynik pracy [II] jest poprawny – półgrupa $\{P(t)\}_{t \geq 0}$ jest asymptotycznie stabilna.

3.2 Sezonowość w modelach populacyjnych

Jedną z istotnych cech wielu biomów jest występowanie sezonów klimatycznych. Ponieważ reprezentują one niemal okresową zmienność, takich czynników jak temperatura powietrza czy wilgotność gleby, ich występowanie silnie wpływa na liczne zmienne środowiskowe uwzględniane w pomiarach eksperymentalnych oraz teoretycznych badaniach ekologów. Mimo tego większość rozważań teoretycznych – z powodu niedostępności wygodnych narzędzi formalnych – nie uwzględnia bezpośrednio samego zjawiska sezonowości w badanych modelach, a istniejące w literaturze próby matematycznego opisu takich modeli w większości przypadków ograniczają się do symulacji numerycznych czy analizy bifurkacji [29].

Podejmujemy problem sezonowości w modelach populacyjnych, wykorzystując ponownie odpowiednio zdefiniowane PDMPs. Poniżej opisujemy naszą propozycję opisu takich modeli z sezonowością i prezentujemy zasadnicze wyniki pracy [III], posiłkując się – jako konkretnymi przykładami – rozbudowanymi modelami sawanny z prac poprzednich.

Aby do dotychczas używanych PDMPs wprowadzić bezpośrednio sezony, potrzebujemy dodatkowej zmiennej czasowej ζ – mierzącej czas jaki upłynął od ostatniej zmiany sezonu (lub czas „pobytu" w aktualnym sezonie) – oraz numeracji sezonów zmienną $i \in \{0, 1, \ldots, k-1\}$, gdzie wartość k jest liczbą rozpatrywanych sezonów. Każdy z nich ma ustalony czas trwania ζ_m^i i rozważamy dla niego układ dynamiczny opisujący rozwiązania zwyczajnego równania różniczkowego

$$\xi'(t) = b^i\big(\xi(t)\big), \quad i = 0, \ldots, k-1. \tag{3.6}$$

Zakładamy istnienie takiego borelowskiego podzbioru X_i przestrzeni euklidesowej, że dla każdego $\xi_0 \in X_i$ rozwiązanie $\xi(t)$ równania (3.6) z warunkiem początkowym $\xi(0) = \xi_0$ istnieje oraz $\xi(t) \in X_i$ dla $t \geq 0$. Oznaczamy to rozwiązanie przez $\pi_t^i(\xi_0)$. Przechodzimy więc do opisu stanu x całego procesu za pomocą trójki (ξ, ζ, i), która zmienia się w czasie zgodnie z układem

$$\begin{cases} \xi'(t) = b^{i(t)}\big(\xi(t)\big), \\ \zeta'(t) = 1, \\ i'(t) = 0. \end{cases}$$

W związku z tym, jak w (2.1), otrzymujemy układ dynamiczny ϕ zadany rozwiązaniami powyższego układu równań

$$\phi_t(x) = \phi_t(\xi, \zeta, i) = \big(\pi_t^i(\xi), \zeta + t, i\big).$$

W takiej sytuacji przestrzeń stanów ma postać

$$X = \bigcup_i X_i \times [0, \zeta_m^i) \times \{i\}$$

i $\{\phi_t\}$ może z niej wychodzić w skończonym czasie przez aktywny brzeg

$$\Gamma = \bigcup_i X_i \times \{\zeta_m^i\} \times \{i\}.$$

Czas pierwszego wyjścia wynosi $t_+(x) = \zeta_m^i - \zeta$ dla $x = (\xi, \zeta, i) \in X$. Jeżeli (ξ, ζ_m^i, i) jest stanem procesu pod koniec i-ego sezonu, to na początku kolejnego sezonu proces wykonuje skok do $(\xi, 0, (i+1)_{\mathrm{mod}\, k})$. Gdy proces znajduje się w danym sezonie może dodatkowo w losowych momentach ulegać losowym zmianom, co opisujemy następującą funkcją przejścia

$$\mathcal{P}((\xi, \zeta, i), B) = \int_\Theta \mathbf{1}_B\big((S_\theta^i(\xi), \zeta, i)\big) p_\theta^i(\xi, \zeta)\nu^i(d\theta), \quad (\xi, \zeta, i) \in X, B \in \mathcal{B}(X),$$

gdzie Θ jest pewnym podzbiorem przestrzeni euklidesowej z miarą borelowską ν^i, transformacja $S_\theta^i(\xi)$ opisuje wartość stanu populacji ξ po losowej zmianie, natomiast $p_\theta^i(\xi, \zeta)\nu^i(d\theta)$ jest pewnym rozkładem prawdopodobieństwa, tzn.

$$\int_\Theta p_\theta^i(\xi, \zeta)\nu^i(d\theta) = 1,$$

przy czym zakładamy, że odwzorowania $(\theta, \xi) \mapsto S_\theta^i(\xi)$ oraz $(\theta, \xi, \zeta) \mapsto p_\theta^i(\xi, \zeta)$ są ciągłe. Jako funkcję intensywności przyjmujemy $q(\xi, \zeta, i) = \lambda^i(\xi, \zeta)$, gdzie każda λ^i jest ciągłą nieujemną funkcją opisującą występowanie losowych zmian populacji w i-tym sezonie. W ten sposób uzyskujemy PDMP z charakterystykami $(\phi, q, \mathcal{P})$, który oznaczamy przez $\Phi = \{\Phi(t)\}_{t \geq 0}$.

Zauważmy, że uwzględnienie sezonowości w zaproponowany przez nas sposób prowadzi do procesu Markowa jednorodnego w czasie w rozszerzonej przestrzeni stanów, gdzie jedna ze współrzędnych jest funkcją okresową (ζ). Wobec tego – zamiast badania zbieżności rozkładów do rozkładu stacjonarnego – badamy zbieżność średnich z rozkładów takich procesów. Mówimy, że proces Φ jest *ergodyczny w średniej (Cesáro-ergodic)*, jeżeli dla każdej miary probabilistycznej μ na przestrzeni X istnieje taka miara skończona $\mu\Pi$ na tej samej przestrzeni, że średnie w czasie z rozkładów, tzn. miary

$$\mu(t)(B) := \frac{1}{t}\int_0^t \int_X \mathbb{P}_x(\Phi(s) \in B)\mu(dx)ds, \quad B \in \mathcal{B}(X),\ t > 0,$$

są zbieżne w normie całkowitego wahania do miary $\mu\Pi$, czyli

$$\lim_{t\to\infty} \sup_{B \in \mathcal{B}(X)} |\mu(t)(B) - \mu\Pi(B)| = 0.$$

Zauważmy, że każda miara $\mu\Pi$ jest miarą niezmienniczą dla procesu Φ. Przyjmujemy definicję

$$\Pi(x, B) = \delta_x \Pi(B), \quad B \in \mathcal{B}, \; x \in X,$$

gdzie δ_x jest miarą punktową w punkcie x (*deltą Diraca*).

W pracy [III] podajemy warunki wystarczające na to, aby dowolny proces Markowa był ergodyczny w średniej. Aby przejść do wypowiedzenia zasadniczego wyniku, musimy jeszcze przypomnieć pojęcie T-*procesu* wprowadzone w [27, 17]. Mianowicie proces Φ nazywamy T-procesem jeżeli dla pewnej miary probabilistycznej a na $\mathbb{R}_+$ funkcja przejścia zdefiniowana przez

$$K_a(x, B) = \int_0^\infty \mathbb{P}_x(\Phi(t) \in B) a(dt)$$

ma nietrywialną część ciągłą, tzn. istnieje takie jądro T, że zachodzą następujące warunki: $K_a(x, B) \geq T(x, B)$ dla $x \in X$, $B \in \mathcal{B}(X)$, funkcja $x \mapsto T(x, B)$ jest półciągła z dołu dla każdego $B \in \mathcal{B}(X)$ oraz $T(x, X) > 0$. Jeżeli a odpowiada rozkładowi wykładniczemu, tj. $a(dt) = e^{-t} dt$, to funkcja K_a jest *rezolwentą procesu* – funkcją przejścia dla łańcucha Markowa (zwanego R-*łańcuchem*) zdefiniowanego przez obserwacje procesu Φ w momentach skoku procesu Poissona z intensywnością 1 (niezależnego od procesu Φ).

Zakładamy teraz, że spełniony jest następujący warunek typu Fostera-Lapunowa (odpowiadający warunkowi (CD2) z pracy [18]):

$$\mathcal{L}V(x) \leq -cf(x) + d\mathbf{1}_C(x), \quad x \in X,$$

dla pewnych: $V \in \mathcal{D}(\mathcal{L})$, funkcji mierzalnej $f\colon X \to [1, \infty)$, zbioru zwartego C oraz stałych dodatnich c i d. Wtedy – jeżeli Φ jest T-procesem – prawdziwy jest wynik [III, Theorem 5.1], mianowicie Φ jest ergodyczny w średniej oraz zachodzi

$$\mathbb{P}_x \left(\lim_{t\to\infty} \frac{1}{t} \int_0^t f(\Phi(s)) ds = \int f d\tilde{\Pi} \right) = 1$$

dla dowolnej ograniczonej i mierzalnej f oraz miary losowej $\tilde{\Pi}$, która spełnia $\Pi(x, B) = \mathbb{E}_x \tilde{\Pi}(B), \quad B \in \mathcal{B}(X), \; x \in X$. Okazuje się, że ergodyczność w średniej dla procesu Φ jest równoważna ergodyczności w średniej dla R-łańcucha [III, Lemma 6.2]. W związku z tym dowód wspomnianego wyniku [III, Theorem 5.1] polega na badaniu R-łańcucha w oparciu o metody wypracowane przez S. Meyna i R. L. Tweediego w pracach [16, 17, 18].

Opiszemy teraz sezonowe modele dynamiki populacyjnej na sawannie, uogólniające podejścia przedstawione w pracach [I] oraz [II], a w szczególności podamy warunki wystarczające aby opisujące je PDMPs były ergodyczne w średniej. Ponownie wykorzystujemy znormalizowane zmienne $g, w \in [0, 1]$ na oznaczenie biomas roślin trawiastych oraz drzew.

Dodatkowo uwzględniamy jeszcze zmiany tych biomas w wyniku występowania na danym terenie populacji zwierząt roślinożernych. Tacy roślinożercy często „specjalizują się” w trawieniu danego typu roślin, co uwzględniamy poprzez wprowadzenie populacji dwóch grup zwierząt. Populację tych odżywiających się przede wszystkim trawami wprowadzamy jako liczebność osobników h_G (G z ang. *grazers*). Analogicznie – przez h_B (B z ang. *browsers*) – opisujemy populację zwierząt jedzących przede wszystkim fragmenty drzew. Deterministyczną sytuację zależności populacyjnych na sawannie opisujemy teraz jako poniższy układ równań (korzystamy z równań opisujących populacje roślinożerców z [28]):

$$\begin{cases} \frac{dw}{dt} = r_w w\,(1-w) - c_w h_B w, \\ \frac{dg}{dt} = r_g g\,(1-g-w) - c_g h_G g, \\ \frac{dh_G}{dt} = e_g h_G\,(g - h_G)\,, \\ \frac{dh_B}{dt} = e_w h_B\,(w - h_B)\,, \end{cases}$$

gdzie r_w, r_g oznaczają jak wcześniej współczynniki wzrostu dla traw i drzew, stałe e_w, e_g opisują jak „efektywnie” roślinożercy przetwarzają biomasę odpowiedniego typu roślin, natomiast wartości c_w, c_g zależą między innymi od współczynników wymierania odpowiednich grup zwierząt. Uwzględniamy teraz sezonowość na sawannie – charakteryzuje ją podział roku na porę mokrą oraz porę suchą, wobec czego przyjmujemy $k = 2$. Zmianę dynamiki wzrostu roślin względem zmiany opadów między nimi wprowadzamy przez przypisanie porze suchej ($i = 0$) oraz porze mokrej ($i = 1$) oddzielnych współczynników wzrostu r^i. Nie wprowadzamy bezpośrednio zależności populacji roślinożerców od występowania sezonów. W każdym z sezonów rozważamy ten układ na przestrzeni stanów

$$X_i = (0,1) \times (0,1] \times (0,\infty) \times (0,\infty).$$

Pozostało nam uwzględnić straty biomas roślin spowodowane występowaniem pożarów. Jako odpowiednią transformację bierzemy:

$$S^i_\theta(\xi) = \big((1-\theta_w)w, (1-\theta_g)g, h_g, h_B\big), \quad \xi = (w, g, h_G, h_B) \in X_i,\ \theta = (\theta_w, \theta_g).$$

Zauważmy, że w analogicznej sytuacji (bez uwzględniania sezonowości), jeżeli przyjmiemy $h_B = h_G = 0$, to uzyskamy sytuację rozważaną w pracy [II] uogólnioną o losowe straty biomas (w miejsce stałych M_w, M_g) – czyli dwuwymiarową wersję modelu z [I]. Wobec tego nasz model sawanny, opisywany procesem Φ, jest przykładem PDMP z dwoma sezonami. Przyjmując, że funkcja intensywności oraz rozkłady strat biomasy nie zależą bezpośrednio od liczebności populacji roślinożerców oraz dopuszczając możliwość wystąpienia pożaru w każdym z sezonów (warunki (i) oraz (ii) ze str. 129 w [III]) pokazujemy, że Φ jest T-procesem [III, Theorem 5.3]. Dodatkowo, przyjmując odpowiednie warunki techniczne (warunki (iii), (iv) ze str. 129 w [III]), dowodzimy że zachodzi warunek typu Fostera-Lapunowa [III, Theorem 5.3]. W rezultacie Φ spełnia założenia przytoczonego wcześniej głównego wyniku [III, Theorem 5.1] i jest ergodyczny w średniej. W szczególności, dla modelu z proporcjonalnymi (do nagromadzonej biomasy) stratami w wyniku pożarów (jak w pracy [II]), wystarczy aby zachodził warunek (3.5) w każdym z sezonów, tzn.

$$r_w^i + \bar{\lambda}^i(1 - M_w^i) > 0, \quad i = 0, 1,$$

gdzie $\bar{\lambda}^i$ jest ograniczeniem górnym dla funkcji λ^i (zobacz [III, Corollary 4.2]). Otrzymana ergodyczność w średniej dla rozważanych modeli sawanny implikuje istnienie rozkładów stacjonarnych określonych na przestrzeni

$$X = (0, 1) \times (0, 1] \times (0, \infty) \times (0, \infty) \times \bigcup_{i=0}^{1} [0, \zeta_m^i) \times \{i\},$$

dowodząc możliwości współistnienia populacji wszystkich rozważanych gatunków (przede wszystkim traw i drzew).

3.3 Półgrupy stochastyczne z losowymi przełączeniami

W ostatniej części rozprawy przyglądamy się procesom, w których dynamika układu ulega zmianom – podobnie jak w sytuacji z występowaniem sezonów – ale nie w stałych tylko w losowych momentach, tj. zgodnie z jakimś łańcuchem Markowa. Przykładami zastosowania takiego opisu w naukach biologicznych mogą być np. modele odpowiedzi układów regulacji metabolizmu czy ekspresji genów na bodźce środowiskowe [3].

Wychodzimy od prostego modelu dynamiki populacji. Rozważamy pewną populację wielkości $x \geq 0$ o współczynniku śmiertelności μ i różnych, zmieniających się zgodnie z dyskretnymi zmianami warunków środowiska, współczynnikami urodzeń β_0 oraz β_1. Zmiany liczebności populacji opisuje równanie $x'(t) = b_i(x(t)),\ i \in \{0, 1\}$, gdzie zmiany wartości współczynnika i opisuje pewien łańcuch Markowa $i(t) \in \{0, 1\}$, natomiast funkcje b_i są postaci

$$b_0(x) = (\beta_0 - cx)x - \mu x \quad \text{oraz} \quad b_1(x) = (\beta_1 - cx)x - \mu x.$$

Zauważmy, że dla każdego i równanie $x'(t) = b_i(x(t))$ indukuje półgrupę stochastyczną $\{P_i(t)\}_{t\geq 0}$. Jeśli przyjmiemy warunki początkowe, gdzie wychodzimy od liczebności populacji opisywanej i-tym równaniem przy gęstości rozkładu g, to po pewnym czasie $t > 0$ rozkład liczebności populacji wyznacza gęstość dana przez $P_i(t)g$.

Przyjrzymy się takiej sytuacji z punktu widzenia całej populacji, tj. przejdziemy do analizy na przestrzeni gęstości. Rozważamy wtedy przełączanie pomiędzy półgrupami stochastycznymi $\{P_0(t)\}_{t\geq 0}$ i $\{P_1(t)\}_{t\geq 0}$ – zgodnie z wcześniej wprowadzonym łańcuchem

Markowa $i(t)$. Prowadzi to do badania równania zaproponowanego przez P.C. Bressloffa w [5] (autor posługuje się nazwą *stochastyczne równanie Liouville'a*):

$$\frac{\partial u(t,x)}{\partial t} = -\frac{\partial\big(b_{i(t)}(x)u(t,x)\big)}{\partial x}.$$

Możemy uogólnić to podejście na dowolne modele populacyjne opisywane układem równań różniczkowych (2.1) z przestrzenią stanów będącą podzbiorem przestrzeni euklidesowej, w których cała rozważana populacja żyje w środowisku ulegającym losowym zmianom. Podobnie jak wyżej opisuemy je pewnym łańcuchem Markowa $i(t) \in I$, gdzie I jest skończonym zbiorem. W takiej sytuacji, przyjmując gęstość początkową $u(0,x) = g(x)$, uzyskujemy ogólniejszą wersję stochastycznego równania Liouville'a:

$$\frac{\partial u(t,x)}{\partial t} = -\operatorname{div}(b_{i(t)}(x)u(t,x)). \tag{3.7}$$

W literaturze rozważa się też analogiczną sytuację, ze środowiskiem ulegającym losowym zmianom, w kontekście procesów dyfuzji – takie wspólne źródło stochastyczności prowadzi do odpowiedniego równania parabolicznego [15], będącego analogiem (3.7).

W pracy [IV] uogólniamy wszystkie te sytuacje – badając całą klasę modeli opisywanych za pomocą *półgrup stochastycznych z losowymi przełączeniami.*

Wychodzimy od $L^1(E) = L^1(E, \mathcal{B}(E), m)$ dla pewnej ośrodkowej przestrzeni mierzalnej (E, ρ) i σ-skończonej miary m. Dla każdego i ze skończonego zbioru $I = \{0, 1, \dots, k\}$ rozważamy półgrupę stochastyczną $\{P_i(t)\}_{t\geq 0}$ na $L^1(E)$ oraz, do opisu przełączań pomiędzy nimi, wprowadzamy łańcuch Markowa $\{i(t)\}_{t\geq 0}$ z przestrzenią stanów I i macierzą intensywności $Q = [q_{ij}]_{i,j\in I}$. Na przestrzeni stanów $X = L^1(E) \times I$ rozważamy semi-układ dynamiczny ϕ_t opisywany równaniem różniczkowym

$$\begin{cases} u'(t) = A_{i(t)}u(t), \\ i'(t) = 0, \end{cases}$$

gdzie A_i jest generatorem półgrupy $\{P_i(t)\}_{t\geq 0}$. Określając funkcję przejścia

$$\mathcal{P}((f,i), \{(f,j)\}) = \frac{q_{ij}}{q_i}, \quad \text{gdzie } q_i = \sum_{j\neq i} q_{ij}$$

i funkcję intensywności $q(f,i) = q_i$ dla $(f,i) \in L^1(E) \times I$, otrzymujemy proces $\xi(t) = (U(t)g, i(t))$ startujący z $\xi(0) = (g, i(0))$, który jest PDMP z charakterystykami $(\phi, q, \mathcal{P})$.

Badamy długookresowe zachowanie średniej procesu $u(t,x) = U(t)g(x)$, $x \in E$. W tym celu wprowadzamy funkcje

$$V_i(t,x) = \mathbb{E}(\mathbf{1}_{\{i(t)=i\}}u(t,x)), \quad x \in E,\ i \in I,\ t \geq 0,$$

i badamy asymptotykę średniej tego procesu, czyli funkcji

$$V(t,x) = \mathbb{E}(u(t,x)) = \sum_{i\in I} V_i(t,x), \quad x \in E,\ t \geq 0.$$

Jeżeli istnieje takie $V^* \in L^1(E)$, że

$$\lim_{t\to\infty} \int_E |V(t,x) - V^*(x)|\, m(dx) = 0,$$

to funkcję V^* nazywamy *średnią tego procesu w długim czasie.*

Z głównego twierdzenia pracy [IV, Theorem 5.1] wynika [IV, Corollary 5.3], że funkcje $(V_i)_{i\in I}$ spełniają równania

$$\frac{\partial}{\partial t} V_i = A_i V_i + \sum_j q_{ji} V_j, \quad i \in I,$$

których rozwiązania stanowią półgrupę stochastyczną $\{P(t)\}_{t\geq 0}$ na przestrzeni $L^1(E\times I)$. W twierdzeniu tym zakładamy, że spełnione są warunki (I)-(II) z artykułu [IV, str. 6]. W sytuacji opisanej równaniem (3.7) warunki te zachodzą [IV, Corollary 5.2], a półgrupa $\{P(t)\}_{t\geq 0}$ jest półgrupą stochastyczną indukowaną przez PDMP odpowiadający układom dynamicznym generowanym przez równania różniczkowe $x'(t) = b_i(x(t))$ z losowymi przełączeniami zgodnie z łańcuchem Markowa $\{i(t)\}_{t\geq 0}$. W szczególności warunkiem wystarczającym na istnienie średniej procesu w długim czasie V^* jest asymptotyczna stabilność półgrupy $\{P(t)\}_{t\geq 0}$ i wtedy $V^*(x) = \sum_{i\in I} f_i^*(x)$, gdzie $f^* = (f_i^*)_{i\in I}$ jest gęstością niezmienniczą tej półgrupy. Zgodnie z kolejnym wynikiem pracy [IV, Theorem 7.1] funkcje $(C_i)_{i\in I}$ określone przez

$$C_i(t,x,y) = \mathbb{E}(\mathbf{1}_{\{i(t)=i\}} u(t,x)u(t,y)), \quad x,y \in E,\ i \in I,\ t \geq 0,$$

spełniają równania

$$\frac{\partial}{\partial t} C_i = (A_i \otimes \mathrm{Id})C_i + (\mathrm{Id} \otimes A_i)C_i + \sum_{j\in I} q_{ji} C_j, \quad i \in I, \tag{3.8}$$

gdzie $\otimes$ oznacza iloczyn tensorowy operatorów. Ponownie zakładamy tutaj prawdziwość warunków (I)-(II) [IV, str. 6]. Ponadto rozwiązania równań (3.8) stanowią półgrupę stochastyczną na przestrzeni $L^1(E^2 \times I)$.

Extended Abstract

4 Introduction and Motivation

Mathematical modelling of natural phenomena uses a wide range of diverse mathematical theories. In this dissertation, we consider stochastic models that use *piecewise deterministic Markov processes* (abbreviated as PDMP, similarly PDMPs for plural). This is a special type of Markov process with continuous time, which is associated with an increasing sequence of random moments in time – called jump times. Between such "jumps", the trajectory of the process is described deterministically – usually by ordinary differential equations. A jump time is a discrete event that changes the dynamics of the system, or literally an immediate "jump" to another point in the phase space. Models based on PDMPs are proving to be a fairly versatile tool in the life sciences, useful for a broad range of varied applications [23].

In the papers presented here, we develop methods for using PDMPs to model environmental disturbances that directly and indirectly affect populations. In particular, we use these processes to describe and predict the impact of phenomena that change population number significantly in the short term (such as fires), as well as those that have a significant impact on the dynamics of a system (for example, the effect of the seasons change on vegetation growth rates). A common research problem that links the articles that constitute this PhD thesis, is the analysis of the impact of different types of disturbances on population dynamics models based on PDMPs and the development of methods to study such models.

In the first part of the overview of the most important results, we will describe the so-called "savanna problem" (our primary application in ecology), which – several decades since it was first described – still remains not fully understood and without a comprehensive theoretical model. An immanent feature of a typical savanna (a widely distributed biome) is the relatively stable coexistence of – competing for living space, water and minerals – grasses and woody plants, which persists over the long term (even though usually, in analogous situations, this ends in the dominance of one of the plant groups – transition of the biome into a forest or a grassland). Research by ecologists points to the particular importance of a variety of phenomena in maintaining such a situation: partitioning of below-ground resources (root-niche separation) [13], losses caused by fire outbreaks (see e.g. [25]), the impact of herbivores by grazing and browsing (e.g. [24], [31]), or seasonality (occurrence of wet and dry seasons) (e.g. [8], [12]). In the literature, we find a wide variety of ideas for modelling the effects of these factors on grass and tree populations in the savanna (often – for practical reasons – expressed not as "number of individuals", but as the amount of biomass of a given plant type). However, available models – due to the difficulties in formal analysis – usually do not directly account for the stochasticity of fires, and use deterministic descriptions. Formally, even the graph loop analysis for network models was used [4], but the most popular approach to include fire events are models based on impulsive systems: of ordinary differential equations (e.g. [30], [11]) or – introducing space-explicit description – reaction-diffusion equations (e.g. [1],[26]).

In the first two papers [I, II] we consider one and two dimensional model of tree-grass coexistence in savanna, based on ordinary differential equations, and we include the stochastic nature of fires by defining the appropriate stochastic process (PDMP). Using the methods of stochastic semigroup theory, we prove the results about the existence of stationary grass and tree biomass distributions (and their asymptotic stability).

In the next part of the dissertation, we extend our models by including a factor that is very important from the point of view of ecology – but almost non-present in typical mathematical models – the seasonality (dry and wet seasons for savannas). A given season not only influences directly the population dynamics (e.g. the growth rates of plants, significantly decreasing it in the dry season due to sparse rainfall), but also indirectly – affecting the probability of occurrence and severity of some environmental disturbances (e.g. the possibility of fire outbreak and the extent of the damage caused to vegetation). The work [III] – as a main application example – again refers to the tree-grass coexistence in savanna, but the results obtained are general and can be applied to a whole class of population models. Namely, the ones based on PDMPs with random environmental disturbances (discrete population losses in jump times of a given PDMP), that additionally include seasonality (as dynamics changes between fixed intervals – corresponding to the average duration of the respective seasons).

The last part of the overview of the major results deals with random disturbances of the PDMP models from the perspective of the entire population – as opposed to the usual individual perspective. Mathematically, it requires studying processes on an infinite-dimensional state space. In the paper [IV], we introduced the concept of *randomly switching stochastic semigroups* and study a family of stochastic evolution equations on the density space (L_1). In the case of diffusion processes, P. C. Bessloff identified the average of such a randomly switching environment process over a long time with certain solutions of the (*stochastic version of the Liouville equation*) [5] and provided moment equations of the considered process. We generalize and justify analytically these results for a broader class of models (the introduced randomly switching stochastic semigroups). Furthermore, we study in detail the second moments of the stochastic evolution equations and describe how to extend our reasoning by analogy for higher moments.

Before giving a more detailed presentation of the essential results of the publications [I-IV], in the next preliminary part we will briefly summarize the most important definitions and facts about PDMPs, as well as their relations with the stochastic semigroups theory. These references allow for more clear and concise presentation of main theorems and population models.

5 PDMPs and Stochastic Semigroups

PDMPs were introduced by M.H.A. Davis in the paper [6]. We say, that a continuous time stochastic process $\{\xi(t)\}_{t\geq 0}$ is piecewise deterministic, if there exists an increasing sequences of the so-called jump times $(t_n)_{n\geq 1}$, such that between two consecutive "jumps" the process is deterministic (for example, described by autonomous system of ordinary differential equations). Values of this process at jump times $\xi(t_1),\ \xi(t_2),\ \xi(t_3),\ \ldots$ are chosen according to probability distribution depending on the state of the process at the moment before the jump, while the jump intensity depends on the current state of the process.

Formally, a PDMP is defined by three local characteristics $(\pi, q, \mathcal{P})$, where π is a semidynamical system describing the deterministic parts of the process, $q(x)$ is a jump intensity (from x) function, and $\mathcal{P}(x, \dot{})$ is the state distribution after this jump. We assume that the set X – the *state space* – is a Borel space. We say that the mapping $\pi\colon \mathbb{R}_+ \times X \to X$, $(t, x) \mapsto \pi_t x$ is a *semidynamical system* on X if ([14, Section 7.2]):

a) $\pi_0 x = x$,

b) $\pi_{t+s}x = \pi_t(\pi_s x)$ for $x \in X$ and $s, t \in \mathbb{R}_+$,

c) $(t, x) \mapsto \pi_t x$ is continuous.

We make an important assumption that $\pi_t(X) \subseteq X$ for each $t \geq 0$. For the *jump intensity function* $q\colon X \to [0, \infty)$ we require that it is Borel, that the mapping $s \mapsto q(\pi_s x)$ is integrable on each interval $[0, t)$ for $t > 0$, and we assume that:

$$\lim_{t\to\infty} \int_0^t q(\pi_s x) ds = +\infty, \quad x \in X.$$

For the transition function $\mathcal{P}\colon X \times \mathcal{B}(X) \to [0, 1]$ we require that $\mathcal{P}(x, X \setminus \{x\}) = 0$ for all $x \in X$. Let us remind that $\mathcal{P}\colon X \times \mathcal{B}(X) \to [0, 1]$ is called a *transition function* *(a kernel)*, if for each $x \in X$ the function $\mathcal{P}(x, \cdot)$ is a probability measure (a finite measure) and for each $B \in \mathcal{B}(X)$ the function $\mathcal{P}(\cdot, B)$ is measurable. Now we briefly summarize how to construct a PDMP $\{\xi(t)\}_{t\geq 0}$ with local characteristics $(\pi, q, \mathcal{P})$ ([6, 7]). Let us define a function

$$F_x(t) = \exp\{-\int_0^t q(\pi_s x) ds\}, \quad t \geq 0,\ x \in X$$

and note that assumptions for q imply that $1 - F_x$ is a distribution function of a finite and nonnegative random variable for each $x \in X$. Assume that $t_0 = 0$ and let $\xi(0) = \xi_0$ be a random variable taking values in X. As the n-th *jump time* t_n (for any $n \geq 1$) we can take any nonnegative random variable for which:

$$\Pr(t_n - t_{n-1} > t | \xi_{n-1} = x) = F_x(t), \quad t \geq 0.$$

We determine

$$\xi(t) = \begin{cases} \pi_{t-t_{n-1}}(\xi_{n-1}) & \text{for } t_{n-1} \leq t < t_n, \\ \xi_n & \text{for } t = t_n, \end{cases}$$

where the n-th *position after jump* ξ_n is a random variable with values from X such that $\Pr(\xi_n \in B | \xi(t_n-) = x) = \mathcal{P}(x, B)$ and $\xi(t_n-) = \lim_{t\uparrow t_n} \xi(t) = \pi_{t_n - t_{n-1}}(\xi_{n-1})$. Then the trajectory of the process is defined for all $t < t_\infty := \lim_{n\to\infty} t_n$. We extend the definition for all t by taking $\xi(t) = \Delta$ for $t \geq t_\infty$, where $\Delta \notin X$ denotes an additional state (not an element of the state space). The process $\{\xi(t)\}_{t\geq 0}$ is called the *minimal PDMP* corresponding to $(\pi, q, \mathcal{P})$ – and we say that it is *non-explosive* – if $\mathbb{P}_x(t_\infty = \infty) = 1$ for all $x \in X$, where $\mathbb{P}_x$ is the distribution of the process starting from x. Note that if the function q is bounded then the process is non-explosive. A probability measure μ is *invariant* for the process ξ, if for all sets $B \in \mathcal{B}(X)$:

$$\mu(B) = \int_X \mathbb{P}_x(\xi(t) \in B) \mu(dx), \quad t \geq 0.$$

M. H. A. Davis in his definition of PDMP in [6] takes a subset of a Euclidean space as the state space and – instead of a semidynamical system – considers a local dynamical system $\pi_t x$ describing solutions of an ordinary differential equation

$$x'(t) = b(x(t)) \tag{5.1}$$

with initial value $x(0) = x$ chosen from an open set X^0, while a mapping $b\colon \mathbb{R}^d \to \mathbb{R}^d$ is required to be (locally) Lipschitz. These solutions may (in finite time) leave the state space X – which is a subset of the closure of the set X^0. Therefore we specify a first exit time $t_+(x)$ and a set $\Gamma = \{x : t_+(x) < \infty\}$. If this set is nonempty, it is called an *active boundary* and then the transition function must be defined also on Γ – but only jumps into the state space are considered: $\mathcal{P}(x, X \setminus \{x\}) = 1$ for $x \in X \cup \Gamma$. Assuming the definition

$$F_x(t) = \mathbf{1}_{[0,t_+(x))}(t) \exp\left\{-\int_0^t q(\pi_r x)dr\right\}, \quad t \geq 0,$$

we can construct a process analogically to the scheme used earlier.

In [6, 7] M. H. A. Davis determines the *extended generator* $\mathcal{L}$ of the process ξ as a linear operator defined on the space of Borel functions on X, given by [7, Proposition 26.14]:

$$\mathcal{L}V(x) = \mathcal{L}_0 V(x) + q(x) \int_X (V(y) - V(x))\mathcal{P}(x, dy), \quad x \in X,$$

and its domain $\mathcal{D}(\mathcal{L})$ contains especially all measurable bounded functions $V\colon X \to \mathbb{R}$ for which:

a) the function $t \mapsto V\big(\phi_t(x)\big)$ is absolutely continuous on $[0, t_+(x))$ for $x \in X$,

b) when extending V onto the active boundary by $V(x) = \lim_{t\to 0} V(\pi_{-t}x)$ for $x \in \Gamma$ it holds that

$$V(x) = \int_X V(y)\mathcal{P}(x, dy), \quad x \in \Gamma,$$

c) $\mathcal{L}_0$ corresponds to the system π:

$$\mathcal{L}_0 V(x) = \lim_{t\downarrow 0} \frac{V\big(\pi_t(x)\big) - V(x)}{t}.$$

Now let m be a σ-finite measure on $\mathcal{B}(X)$, and let D be a subset of the space $L^1 = L^1(X, \mathcal{B}(X), m)$ that contains all densities:

$$D = \{f \in L^1 : f \geq 0, \|f\| = 1\}, \quad \text{where } \|f\| = \int_X |f(x)|m(dx).$$

If a linear operator $P\colon L^1 \to L^1$ satisfies $P(D) \subset D$, then we call it a *stochastic operator*. The family of such operators $\{P(t)\}_{t\geq 0}$ forms a *stochastic semigroup* ([14]) when the following conditions are true:

a) $P(0) = \mathrm{Id}$,

b) $P(t+s) = P(t) \circ P(s)$ for $t, s > 0$,

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

For a semigroup $\{P(t)\}_{t\geq 0}$ we define its *infinitesimal generator* A by

$$Af = \lim_{t\downarrow 0} \frac{1}{t}(P(t)f - f), \quad f \in \mathcal{D}(A),$$

where its domain $\mathcal{D}(A)$ contains all functions from L^1 for which this limit exist.

A stochastic semigroup $\{P(t)\}_{t\geq 0}$ is *asymptotically stable*, if there exists $f_* \in D$ such that for all $t \geq 0$ it holds that $P(t)f_* = f_*$ and

$$\lim_{t\to\infty} \|P(t)f - f_*\| = 0, \quad f \in D.$$

Then the density f_* is called *invariant*. General results regarding asymptotic stability of stochastic semigroups belong to R. Rudnicki [22], and their extensions to K. Pichór and R. Rudnicki [19, 20, 21].

Let $\{\xi(t)\}_{t\geq 0}$ be a non-explosive PDMP with characteristics $(\pi, q, \mathcal{P})$, defined on a state space X without an active boundary. Such process induces a *stochastic semigroup* $\{P(t)\}_{t\geq 0}$ on L^1, if for all $B \in \mathcal{B}(X)$, $t > 0$ and for each density f there is

$$\int_B P(t)f(x)m(dx) = \int_X \mathbb{P}_x(\xi(t) \in B)f(x)m(dx).$$

Hence, if f is a density of $\xi(0)$, then $P(t)f$ is a density of $\xi(t)$ in each time t. Infinitesimal generator of such semigroup takes the form [23]

$$Af = A_0 f - qf + P(qf),$$

where A_0 denotes the generator of the stochastic semigroup induced by a dynamical system π, and $P\colon L^1 \to L^1$ is a *transition operator* corresponding to the transition function $\mathcal{P}$, that is:

$$\int_X \mathcal{P}(x, B)f(x)m(dx) = \int_B Pf(x)m(dx), \quad B \in \mathcal{B}(X),\ f \in D.$$

When the system π describes the solutions of (2.1), and the function b is C^1, then for smooth f we have $A_0 f(x) = -\operatorname{div}(b(x)f(x))$ for all $x \in X$.

6 Overview of the Main Results

In three sections below, we discuss the main results obtained in the papers [I, II, III, IV]. The full-text versions of original papers are attached as the dissertation parts following the extended abstract and bibliography.

6.1 Models of Tree-Grass Coexistence in Savannas

We begin our study with a description of the two models of tree-grass coexistence in savannas, as introduced in papers [I] and [II], and a summary of the results established for them.

We introduce a state variable $v \in [0,1]$ denoting the biomass of trees, where 0 corresponds to the situation with the minimum occurrence of trees in a given area, while the value of 1 denotes maximum afforestation. Following [9] we use the following simplification: instead of introducing an additional variable describing the biomass of grasses – and taking interspecies competition directly into account – we assume that grasses grow over all available space (remaining between trees) and in proportion to the remaining resources $(1-v)$. We model such a situation (without disturbances) with the classical logistic equation

$$v'(t) = \alpha v(t)(1 - v(t)), \tag{6.1}$$

where $\alpha > 0$ is the growth rate parameter. So actually, apart from the situation in which grasses dominate (stable point $v = 0$), this equation describes the suppression of grass vegetation by trees – up to their total dominance (logistic growth to $v = 1$), and we can easily solve it obtaining

$$\pi_t(w) = v(t) = \frac{w}{w + e^{-\alpha t}(1-w)},$$

for initial condition $v(0) = w \in [0,1]$.

We assume that fires occur at random times $(t_n)_{n\geq 1}$. We describe the biomass of the trees by a stochastic process $\xi(t), t \geq 0$, which changes between fires according to equation (6.1). The loss of biomass from the fire event at each t_n is determined by

$$\xi(t_n) = (1-\theta_n)\xi(t_n^-),$$

where $(\theta_n)_{n\geq 1}$ is a sequence of independent random variables that have values in the interval $(0,1)$ and with density h. Note that taking $\xi(0) = 0$ implies $\xi(t) = 0$ for all t. Therefore, we will limit our analysis to the interval $(0,1]$. We assume that an intensity function $\lambda\colon [0,1] \to \mathbb{R}_+$ is continuous, bounded, and positive in zero. A process defined in this way $\xi(t), t \geq 0$ is an example of PDMP with characteristics $(\pi, \lambda, \mathcal{P})$, the state space $X = (0,1]$, and the transition function $\mathcal{P}$ of the form

$$\mathcal{P}(v, B) = \Pr((1-\theta_n)v \in B) = \int_0^1 \mathbf{1}_B((1-\theta)v)h(\theta)d\theta, \quad v \in (0,1],\ B \in \mathcal{B}((0,1]),$$

where h is the probability density of θ_n.

In the state space X we take m to be the Lebesgue measure, so the transition operator on L^1 is of the form

$$Pf(v) = \int_v^1 h\left(1 - \frac{v}{w}\right)\frac{1}{w}f(w)dw.$$

The process $\{\xi(t)\}_{t\geq 0}$ induces a stochastic semigroup $\{P(t)\}_{t\geq 0}$ with generator given by

$$Af(v) = -\frac{\partial}{\partial v}\big(\alpha v(1-v)f(v)\big) - \lambda(v)f(v) + \int_v^1 h\left(1 - \frac{v}{w}\right)\frac{\lambda(w)}{w}f(w)dw.$$

Assuming that the function λ is continuous and strictly positive on the interval $[0,1]$, we consider the following two conditions:

$$\alpha + \lambda(0)\int_0^1 \ln(1-z)h(z)dz > 0 \tag{6.2}$$

and

$$\alpha\bar{\lambda} + \underline{\lambda}^2\int_0^1 \ln(1-z)h(z)dz < 0, \tag{6.3}$$

where we use the shortened notation for the upper and lower bounds, namely $\bar{\lambda} = \sup\{\lambda(v) : v \in [0,1]\}$ and $\underline{\lambda} = \inf\{\lambda(v) : v \in [0,1]\}$. Additionally note that

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

and it is equality for λ being a constant function.

In paper [I] we proved [I, Theorem 2.1] that if (3.2) is fulfilled, then the semigroup $\{P(t)\}_{t\ge 0}$ is asymptotically stable. However, if condition (3.3) is true, then this semigroup has no invariant density.

Now we switch to the description of the two-dimensional model presented in paper [II], where we use modified equations from [2].

Again, we consider changes in the amount of vegetation biomass in savanna in the presence of fire outbreaks, but this time we directly include the competition between grasses (biomass amount denoted as g) and trees (biomass w – from wood). The deterministic model is described by the system:

$$\begin{cases} w'(t) = r_w w(t)\big(1 - w(t)\big), \\ g'(t) = r_g g(t)\big(1 - g(t) - w(t)\big), \end{cases} \tag{6.4}$$

where the constants $r_w,\ r_g$ are the respective growth rates and $w(t),\ g(t) \in [0,1]$. Next we add random jump times $(t_n)_{n\ge 1}$, denoting fire outbreak events. Assume $t_0 = 0$, and choose some initial values (from $[0,1]$) for biomasses $w(t_0) = w_0$ and $g(t_0) = g_0$. In this model, we assume that the damage caused to vegetation by a fire event is proportional to the accumulated biomass – we express the loss at each t_n (for any $n \ge 1$) by

$$\begin{cases} w(t_n) = w(t_n^-) - M_w\, w(t_n^-), \\ g(t_n) = g(t_n^-) - M_g\, g(t_n^-), \end{cases}$$

for some given constants M_w and M_g chosen from interval $(0,1)$.

The stochastic process $\xi(t)$ determining biomasses $(w(t), g(t))$ is a PDMP, and again we demand that its jump intensity function $\lambda\colon [0,1]^2 \to \mathbb{R}_+$ is bounded, non-negative and continuous. Additionally we assume:

$$\lambda(w,0) = 0 \quad \text{for } w \ge 0 \qquad \text{and} \qquad \lambda(w,g) > 0 \quad \text{for } w \ge 0,\ g > 0,$$

since – according to ecological data – fires are fueled mainly by dry grasses (with amount proportional to accumulated biomass g). Therefore, when taking initial values $g(0) = 0$ and $w(0) > 0$, the grass biomass will remain to be zero at all times and – according to conditions imposed on λ – there will be no fire outbreaks. In such situation woody biomass grows indefinitely, until reaching the "forest" state ($w = 1$ limit). Hence the point measure $\delta_{\{(1,0)\}}$ is invariant for the process ξ. Similarly – when starting with zeroth biomasses for both vegetation types – they will stay zero at any time, and hence the invariant measure of ξ is then $\delta_{\{(0,0)\}}$. Finally we consider zero initial biomass for trees but $g(0) > 0$. Then again $w(t)$ would remain to be zero – but there would be fires. So under this assumption we get a very similar situation to the one dimensional model from the paper [I], with the difference that – instead of describing the biomass of trees v – it determines the amount of grass biomass $g(t) = 1 - v(t)$ (observe that positive intensity function value at zero corresponds to the upper bound for λ). Thus let us assume that

$$r_g + \bar{\lambda}_0(1 - M_g) > 0,$$

where $\bar{\lambda}_0 = \sup\{\lambda(0, g) : g \in [0, 1]\}$. Then the process ξ has an invariant measure that is a product measure of $\delta_{\{0\}}$ and an absolutely continuous measure with invariant density obtained for the one dimensional model.

Here we take the opportunity to fix an oversight from the paper [II]. According to the above observations, as a state space for our two dimensional model we take $X = (0, 1) \times (0, 1]$, and additionally we assume that

$$r_w + \bar{\lambda}(1 - M_w) > 0, \tag{6.5}$$

where $\bar{\lambda} = \sup\{\lambda(w, g) : w, g \in [0, 1]\}$.

The process ξ is a PDMP with characteristics $(\pi, \lambda, \mathcal{P})$, where the mapping π is a semi-dynamical system corresponding to (6.4), and the transition function is given by

$$\mathcal{P}((w, g), B) = \mathbf{1}_B(S(w, g)), \quad B \in \mathcal{B}(X),$$

with S being a linear transformation determining the values for the process at jump times via

$$S(w, g) = ((1 - M_w)w, (1 - M_g)g).$$

Consequently, the stochastic operator

$$Pf(w, g) = (1 - M_w)^{-1}(1 - M_g)^{-1}f(S^{-1}(w, g)).$$

corresponds to the function $\mathcal{P}$. The process $\{\xi(t)\}_{t\geq 0}$ induces a stochastic semigroup $\{P(t)\}_{t\geq 0}$ with generator

$$Af(w,g) = -\frac{\partial\big(r_w w(1-w)f(w,g)\big)}{\partial w} - \frac{\partial\big(r_g g(1-g-w)f(w,g)\big)}{\partial g} \\ - \lambda(w,g)f(w,g) + \frac{\lambda\big(S^{-1}(w,g)\big)f\big(S^{-1}(w,g)\big)}{(1-M_w)(1-M_g)}.$$

The proof of asymptotic stability of the semigroup $\{P(t)\}_{t\geq 0}$ is the main result of the paper [II, Theorem 2.1] and it uses results from the article [21, Theorem 2.2] (in a version as in the monograph [23, Theorem 5.6]). To show condition (WT) we introduce an appropriate *Hasminsky function* V (see [23, Section 5.2.4]). It is a measurable function for which the function $\mathcal{L}V$, where $\mathcal{L}$ denotes the extended generator, is well defined, and – for some compact set $F \subset X$ – this function $\mathcal{L}V$ is bounded on this set, while it is negative and separated from zero in all points outside of F. In paper [II] we consider the state space $X = (0,1]^2$ (the oversight mentioned earlier), and then the proposed function

$$V(w,g) = -\ln(w) - \ln(g)$$

is not a Hasminsky function. Namely $\mathcal{L}V$ converges to zero when w converges to one, and g to zero. But – assuming condition (6.5), taking $X = (0,1) \times (0,1]$, and defining

$$V(w,g) = \frac{1}{w^{a_w}} + \frac{1}{g^{a_g}} - \ln(1-w),$$

for suitably chosen constants $a_w,\ a_g \in (0,1]$ – the essential result of [II] remains true, i.e. the semigroup $\{P(t)\}_{t\geq 0}$ is asymptotically stable.

6.2 Population Dynamics Models and Seasonality

One of the most important features of many biomes is the occurrence of seasons. Since they represent near-periodic variability, such as air temperature or soil moisture, their occurrence strongly influences numerous environmental variables considered in experimental measurements and theoretical studies by ecologists. Despite this, most theoretical considerations – due to the unavailability of convenient formal tools – do not directly include seasonality in the models. Most existing attempts in the literature (to mathematically describe such models) are usually restricted to numerical simulations or bifurcation analysis [29].

We address the problem of seasonality in population models by the use of appropriately defined PDMPs. In this section we describe our proposal for such models with seasonality, and present the main results of the work [III], where – as the examples – we introduce the extended savanna models from previous papers.

To incorporate seasons directly into the PDMPs used so far, we need to introduce an additional time variable ζ. It measures the time elapsed since the last season change (or the "time of stay" in the current season). Moreover, we consider the numbering of the seasons with the variable $i \in \{0, 1, \ldots, k-1\}$, where k is the number of seasons considered. Each such season has a fixed duration of ζ_m^i and we consider for it a dynamical system describing the solutions of the ordinary differential equation

$$\xi'(t) = b^i\big(\xi(t)\big), \quad i = 0, \ldots, k-1. \tag{6.6}$$

We assume the existence of a Borel subset X_i of Euclidean space such that for every $\xi_0 \in X_i$ the solution $\xi(t)$ of (6.6), with initial condition $\xi(0) = \xi_0$, exists and moreover $\xi(t) \in X_i$ for $t \geq 0$. We denote this solution by $\pi_t^i(\xi_0)$. So now, to describe a state x of the process, we use the triple (ξ, ζ, i) determined by

$$\begin{cases} \xi'(t) = b^{i(t)}\big(\xi(t)\big), \\ \zeta'(t) = 1, \\ i'(t) = 0. \end{cases}$$

Therefore, as in (5.1), we obtain the dynamical system ϕ given by the solutions of the above system of equations

$$\phi_t(x) = \phi_t(\xi, \zeta, i) = \big(\pi_t^i(\xi), \zeta + t, i\big).$$

The state space here is

$$X = \bigcup_i X_i \times [0, \zeta_m^i) \times, \{i\}$$

and $\{\phi_t\}$ may leave it in finite time through the active boundary

$$\Gamma = \bigcup_i X_i \times \{\zeta_m^i\} \times \{i\}.$$

The first exit time is $t_+(x) = \zeta_m^i - \zeta$ for $x = (\xi, \zeta, i) \in X$. If (ξ, ζ_m^i, i) is the state of the process at the end of the i-th season, then – at the beginning of the next one – the process jumps to $(\xi, 0, (i+1)_{\mathrm{mod}\ k})$.

When the process is in a given season, it can additionally undergo random changes at random times according to the following transition function

$$\mathcal{P}((\xi, \zeta, i), B) = \int_\Theta \mathbf{1}_B\big((S_\theta^i(\xi), \zeta, i)\big) p_\theta^i(\xi, \zeta) \nu^i(d\theta), \quad (\xi, \zeta, i) \in X, B \in \mathcal{B}(X),$$

where Θ is a subset of Euclidean space with Borel measure ν^i, transformation $S^i_\theta(\xi)$ determines the value of ξ after a jump, while $p^i_\theta(\xi,\zeta)\nu^i(d\theta)$ is some probability distribution, that is

$$\int_\Theta p^i_\theta(\xi,\zeta)\nu^i(d\theta) = 1,$$

where we assume that the mappings $(\theta,\xi) \mapsto S^i_\theta(\xi)$ and $(\theta,\xi,\zeta) \mapsto p^i_\theta(\xi,\zeta)$ are continuous.

As the intensity function we take $q(\xi,\zeta,i) = \lambda^i(\xi,\zeta)$, where each λ^i is a continuous and nonnegative function that describes the intensity of random changes to population in the i-th season. Therefore we obtain a PDMP with characteristics $(\phi, q, \mathcal{P})$, and we denote it as $\Phi = \{\Phi(t)\}_{t\geq 0}$.

Note that including seasonality in the way we propose, leads to a time-homogeneous Markov process (in an extended state space) with one of the coordinates being a periodic function (ζ). Therefore – instead of studying the convergence of distributions to the stationary distribution – we study the convergence of the time averages of the distributions of such processes. We say that a process Φ is *mean ergodic (Cesáro-ergodic)* if, for every probability measure μ on the space X, there exists a finite measure $\mu\Pi$ on the same space such that the time averages of the distributions, i.e. the measures

$$\mu(t)(B) := \frac{1}{t}\int_0^t \int_X \mathbb{P}_x(\Phi(s) \in B)\mu(dx)ds, \quad B \in \mathcal{B}(X),\ t > 0,$$

are convergent (in the total variation norm) to $\mu\Pi$, namely

$$\lim_{t\to\infty} \sup_{B\in\mathcal{B}(X)} |\mu(t)(B) - \mu\Pi(B)| = 0.$$

Note that each measure $\mu\Pi$ is invariant for the process Φ. Let us define

$$\Pi(x,B) = \delta_x\Pi(B), \quad B \in \mathcal{B},\ x \in X,$$

where δ_x is the point measure in x (*Dirac delta*).

In the paper [III] we provide sufficient conditions for a Markov process to be mean ergodic. To summarize essential results of this publication we need to recall the notion of a *T-process*, as introduced in [27, 17]. We say that a process Φ is a T-process if – for some probability measure a on $\mathbb{R}_+$ – the transition function defined by

$$K_a(x,B) = \int_0^\infty \mathbb{P}_x(\Phi(t) \in B)a(dt)$$

has nontrivial continuous term, i.e. there exists a kernel T such that the following conditions hold: $K_a(x,B) \geq T(x,B)$ for $x \in X$, $B \in \mathcal{B}(X)$, the function $x \mapsto T(x,B)$ is lower semicontinuous for each $B \in \mathcal{B}(X)$, and $T(x,X) > 0$ for all x. If a corresponds to the exponential distribution, that is $a(dt) = e^{-t}dt$, then the function K_a is the *resolvent kernel* – a transition function for the Markov chain (called *R-chain*) defined by observing Φ at jump times of a Poisson process with intensity 1 (and independent of the process Φ).

We assume that the following Foster-Lyapunov type condition holds (it corresponds to (CD2) from [18]):

$$\mathcal{L}V(x) \leq -cf(x) + d\mathbf{1}_C(x), \quad x \in X,$$

for: some $V \in \mathcal{D}(\mathcal{L})$, a measurable function $f\colon X \to [1, \infty)$, a compact set C, and positive constants c, d. Then – whenever Φ is a T-process – the following result is true [III, Theorem 5.1]: Φ is mean ergodic and moreover

$$\mathbb{P}_x \left(\lim_{t\to\infty} \frac{1}{t} \int_0^t f(\Phi(s))ds = \int f d\tilde{\Pi} \right) = 1$$

for any bounded and measurable f, and random measure $\tilde{\Pi}$ for which $\Pi(x, B) = \mathbb{E}_x\tilde{\Pi}(B), \quad B \in \mathcal{B}(X),\ x \in X$. It appears that mean ergodicity of the process Φ is equivalent to mean ergodicity of the R-chain [III, Lemma 6.2]. Therefore the proof of the stated result [III, Theorem 5.1] involves studying the R-chain using the methods developed by S. Meyn and R. L. Tweedie in papers [16, 17, 18].

Now we describe seasonal models of population dynamics in savanna – generalising the ones presented in papers [I] and [II] – and, in particular, we provide sufficient conditions for the PDMPs describing them to be mean ergodic. We use again the variables $g, w \in [0, 1]$ to denote the grass and woody biomasses. Additionally, we further account for changes in these biomasses due to the presence of herbivore populations in the area (separated into populations: h_G of grazers - herbivores digesting mainly grassland plants, and the population h_B of browsers that mostly eat different parts of trees). We describe the deterministic situation in the savanna by the following system (the equations determining herbivore populations are taken from [28]):

$$\begin{cases} \frac{dw}{dt} = r_w w\,(1-w) - c_w h_B w, \\ \frac{dg}{dt} = r_g g\,(1-g-w) - c_g h_G g, \\ \frac{dh_G}{dt} = e_g h_G\,(g - h_G)\,, \\ \frac{dh_B}{dt} = e_w h_B\,(w - h_B)\,, \end{cases}$$

where r_w, r_g are trees and grasses growth rates, constants e_w, e_g correspond to vegetation biomass conversion efficiency for herbivores, while values c_w, c_g are related to death rates of these animals. Now we introduce seasonality – savannas are in this regard characterized by wet and dry seasons so we take $k = 2$. We include changes in population dynamics for vegetation, related to soil moisture differences between seasons, by taking different growth rates r^i for dry ($i = 0$) and wet ($i = 1$) seasons. We do not consider the direct dependence on herbivore populations of the occurrence of seasons. In each season we consider this system on the state space

$$X_i = (0, 1) \times (0, 1] \times (0, \infty) \times (0, \infty).$$

Finally we consider the losses of vegetation biomasses due to the fire outbreaks. As the appropriate transformation we take:

$$S^i_\theta(\xi) = \big((1 - \theta_w)w, (1 - \theta_g)g, h_g, h_B\big), \quad \xi = (w, g, h_G, h_B) \in X_i,\ \theta = (\theta_w, \theta_g).$$

Note that in such situation – but without seasonality – if we consider $h_B = h_G = 0$, then we get a model from [II] generalized by including random biomass losses (instead of using constants M_w, M_g), and hence it is also a two dimensional version of the model from [I]. So our savanna model, described by the process Φ, is an example of PDMP with two seasons. Assuming that intensity function and biomass loss distributions do not directly depend on herbivore populations, and considering the possibility of fire events in each season (conditions (i) and (ii) from page 129 in [III]), we show that Φ is a T-process [III, Theorem 5.3]. Moreover, under appropriate technical assumptions (conditions (iii), (iv) from page 129 in [III]), we prove that Foster-Lyapunov type condition holds [III, Theorem 5.3]. In consequence Φ fulfills all assumptions in the main result mentioned earlier [III, Theorem 5.1] and hence it is mean ergodic. Especially, in the case of the model with proportional (to accumulated biomass amount) losses due to fires (as in [II]), it is enough when the condition (6.5) holds in each season, i.e.

$$r^i_w + \bar{\lambda}^i(1 - M^i_w) > 0, \quad i = 0, 1,$$

where $\bar{\lambda}^i$ is an upper bound for the function λ^i (see [III, Corollary 4.2]). Obtained mean ergodicity for savanna models implies the existence of stationary distributions in the space

$$X = (0, 1) \times (0, 1] \times (0, \infty) \times (0, \infty) \times \bigcup_{i=0}^{1} [0, \zeta^i_m) \times \{i\},$$

for all considered populations, formally justifying the possibility of their coexistence (especially of trees and grasses).

6.3 Randomly Switching Stochastic Semigroups

In the last part of the thesis, we consider processes in which the dynamics of the system changes – similarly to the situation with seasonality – but at *random* moments, i.e.

according to some Markov chain. Such approach can be used in the biological sciences – for example to describe the response of the metabolic system of the baker's yeast to an environmental stimulus [3].

We start with a simple model of population dynamics. We consider a certain population of size $x \geq 0$ with a death rate μ and two different – varying according to discrete changes in environmental conditions – birth rates β_0 and β_1. Changes in the population size are described by the equation $x'(t) = b_i(x(t)),\ i \in \{0,1\}$, where i changes according to some Markov chain $i(t) \in \{0,1\}$, and the functions b_i are of the form

$$b_0(x) = (\beta_0 - cx)x - \mu x \quad \text{and} \quad b_1(x) = (\beta_1 - cx)x - \mu x.$$

Note that for each i equation $x'(t) = b_i(x(t))$ induces a stochastic semigroup $\{P_i(t)\}_{t\geq 0}$. If we initially start with a distribution density g for the population described by the i-th equation, then – after a certain time $t > 0$ – the population distribution is determined by the density $P_i(t)g$.

We look at this situation from a perspective of an entire population, i.e. we switch to analysis on the space of densities. We consider switching between stochastic semigroups $\{P_0(t)\}_{t\geq 0}$ and $\{P_1(t)\}_{t\geq 0}$ – according to Markov chain $i(t)$ that we introduced above. It leads to a study of the equation proposed by P.C. Bressloff in [5] (the author used the name *stochastic Liouville equation*):

$$\frac{\partial u(t,x)}{\partial t} = -\frac{\partial\big(b_{i(t)}(x)u(t,x)\big)}{\partial x}.$$

We generalize this approach to population models described by a system of differential equations (5.1) with state space that is a subset of Euclidean space, in which the entire population lives in an environment that is affected by random disturbances. Again, we will describe these random changes via a Markov chain $i(t) \in I$, where I is some finite set. Then, assuming initial density $u(0,x) = g(x)$, we get a more general version of stochastic Liouville equation:

$$\frac{\partial u(t,x)}{\partial t} = -\operatorname{div}(b_{i(t)}(x)u(t,x)). \tag{6.7}$$

In the literature, an analogous situation is also considered (with the environment undergoing random changes) in the context of diffusion processes – such a common source of stochasticity leads to the corresponding parabolic equation [15], which is the analog of (6.7).

In paper [IV] we generalize these approaches, and study the entire class of models described by *randomly switching stochastic semigroups*.

As in [IV] we start by defining $L^1(E) = L^1(E, \mathcal{B}(E), m)$ for some separable measurable space (E,ρ) and σ-finite measure m. For each i from a finite set $I = \{0,1,\ldots,k\}$ we consider a stochastic semigroup $\{P_i(t)\}_{t\geq 0}$ on $L^1(E)$ and – to describe switching between them – we introduce a Markov chain $\{i(t)\}_{t\geq 0}$ with state space I and intensity matrix $Q = [q_{ij}]_{i,j\in I}$. On a space $X = L^1(E) \times I$ we consider a semi-dynamical system ϕ_t given by

$$\begin{cases} u'(t) = A_{i(t)}u(t), \\ i'(t) = 0, \end{cases}$$

where A_i is the generator of the semigroup $\{P_i(t)\}_{t\geq 0}$. By determining a transition function as

$$\mathcal{P}((f,i),\{(f,j)\}) = \frac{q_{ij}}{q_i}, \quad \text{where } q_i = \sum_{j\neq i} q_{ij}$$

and an intensity function by $q(f,i) = q_i$ for $(f,i) \in L^1(E) \times I$, obtain a process $\xi(t) = (U(t)g, i(t))$ starting from $\xi(0) = (g, i(0))$, that is a PDMP with characteristics $(\phi, q, \mathcal{P})$.

We study the mean of such process at large time $u(t,x) = U(t)g(x)$, $x \in E$. For this aim we introduce a function

$$V_i(t,x) = \mathbb{E}(\mathbf{1}_{\{i(t)=i\}}u(t,x)), \quad x \in E, i \in I, t \geq 0.$$

and study an asymptotic behaviour of the mean of such process, i.e. of the function

$$V(t,x) = \mathbb{E}(u(t,x)) = \sum_{i\in I} V_i(t,x), \quad x \in E, t \geq 0.$$

If there exists $V^* \in L^1(E)$ such that

$$\lim_{t\to\infty} \int_E |V(t,x) - V^*(x)|\, m(dx) = 0$$

then we call the function V^* a *mean of the process at large time.*

From the main theorem of the paper [IV, Theorem 5.1] it follows [IV, Corollary 5.3], that functions $(V_i)_{i\in I}$ satisfy the equations

$$\frac{\partial}{\partial t} V_i = A_i V_i + \sum_j q_{ji} V_j, \quad i \in I, \tag{6.8}$$

and their solutions form a stochastic semigroup $\{P(t)\}_{t\geq 0}$ on the state space $L^1(E \times I)$. In this theorem we assume that the conditions (I)-(II) from [IV, p. 6] are met. In the case described by equations (6.7) these conditions indeed are fulfilled [IV, Corollary 5.2], and $\{P(t)\}_{t\geq 0}$ is a stochastic semigroup induced by PDMP corresponding to dynamical systems generated by differential equations $x'(t) = b_i(x(t))$ with stochastic switching according to the Markov chain $\{i(t)\}_{t\geq 0}$. Especially, for a mean of the process at large time V^* to exist, it is enough that $\{P(t)\}_{t\geq 0}$ is asymptotically stable, and then

$V^*(x) = \sum_{i\in I} f_i^*(x)$, where $f^* = (f_i^*)_{i\in I}$, is an invariant density of this semigroup. According to the next result [IV, Theorem 7.1], functions $(C_i)_{i\in I}$ given by

$$C_i(t,x,y) = \mathbb{E}(\mathbf{1}_{\{i(t)=i\}}u(t,x)u(t,y)), \quad x,y \in E,\ i \in I,\ t \geq 0.$$

satisfy the equations

$$\frac{\partial}{\partial t} C_i = (A_i \otimes \mathrm{Id})C_i + (\mathrm{Id} \otimes A_i)C_i + \sum_{j\in I} q_{ji} C_j, \quad i \in I, \tag{6.9}$$

where $\otimes$ denotes the tensor product of operators. Again, we assume here that conditions (I)-(II) [IV, str. 6] are fulfilled. Furthermore, the solutions of equations (6.9) form a stochastic semigroup on $L^1(E^2 \times I)$.

References

[1] J. Banasiak, Y. Dumont, and I. V. Yatat Djeumen. Spreading speeds and traveling waves for monotone systems of impulsive reaction–diffusion equations: application to tree–grass interactions in fire-prone savannas. *Differential Equations and Dynamical Systems*, pages 1–34, 2020.

[2] B. Beckage, L. J. Gross, and W. J. Platt. Grass feedbacks on fire stabilize savannas. *Ecological Modelling*, 222(14):2227–2233, 2011.

[3] A. Belle, A. Tanay, L. Bitincka, R. Shamir, and E. K. O'Shea. Quantification of protein half-lives in the budding yeast proteome. *Proceedings of the National Academy of Sciences*, 103(35):13004–13009, 2006.

[4] A. Bodini and N. Clerici. Vegetation, herbivores and fires in savanna ecosystems: A network perspective. *Ecological Complexity*, 28:36–46, 2016.

[5] P. C. Bressloff. Stochastic Liouville equation for particles driven by dichotomous environmental noise. *Phys. Rev. E*, 95(1):012124, 2017.

[6] M. H. A. Davis. Piecewise-deterministic Markov processes: a general class of non-diffusion stochastic models. *J. Roy. Statist. Soc. Ser. B*, 46(3):353–388, 1984.

[7] M. H. A. Davis. *Markov models and optimization*, volume 49 of *Monographs on Statistics and Applied Probability*. Chapman & Hall, London, 1993.

[8] J. de Abreu Araújo, L. S. Galvão, and R. Dalagnol. Sensitivity of hyperspectral vegetation indices to rainfall seasonality in the brazilian savannahs: an analysis using prisma data. *Remote Sensing Letters*, 14(3):277–287, 2023.

[9] P. D'Odorico, F. Laio, and L. Ridolfi. A probabilistic analysis of fire-induced tree-grass coexistence in savannas. *The American Naturalist*, 167(3):E79–E87, 2006.

[10] R. M. Holdo and J. B. Nippert. Linking resource- and disturbance-based models to explain tree–grass coexistence in savannas. *New Phytologist*, 237(6):1966–1979, 2023.

[11] A. Hoyer-Leitzel and S. Iams. Impulsive fire disturbance in a savanna model: tree–grass coexistence states, multiple stable system states, and resilience. *Bull. Math. Biol.*, 83(11):Paper No. 113, 2021.

[12] A. T. Karp, K. T. Uno, M. A. Berke, J. M. Russell, C. A. Scholz, J. R. Marlon, J. T.

Faith, and A. C. Staver. Nonlinear rainfall effects on savanna fire activity across the african humid period. *Quaternary Science Reviews*, 304:107994, 2023.

[13] A. Kulmatiski and K. H. Beard. A modern two-layer hypothesis helps resolve the 'savanna problem'. *Ecology Letters*, 25(9):1952–1960, 2022.

[14] A. Lasota and M. C. Mackey. *Chaos, fractals, and noise: stochastic aspects of dynamics*, volume 97. Springer Science & Business Media, 1994.

[15] S. D. Lawley. Boundary value problems for statistics of diffusion in a randomly switching environment: Pde and sde perspectives. *SIAM Journal on Applied Dynamical Systems*, 15(3):1410–1433, 2016.

[16] S. P. Meyn and R. L. Tweedie. Stability of Markovian processes. I. Criteria for discrete-time chains. *Adv. in Appl. Probab.*, 24(3):542–574, 1992.

[17] S. P. Meyn and R. L. Tweedie. Stability of Markovian processes. II. Continuous-time processes and sampled chains. *Adv. in Appl. Probab.*, 25(3):487–517, 1993.

[18] S. P. Meyn and R. L. Tweedie. Stability of Markovian processes. III. Foster-Lyapunov criteria for continuous-time processes. *Adv. in Appl. Probab.*, 25(3):518–548, 1993.

[19] K. Pichór and R. Rudnicki. Continuous Markov semigroups and stability of transport equations. *J. Math. Anal. Appl.*, 249:668–685, 2000.

[20] K. Pichór and R. Rudnicki. Asymptotic decomposition of substochastic operators and semigroups. *J. Math. Anal. Appl.*, 436(1):305–321, 2016.

[21] K. Pichór and R. Rudnicki. Stability of stochastic semigroups and applications to Stein's neuronal model. *Discrete Contin. Dyn. Syst. Ser. B*, 23(1):377–385, 2018.

[22] R. Rudnicki. On asymptotic stability and sweeping for Markov operators. *Bull. Polish Acad. Sci. Math.*, 43(3):245–262, 1995.

[23] R. Rudnicki and M. Tyran-Kamińska. *Piecewise Deterministic Processes in Biological Models*. Springer Briefs in Applied Sciences and Technology. Springer, Cham, 2017. Springer Briefs in Mathematical Methods.

[24] A. C. Staver, J. O. Abraham, G. P. Hempson, A. T. Karp, and J. T. Faith. The past, present, and future of herbivore impacts on savanna vegetation. *Journal of Ecology*, 109(8):2804–2822, 2021.

[25] T. Strydom, I. P. J. Smit, N. Govender, C. Coetsee, J. Singh, A. B. Davies, and B. W. van Wilgen. High-intensity fires may have limited medium-term effectiveness

for reversing woody plant encroachment in an african savanna. *Journal of Applied Ecology*, 60(4):661–672, 2023.

[26] S. Tega, I. Yatat-Djeumen, J. Tewa, and P. Couteron. Spatio-temporal modelling of tree-grass dynamics in humid savannas: Interplay between nonlocal competition and nonlocal facilitation. *Applied Mathematical Modelling*, 104:587–627, 2022.

[27] P. Tuominen and R. L. Tweedie. The recurrence structure of general Markov processes. *Proc. London Math. Soc. (3)*, 39(3):554–576, 1979.

[28] F. van Langevelde, C. A. D. M. van de Vijver, H. H. T. Prins, and T. A. Groen. Effects of grazing and browsing on tropical savanna vegetation. In I. J. Gordon and H. H. T. Prins, editors, *The Ecology of Browsing and Grazing II*, pages 237–257. Springer, 2019.

[29] E. R. White and A. Hastings. Seasonality in ecology: Progress and prospects in theory. *Ecological Complexity*, 44:100867, 2020.

[30] V. Yatat, P. Couteron, J. J. Tewa, S. Bowong, and Y. Dumont. An impulsive modelling framework of fire occurrence in a size-structured model of tree–grass interactions for savanna ecosystems. *Journal of mathematical biology*, 74:1425–1482, 2017.

[31] I. V. Yatat Djeumen, Y. Dumont, A. Doizy, and P. Couteron. A minimalistic model of vegetation physiognomies in the savanna biome. *Ecological Modelling*, 440:109381, 2021.

I

Revisiting the logistic growth with random disturbances

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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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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:

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

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

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

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

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

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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6. References

[1] B. Beckage, L. J. Gross, and W. J. Platt. Grass feedbacks on fire stabilize savannas. *Ecological Modelling*, 222(14):2227 – 2233, 2011. ISSN 0304-3800. doi: 10.1016/j.ecolmodel.2011.01.015. Cited on p. 178.

[2] W. Biedrzycka and M. Tyran-Kamińska. Existence of invariant densities for semiflows with jumps. *J. Math. Anal. Appl.*, 435(1):61–84, 2016. ISSN 0022-247X. doi: 10.1016/j.jmaa.2015.10.019. URL `https://doi.org/10.1016/j.jmaa.2015.10.019`. Cited on p. 182.

[3] A. Bodini and N. Clerici. Vegetation, herbivores and fires in savanna ecosystems: A network perspective. *Ecological Complexity*, 28:36–46, 2016. Cited on p. 177.

[4] M. H. A. Davis. Piecewise-deterministic Markov processes: a general class of nondiffusion stochastic models. *J. Roy. Statist. Soc. Ser. B*, 46 (3):353–388, 1984. Cited on p. 178.

[5] P. D'Odorico, F. Laio, and L. Ridolfi. A probabilistic analysis of fire-induced tree-grass coexistence in savannas. *The American Naturalist*, 167(3):E79–E87, 2006. Cited on pp. 177, 178, 179, 181, 183, and 185.

[6] S. I. Higgins, W. J. Bond, E. C. February, A. Bronn, D. I. Euston-Brown, B. Enslin, N. Govender, L. Rademan, S. O'Regan, A. L. Potgieter, et al. Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology*, 88(5):1119–1125, 2007. Cited on p. 177.

[7] P. Klimasara and M. Tyran-Kamińska. A model for random fire induced tree-grass coexistence in savannas. *Annales Societatis Mathematicae Polonae. Series III. Math. Appl. (Matematyka Stosowana)*, 46(1): 87–96, 2018. ISSN 2299-4009. doi: 10.14708/ma.v46i1.6382. MR 3841813. Cited on pp. 177, 178, 183, and 186.

[8] M. C. Mackey and M. Tyran-Kamińska. Dynamics and density evolution in piecewise deterministic growth processes. *Ann. Polon. Math.*, 94(2): 111–129, 2008. ISSN 0066-2216. doi: 10.4064/ap94-2-2. Cited on pp. 178 and 183.

[9] S. D. Peckham, E. C. Waymire, and P. De Leenheer. Critical thresholds for eventual extinction in randomly disturbed population growth

models. *J. Math. Biol.*, 77(2):495–525, 2018. ISSN 0303-6812. doi: 10.1007/s00285-018-1217-y. MR 3830273. Cited on pp. 178, 179, 180, and 184.

[10] R. Rudnicki and M. Tyran-Kamińska. *Piecewise deterministic processes in biological models.* Springer Briefs in Applied Sciences and Technology, Springer Briefs in Mathematical Methods. Springer, Cham, 2017. doi: 10.1007/978-3-319-61295-9. Cited on pp. 181 and 183.

[11] G. Sarmiento. *The ecology of neotropical savannas.* Harvard University Press, Cambridge, 1984. Sarmiento, Guillermo and Otto Solbrig. 2014. The Ecology of Neotropical Savannas. Cambridge: Harvard University Press. Retrieved 17 Aug. 2019, from https://www.degruyter.com/view/product/254565. Cited on p. 177.

[12] T. M. Scanlon, K. K. Caylor, S. Manfreda, S. A. Levin, and I. Rodriguez-Iturbe. Dynamic response of grass cover to rainfall variability: implications for the function and persistence of savanna ecosystems. *Advances in Water Resources*, 28(3):291–302, 2005. Cited on p. 178.

[13] L. Trollope and L. A. Trollope. Fire effects and management in african grasslands and savannas. *Range and Animal Sciences and Resources Management*, 2:121–145, 2010. Cited on p. 177.

[14] F. van Langevelde, C. van de Vijver, L. Kumar, J. van de Koppel, N. de Ridder, J. van Andel, A. Skidmore, J. Hearne, L. Stroosnijder, W. Bond, H. Prins, and M. Rietkerk. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84(2):337–350, 2 2003. ISSN 0012-9658. URL `https://www.jstor.org/stable/3107889`. Cited on p. 178.

[15] V. Yatat, P. Couteron, J. J. Tewa, S. Bowong, and Y. Dumont. An impulsive modelling framework of fire occurrence in a size-structured model of tree-grass interactions for savanna ecosystems. *J. Math. Biol.*, 74(6):1425–1482, 2017. ISSN 0303-6812. doi: 10.1007/s00285-016-1060-y. MR 3634789. Cited on p. 177.

Ponowna analiza modelu logistycznego z losowymi skokami

Paweł Klimasara

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].

2010 Klasyfikacja tematyczna AMS (2010): Primary: 92D40; Secondary: 60J25, 92D25.

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

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II

A model for random fire induced tree-grass coexistence in savannas

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A model for random fire induced tree-grass coexistence in savannas

Abstract Tree-grass coexistence in savanna ecosystems depends strongly on environmental disturbances out of which crucial is fire. Most modeling attempts in the literature lack stochastic approach to fire occurrences which is essential to reflect their unpredictability. Existing models that actually include stochasticity of fire are usually analyzed only numerically. We introduce a new minimalistic model of tree-grass coexistence where fires occur according to a stochastic process. We use the tools of the linear semigroup theory to provide a more careful mathematical analysis of the model. Essentially we show that there exists a unique stationary distribution of tree and grass biomasses.

2010 Mathematics Subject Classification: Primary: 92D40; Secondary: 60J25, 92D25.

Key words and phrases: savanna, ecology, fire-vegetation feedbacks, tree-grass coexistence, stochastic modelling, piecewise deterministic Markov processes.

1. Introduction. Savanna covers around 20% of the Earth's land surface. It is a mixed woodland-grassland ecosystem with canopy open enough to support the existence of continuous herbaceous layer dominated by grass. In order to find the explanation of such tree-grass codominance many theoretical models were introduced. Beside the interspecies competition (e.g. [11]), this coexistence is believed to have been driven by various environmental disturbances, primarily rainfall (e.g. [17], [15]), grazing and browsing (e.g. [6]), and fire [14]. Some models consider additional factors like the competition of tree seedlings with grass [2] or varying flammability of trees [3]. From the mathematical point of view, models containing many different factors lack stochasticity and differ in methodology (see e.g. the loop analysis for graphs in [6] or models based on impulsive differential equations [16], [18]).

Realistically, the appearance of fire is stochastic and its frequency can vary significantly [1]. Usually studies with stochastic fire focus on the numerical analysis (see e.g. [10], [2], [4], [9], and [15]). We introduce a simple model where fire occurrences are stochastic and study it in terms of the linear semi-group

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theory. We find that biomasses of grass and trees have a unique stationary distribution and hence this simple model can describe stable savannas driven by stochasticity of fires.

2. Model description. Our model is based on a simplified version of the system of differential equations given in [4], but instead of putting fire disturbances inside these equations we introduce an appropriate stochastic process separately. Similarly to the cited authors we consider only amounts of tree and grass biomasses, fires are events discrete in time, and the strength of grass-fire feedback depends on biomass of grass.

In the absence of fires we represent the dynamics of tree biomass W and grass biomass G (both in $\frac{\text{mass}}{\text{area}}$ units) according to the competition model

$$\begin{cases} W'(t) = r_w W(t)\left(1 - \frac{W(t)}{K_w}\right), \\ G'(t) = r_q G(t)\left(1 - \frac{G(t)}{K_g} - \frac{W(t)}{K_w}\right), \end{cases} \tag{1}$$

where r_w, r_g are the growth rates and K_w, K_g are the carrying capacities for tree and grass biomasses. It is easily seen that (1) has three stationary states: $(0,0)$, $(K_w, 0)$ and $(0, K_g)$. Moreover, the point $(K_w, 0)$ is locally stable, while the points $(0,0)$ and $(0, K_g)$ are unstable. So the system of equations (1) provides a deterministic description of the change of wood and grass biomasses in time where in the long time, due to species competition, the system will end up as a woodland. The solution curves for the system (1) have the qualitative behavior as shown in Figure 1.

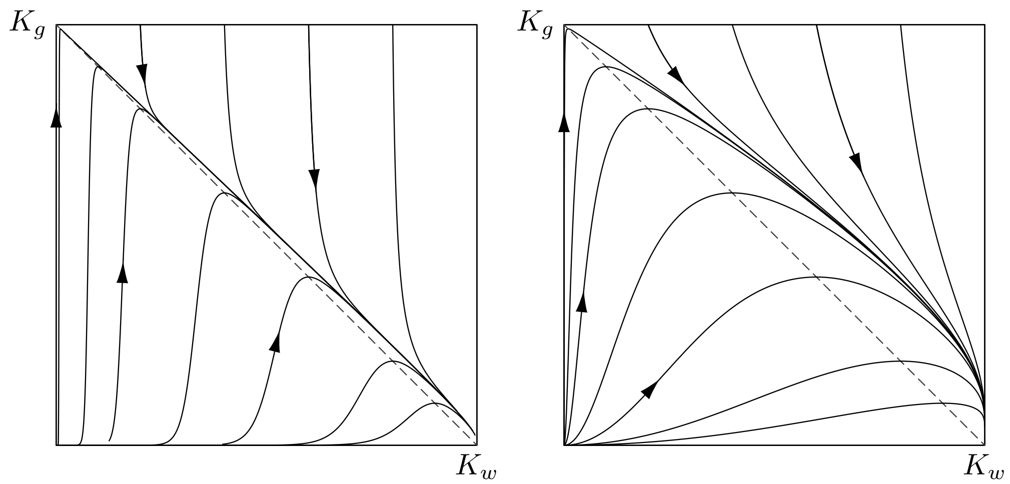


Figure 1: Phase portraits for (1) with parameter values $r_w = 0.08$, $r_g = 1.5$ (left-hand panel) and $r_w = 0.25$, $r_g = 0.5$ (right-hand panel), $K_w = K_g = 1$

Instead of using the amount of biomasses we will relate in our model to ratios of these amounts to maximal capacities of wood and grass, respectively:

$$w(t) = \frac{W(t)}{K_W}, \quad g(t) = \frac{G(t)}{K_G}.$$

Thus $w(t)$ and $g(t)$ take values in the unit interval, i.e. $0 \leqslant w(t), g(t) \leqslant 1$ for any time t. We now allow disturbances of the growth of biomasses due to fires occurring at random times $(t_n)_{n\geqslant 1}$. Let $t_0 = 0$ and $w(t_0) = w_0$, $g(t_0) = g_0$, where $w_0, g_0 \in [0, 1]$ are arbitrary. In periods between fire occurrences the growth of the normalized tree and grass biomasses is modeled with

$$\begin{cases} w'(t) = r_w w(t)\big(1 - w(t)\big), \\ g'(t) = r_g g(t)\big(1 - g(t) - w(t)\big), \end{cases} \tag{2}$$

for $t \in (t_n, t_{n+1})$, $n \geqslant 0$, and a sequence of random variables (τ_n) such that

$$\begin{cases} t_{n+1} = t_n + \tau_{n+1}, \\ \Pr\big(\tau_{n+1} > t | w(t_n) = w_n, g(t_n) = g_n\big) = e^{-\int_0^t \lambda(\pi_s(w_n, g_n))ds}, \end{cases} \tag{3}$$

where $\pi_t(w_n, g_n) = (w(t), g(t))$ is the solution of (2) with the initial condition (w_n, g_n) and λ is a nonnegative bounded continuous function. At each time t_{n+1} the loss of biomasses is given by

$$\begin{cases} w(t_{n+1}) = w(t_{n+1}^-) - M_w\, w(t_{n+1}^-), \\ g(t_{n+1}) = g(t_{n+1}^-) - M_g\, g(t_{n+1}^-), \quad n \geqslant 0, \end{cases} \tag{4}$$

where $M_w, M_g \in (0, 1)$ are constants, $v(t^-) = \lim_{s\to t^-} v(s)$ for $v \in \{w, g\}$. We assume that the function $\lambda\colon [0, 1]^2 \to \mathbb{R}_+$ satisfies

$$\lambda(w, 0) = 0, \quad w \geqslant 0, \quad \lambda(w, g) > 0 \quad \text{for } w \geqslant 0,\ g > 0. \tag{5}$$

In Figure 2 we display graphs of wood and grass biomasses in time, without and with fires. A sample behavior of the overall system in the long run including losses due to random fires is shown in Figure 3.

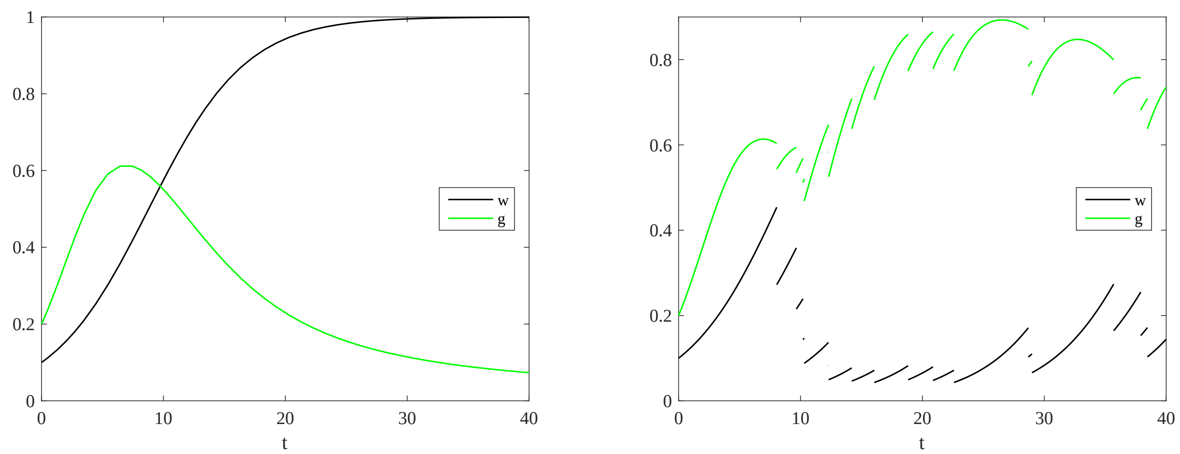


Figure 2: Graphs of system (1) (left-hand panel) and of system (2)–(4) (right-hand panel) with parameter values $r_w = 0.25$, $r_g = 0.5$, $M_w = 0.4$, $M_g = 0.1$, $\lambda(w, g) = g$ and initial condition $w_0 = 0.1$, $g_0 = 0.2$

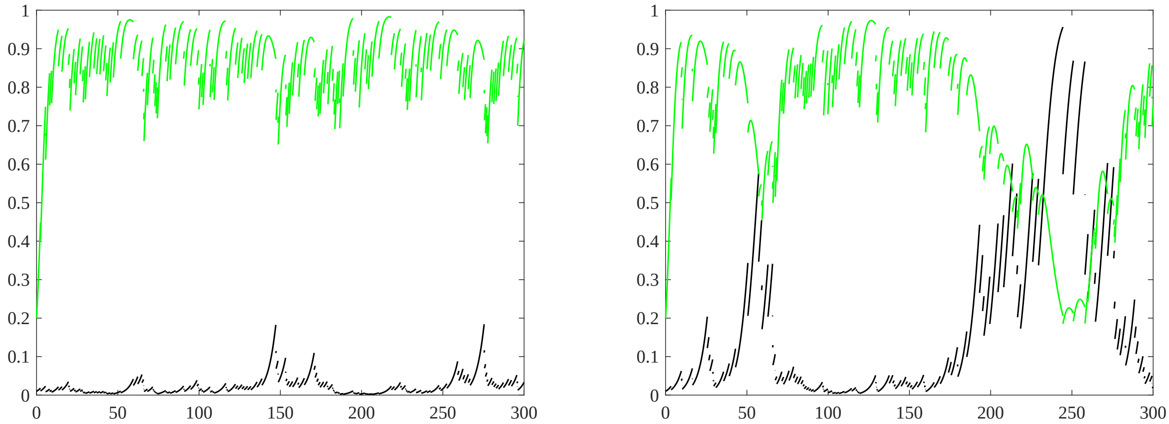


Figure 3: Sample trajectories of the stochastic process in (2)–(4) with parameter values $r_w = 0.25$, $r_g = 0.5$, $M_w = 0.4$, $M_g = 0.1$, $\lambda(w, g) = g$ and initial condition $w_0 = 0.01$, $g_0 = 0.2$

The process $\xi(t) = (w(t), g(t))$, $t \geqslant 0$, with w, g as in (2)–(4), is a piecewise deterministic Markov process ([8]) with state space $[0, 1]^2$. It is an example of a flow with jumps as presented in [13, Section 4.2.4]. We describe the jumps of the stochastic process by a linear transformation S mapping $(w, g) \longmapsto S(w, g)$, where

$$S(w, g) = ((1 - M_w)w, (1 - M_g)g), \quad (w, g) \in [0, 1]^2. \tag{6}$$

Let $p(t, w, g)$ be the probability density of $(w(t), g(t))$, i.e. p is nonnegative, Borel measurable, and satisfies

$$\Pr((w(t), g(t)) \in B) = \int_B p(t, w, g) dw dg$$

for any Borel subset of $[0, 1]^2$ with the integral being equal to one for $B = [0, 1]^2$. Then p is a solution of the following Fokker-Planck type equation

$$\frac{\partial p(t, w, g)}{\partial t} + \frac{\partial\big(r_w w(1 - w)p(t, w, g)\big)}{\partial w} + \frac{\partial\big(r_g g(1 - g - w)p(t, w, g)\big)}{\partial g} \\ = -\lambda(w, g)p(t, w, g) + \frac{\lambda\big(S^{-1}(w, g)\big)p\big(t, S^{-1}(w, g)\big)}{(1 - M_w)(1 - M_g)}, \tag{7}$$

where S^{-1} is the inverse of the transformation S defined in (6). Equation (7) is supplemented with the initial condition

$$p(0, w, g) = f(w, g), \quad \text{where} \quad \int_0^1 \int_0^1 f(w, g)\, dw dg = 1 \tag{8}$$

and f is a nonnegative Borel measurable function, so that f is the probability density of $(w(0), g(0))$. We have the following result - its proof will be given in the next section.

THEOREM 2.1 There exists a unique density $p_*(w,g)$ which is a stationary solution of (7). Moreover, every solution of (7)–(8) converges to p_*, i.e.

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

REMARK 2.1 Let $w_0, g_0 \in [0,1]$ and $w(t), g(t)$ be as in (2)–(4). If $w_0 > 0$ and $g_0 = 0$ then $g(t) = 0$ for all $t > 0$. In this case, assumption (5) implies that fire can not occur when there is no grass biomass. Hence, w is defined for all t as the solution of the differential equation $w'(t) = r_w w(t)(1-w(t))$ with initial condition $w(0) = w_0$. Thus $w(t) > 0$ for all $t > 0$ and $w(t)$ converges to 1 as $t \to \infty$. Consequently, the point measure $\delta_{\{(1,0)\}}$ is an invariant measure for the process ξ. Similarly, if $w_0 = 0$ and $g_0 = 0$ then $w(t) = 0$ and $g(t) = 0$ for all $t > 0$. Thus also the point measure $\delta_{\{(0,0)\}}$ is an invariant measure for the process ξ. Finally, if $w_0 = 0$ and $g_0 > 0$ then $w(t) = 0$ and $g(t) > 0$ for all $t \geqslant 0$. In this case, the process ξ has an invariant distribution which is a product of $\delta_{\{0\}}$ and an absolutely continuous measure, see Remark 3.1.

REMARK 2.2 If instead of (3) we have $t_{n+1} = t_n + \tau$, $n \geqslant 0$ where τ is a constant then such a model is an example of an impulsive system [16, 18].

3. Existence and uniqueness of tree and grass biomasses distribution. Methods in this section are mostly taken from the book [13]. To prove Theorem 2.1 we use the method from [13, Section 6.3.2]. We begin by recalling some notions for stochastic semigroups. Let the triple (X,Σ,m) be a σ-finite measure space. Denote by D the subset of the space $L^1 = L^1(X,\Sigma,m)$ which contains all densities

$$D = \{f \in L^1 : f \geqslant 0,\ \|f\| = 1\}.$$

A linear mapping $P\colon L^1 \to L^1$ is called a *Markov* or *stochastic operator* if $P(D) \subset D$. A family $\{P(t)\}_{t\geqslant 0}$ of stochastic operators which satisfies conditions:

1. $P(0) = \mathrm{id}$, $P(t+s) = P(t)P(s)$ for $s, t \geqslant 0$,
2. for each $f \in L^1$ the function $t \mapsto P(t)f$ is continuous,

is called a *stochastic semigroup.*

Consider a stochastic semigroup $\{P(t)\}_{t\geqslant 0}$. A density f_* is called *invariant* if $P(t)f_* = f_*$ for each $t > 0$. The stochastic semigroup $\{P(t)\}_{t\geqslant 0}$ is called *asymptotically stable* if there is an invariant density f_* such that

$$\lim_{t\to\infty}\|P(t)f - f_*\| = 0 \quad \text{for} \quad f \in D.$$

We will use a result of Pichór and Rudnicki [12] (see also [13, Theorem 5.6]) which requires the following conditions:

(K) For every $y_0 \in X$ there exist $\varepsilon > 0$, $t > 0$, and a measurable function $\eta \geqslant 0$ such that $\int \eta(x)\, m(dx) > 0$ and

$$P(t)f(x) \geqslant \eta(x) \int_{B(y_0,\varepsilon)} f(y)\, m(dy),$$

where $B(y_0, \varepsilon) = \{y \in X : \ \rho(y, y_0) < \varepsilon\}$.

(WI) There exists a point $x_0 \in X$ such that for each $\varepsilon > 0$ and for each density f we have

$$\int\limits_{B(x_0,\varepsilon)} P(t)f(x)\, m(dx) > 0 \quad \text{for some } t = t(\varepsilon, f) > 0.$$

(WT) There exists $\kappa > 0$ such that

$$\sup_{F\in\mathcal{F}} \limsup_{t\to\infty} \int_F P(t)f(x)\, m(dx) \geqslant \kappa$$

for $f \in D_0$, where D_0 is a dense subset of D and $\mathcal{F}$ is the family of all compact subsets of X.

Theorem 3.1 Let $\{P(t)\}_{t\geqslant 0}$ be a stochastic semigroup on $L^1(X, \Sigma, m)$, where X is a separable metric space, Σ is the σ-algebra of Borel subsets of X, and m is a σ-finite measure. Assume that $\{P(t)\}_{t\geqslant 0}$ satisfies conditions (K), (WI), and (WT). Then the semigroup $\{P(t)\}_{t\geqslant 0}$ is asymptotically stable.

Now we are ready to prove the main theorem.

Proof (of Theorem 2.1) Let $X = (0, 1]^2$ and m be the two-dimensional Lebesgue measure on X. It follows from [13, Section 4.2.4] that the process $\xi(t)$, $t \geqslant 0$, induces a stochastic semigroup $\{P(t)\}_{t\geqslant 0}$ on $L^1 = L^1(X, \Sigma, m)$ and that the solution of (7)–(8) is given by $p(t, w, g) = P(t)f(w, g)$, $t \geqslant 0$, $(w, g) \in X$. To apply Theorem 3.1 we need to check conditions (K), (WI), and (WT).

We first show that condition (WT) holds. The extended generator $\widetilde{L}$ of the process ξ is of the form

$$\widetilde{L}V(x) = \langle b(x), \mathrm{grad} V(x)\rangle + \varphi(x)(V(S(x)) - V(x)) \quad \text{for } x = (w, g),$$

where $\mathrm{grad}V(x)$ is the gradient of $V(x)$ and $b(x)$ is the vector with coordinates

$$b_1(x) = r_w w(1 - w), \quad b_2(x) = r_g g(1 - w - g), \quad x = (w, g).$$

The domain $\mathcal{D}(\widetilde{L})$ of the extended generator $\widetilde{L}$ (see [8] or [13, Section 2.3.6]) contains the set of functions $V : X \to \mathbb{R}$ such that for each $x \in X$ the function $t \mapsto V(\pi_t(x))$ is absolutely continuous and for each $t \geqslant 0$, $x \in X$, we have

$$\mathbb{E}\Big(\sum_{t_n\leqslant t} \big|V(\xi(t_n)) - V(\xi(t_n^-))\big| \Big|\xi(0) = x\Big) < \infty.$$

Let $V(w,g) = -\log w - \log g$. Since we have $V(\xi(t_n)) - V(\xi(t_n^-)) = -\log(1 - M_w) - \log(1 - M_g)$ for any n, we see that V belongs to $\mathcal{D}(\widetilde{L})$ and that

$$\widetilde{L}V(w,g) = -r_w(1-w) - r_g(1-w-g) - \lambda(w,g)(\log(1-M_w) + \log(1-M_g)).$$

The function $\widetilde{L}V$ is bounded on $(0,1]^2$ and $\widetilde{L}V(w,g) \to -r_w - r_g$ as $\|(w,g)\| \to 0$, where $\|\cdot\|$ denotes a norm in $\mathbb{R}^2$. Thus we can find a $\delta \in (0,1)$ such that $\widetilde{L}V(w,g) \leqslant -(r_w + r_g)/2$ for $\|(w,g)\| < \delta$. Moreover, we have

$$\int_X \widetilde{L}V(x) f(x) m(dx) = \int_X V(x) A f(x) m(dx), \quad f \in \mathcal{D}(A) \cap \mathcal{D}_V,$$

where $f \in D_V$ iff $\int_X V(x)|f(x)|m(dx) < \infty$ and $(A, \mathcal{D}(A))$ is the generator of the semigroup $\{P(t)\}_{t \geqslant 0}$. We conclude that V is a Hasminskiĭ function for the semigroup $\{P(t)\}_{t \geqslant 0}$ and the compact set $F = \{(w,g) \in X : \|(w,g)\| \geqslant \delta\}$ implying that condition (WT) holds, by [13, Corollary 5.8].

To check condition (K) take $x_0 \in X$ and define $x_1 = S(x_0)$, $x_2 = S(x_1)$,

$$v_1 = S'(x_1)S'(x_0)b(x_0) - b(x_2), \quad v_2 = S'(x_1)b(x_1) - b(x_2). \tag{9}$$

Since S is a linear transformation, we have

$$v_1 = S^2(b(x_0)) - b(S^2(x_0)), \quad v_2 = S(b(S(x_0)) - b(S^2(x_0)),$$

where $S^2(x) = S(S(x))$. It is easily seen that vectors v_1 and v_2 are linearly independent for each $x_0 \in X$. Since the function λ is strictly positive on $(0,1]^2$, we conclude that condition (K) holds (see e.g. [13, Section 6.3.2] or [5, Section 4]).

Finally, if we prove that there exists x_0 such that for each $\varepsilon > 0$ and $x \in X$ we can find n and times $s_1, \dots, s_n, s_{n+1} > 0$ such that $\pi_{s_{n+1}}(x_n) \in B(x_0, \varepsilon)$, where

$$x_n = S(\pi_{s_n}(\dots S(\pi_{s_1}x))), \tag{10}$$

then condition (WI) holds. To this end, we note that the point $(0,1)$ is a saddle point for the two-dimensional system (2) considered on $\mathbb{R}^2$. Its stable manifold is the set $\{(0,g) : g > 0\}$ and its unstable manifold contains a curve joining the point $(0,1)$ with the stable point $(1,0)$, see Figure 1. Let us take $x_0 \in X$ from this curve lying close to the point $(1,0)$. For any point $x \in X$ we can find n and $s_1, \dots, s_n > 0$ such that x_n defined as in (10) is as close to $(0,0)$ as is needed. Since $\pi_s y \to (1,0)$ for $y \in (0,1)^2$, we can find s_{n+1} such that $\pi_{s_{n+1}} x_n \in B(x_0, \varepsilon)$, which completes the proof. ∎

Remark 3.1 The process ξ restricted to the set $\{(0,g) : g \in (0,1]\}$, considered with measure being the product of $\delta_{\{0\}}$ and the Lebesgue, induces a stochastic semigroup on $L^1(\{0\} \times (0,1])$. Using the same type of argument as in the proof of Theorem 2.1 it can be shown that this semigroup satisfies conditions (K), (WI) and (WT), thus this semigroup is asymptotically stable, implying the existence of the invariant measure mentioned in Remark 2.1.

4. Discussion. We showed that there exists the unique, absolutely continuous with respect to the two-dimensional Lebesgue measure, stationary distribution for the positive amount of grass and wood biomasses. The stationary density is strictly positive in the region bounded by the axes and the unstable manifold of the point $(0, 1)$, in particular in a neighborhood of the line $\{(w, 1 - w) : w \in (0, 1]\}$, showing that the coexistence of trees and grass is possible. Finding the actual shape of this distribution, numerical analysis, and further improvements of the model by adding more coefficients reflecting real-world factors regulating savanna biomasses we leave for future work.

Moreover such an analysis can be implemented in models describing different phenomena involving random fires, such as the impact of forest fires on population of pines and bark beetles. Modeling attempts usually are deterministic (see e.g. [7]) and hence could benefit from involving stochastic nature of fire.

References

[1] S. Archibald, D. P. Roy, V. Wilgen, W. Brian, and R. J. Scholes. What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biol.*, 15(3):613–630, 2009. doi: 10.1111/j.1365-2486.2008.01754.x. Cited on p. 87.

[2] M. Baudena, F. D'Andrea, and A. Provenzale. An idealized model for tree–grass coexistence in savannas: the role of life stage structure and fire disturbances. *J. Ecol.*, 98(1):74–80, 2010. doi: 10.1111/j.1365-2745.2009.01588.x. Cited on p. 87.

[3] B. Beckage, W. J. Platt, and L. J. Gross. Vegetation, fire, and feedbacks: a disturbance-mediated model of savannas. *Am. Nat.*, 174(6):805–818, 2009. doi: 10.1086/648458. Cited on p. 87.

[4] B. Beckage, L. J. Gross, and W. J. Platt. Grass feedbacks on fire stabilize savannas. *Ecol. Model.*, 222(14):2227–2233, 2011. doi: 10.1016/j.ecolmodel.2011.01.015. Cited on pp. 87 and 88.

[5] W. Biedrzycka and M. Tyran-Kamińska. Existence of invariant densities for semiflows with jumps. *J. Math. Anal. Appl.*, 435(1):61–84, 2016. doi: 10.1016/j.jmaa.2015.10.019. Cited on p. 93.

[6] A. Bodini and N. Clerici. Vegetation, herbivores and fires in savanna ecosystems: A network perspective. *Ecol. Complex.*, 28:36–46, 2016. doi: 10.1016/j.ecocom.2016.10.001. Cited on p. 87.

[7] B. Chen-Charpentier and M. Leite. A model for coupling fire and insect outbreak in forests. *Ecol. Model.*, 286:26–36, 2014. doi: 10.1016/j.ecolmodel.2014.04.008. Cited on p. 94.

[8] M. H. A. Davis. Piecewise-deterministic Markov processes: a general class of nondiffusion stochastic models. *J. Roy. Statist. Soc. Ser. B*, 46 (3):353–388, 1984. Cited on pp. 90 and 92.

[9] C. De Michele and F. Accatino. Tree cover bimodality in savannas and forests emerging from the switching between two fire dynamics. *PloS one*, 9(3):e91195, 2014. doi: 10.1371/journal.pone.0091195. Cited on p. 87.

[10] P. D'Odorico, F. Laio, and L. Ridolfi. A probabilistic analysis of fire-induced tree-grass coexistence in savannas. *Am. Nat.*, 167(3):E79–E87, 2006. doi: 10.1086/500617. Cited on p. 87.

[11] P. S. Eagleson and R. I. Segarra. Water-limited equilibrium of savanna vegetation systems. *Water Resour. Res.*, 21(10):1483–1493, 1985. doi: 10.1029/WR021i010p01483. Cited on p. 87.

[12] K. Pichór and R. Rudnicki. Stability of stochastic semigroups and applications to Stein's neuronal model. *Discrete Contin. Dyn. Syst. Ser. B*, 23(1):377–385, 2018. doi: 10.3934/dcdsb.2018026. Cited on p. 91.

[13] R. Rudnicki and M. Tyran-Kamińska. *Piecewise deterministic processes in biological models*. Springer Briefs in Applied Sciences and Technology, Springer Briefs in Mathematical Methods. Springer, Cham, 2017. doi: 10.1007/978-3-319-61295-9. Cited on pp. 90, 91, 92, and 93.

[14] M. Sankaran, J. Ratnam, and N. Hanan. Woody cover in african savannas: the role of resources, fire and herbivory. *Global Ecol. Biogeogr.*, 17(2):236–245, 2008. doi: 10.1111/j.1466-8238.2007.00360.x. Cited on p. 87.

[15] A. D. Synodinos, B. Tietjen, D. Lohmann, and F. Jeltsch. The impact of inter-annual rainfall variability on African savannas changes with mean rainfall. *J. Theor. Biol.*, 437:92–100, 2018. doi: 10.1016/j.jtbi.2017.10.019. Cited on p. 87.

[16] A. T. Tamen, Y. Dumont, J. J. Tewa, S. Bowong, and P. Couteron. Tree–grass interaction dynamics and pulsed fires: Mathematical and numerical studies. *Appl. Math. Model.*, 40(11-12):6165–6197, 2016. doi: 10.1016/j.apm.2016.01.019. Cited on pp. 87 and 91.

[17] N. Ursino. Eco-hydrology driven fire regime in savanna. *J. Theor. Biol.*, 355:68–76, 2014. doi: 10.1016/j.jtbi.2014.04.002. Cited on p. 87.

[18] V. Yatat, P. Couteron, J. J. Tewa, S. Bowong, and Y. Dumont. An impulsive modelling framework of fire occurrence in a size-structured model of tree–grass interactions for savanna ecosystems. *J. Math. Biol.*, 74(6):1425–1482, 2017. doi: 10.1007/s00285-016-1060-y. Cited on pp. 87 and 91.

Model koegzystencji traw i drzew na sawannach indukowanej losowymi pożarami

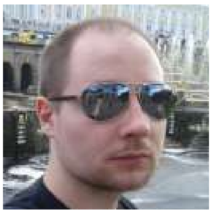
Paweł Klimasara, Marta Tyran-Kamińska

Streszczenie Sawanny zajmują ok. 20% lądowej powierzchni Ziemi. W tym ekosystemie korony drzew są na tyle oddzielone od siebie nawzajem, że do podłoża dociera wystarczająco dużo światła, aby utrzymywała się równomierna warstwa traw. Takie

długotrwałe współistnienie traw i drzew, czyli brak konwersji do łąki lub lasu, jest możliwe dzięki różnym czynnikom. Uważa się, że najważniejsze z nich to powtarzające się pożary, obfitość pory deszczowej oraz uszczuplanie warstwy roślinnej przez roślinożerców i działalność człowieka. Większość dotychchczasowych modeli koegzystencji traw i drzew jest deterministyczna, jeżeli już przyjmuje się stochastyczne występowanie pożarów lub deszczu, to zazwyczaj w bardzo uproszczonej formie, a analiza jest przeprowadzana numerycznie.
W tym artykule wprowadzamy uproszczony model, składający się z układu równań różniczkowych, opisujących wzrost traw i drzew w czasie oraz procesu stochastycznego, odpowiadającego za losowe pojawianie się pożarów. Analizujemy ten proces, korzystając z metod teorii półgrup liniowych, co pozwala nam pokazać, że startując z dowolnego rozkładu początkowego biomasy traw i drzew, po odpowiednio długim czasie rozkład tych biomas się stabilizuje. Istnieje jedyny (absolutnie ciągły względem dwuwymiarowej miary Lebesgue'a) taki rozkład stacjonarny. Planujemy rozbudować zaproponowany model o dodatkowe czynniki środowiskowe wymienione wcześniej oraz konkurencję o zasoby pomiędzy trawami a sadzonkami drzew. Ponadto podobne uwzględnienie stochastycznej natury występowania pożarów można uwzględnić w modelowaniu innych zjawisk przyrodniczych jak związek pomiędzy pożarami lasów a populacją żywiących się korą sosen chrząszczy.

Klasyfikacja tematyczna AMS (2010): 92D40; 60J25; 92D25.

Słowa kluczowe: sawanna, ekologia, sprzężenie zwrotne, koegzystencja roślin, modelowanie stochastyczne, kawałkami deterministyczne procesy Markowa.



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III

A Model of Seasonal Savanna Dynamics

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A MODEL OF SEASONAL SAVANNA DYNAMICS*

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Abstract. We introduce a mathematical model of savanna vegetation dynamics. The usual approach of nonequilibrium ecology is extended by including the impact of wet and dry seasons. We present and rigorously analyze a model describing a mixed woodland-grassland ecosystem with stochastic environmental noise in the form of vegetation biomass losses manifesting fires. Both the probability of ignition and the strength of these losses depend on the current season (as well as vegetation growth rates, etc.). Formally it requires an introduction and analysis of a system that is a piecewise deterministic Markov process with parameters switching between given constant periods of time. We study the long time behavior of time averages for such processes.

Key words. seasonality, savanna, tree-grass coexistence, herbivores, fire-vegetation feedback, piecewise deterministic Markov process

MSC codes. 60J25, 92D25, 92D40

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1. Introduction.

Seasonality is a very important feature of various ecological systems that affects their characterization in many ways. Defined as persistent periodic changes of environmental variables like temperature, rainfall, etc., it is crucial to understand population dynamics of many systems [52]. Despite its importance and universality, seasonality is usually not explicitly present in mathematical modeling attempts in ecology. Existing formal inclusion of seasons in models is often analyzed only numerically or based on Floquet theory [29, 52]. We propose a seasonal model that is formally a stochastic hybrid process that jumps between two piecewise deterministic Markov processes (PDMPs, [14]) reflecting repeated switching between two seasons. Although we focus on the example of the savanna dynamics model, we provide a general theory that can be used for other, formally similar, models or in situations with more than two seasons present.

Savannas are biomes characterized generally as mixed tree-grass systems [43] and cover around 20% of Earth's land surface. The competition for resources between trees and grasses is regulated by many factors including herbivore activity, temporary changes in water availability, and fires [50]. There is a rich literature on savanna models [55] based on incorporating into dynamical system vegetation losses due to fires with constant [26, 54] or random [16, 3] frequency. Despite its ecological significance and prospective impact on model parameters, these approaches do not include explicit representation of seasonality. We take into account facts that in humid/mesic savannas rainfall happens primarily in wet seasons, boosting the vegetation growth, and results in more grass fuel for fires, happening more frequently in dry seasons, that cause then more damage to tree cover (see [53, 40, 1, 51] and the references therein). Most

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up-to-date savanna dynamics models that take rainfall and/or soil moisture into account refer to their mean annual value (e.g., [49, 45, 44]). Even when annual mean rainfall changes each year then these are much smaller variations in water availability than between seasons. Moreover, the duration of wet and dry seasons usually are not the same. Nevertheless, there is no direct presence of wet and dry seasons in these models.

In section 2 we introduce a simple seasonal model of savanna vegetation dynamics. A system of logistic equations describes the growth of tree and grass biomasses, and without disturbances it would result in woodland (the trees outcompete grasses). We add random fire events manifested as discrete biomass losses. The probability of ignition and fire severity increase with grass biomass (fuel load). Later in section 3 we focus on a more complicated version of this model where we introduce two more equations describing grazer and browser populations that additionally impact the vegetation dynamics. We provide figures of sample trajectories illustrating the behavior of these systems. The resulting models are stochastic only due to randomly occurring fires. The seasons are present in these models as repeated deterministic switching of growth rate parameters. This is entirely different setting than random switching between model parameters that has been used recently in PDMP models, e.g., in ecological dynamics [7, 5, 10, 24, 23, 20, 21], epidemiology [8], or population genetics [19].

To follow seasonal changes we introduce an additional time variable measuring the duration of stay in a given season. This allows us to represent the savanna models as PDMPs in section 4 and provide sufficient conditions for their ergodicity (Theorem 4.1). Due to periodic changes we cannot study the usual convergence of distributions of such processes, and we must look at the convergence of time averages. In section 5 we explore formally the long time behavior of averages of homogeneous Markov processes, and we formulate one of the main results of the paper that T-processes, as in [47, 36], satisfying a Foster–Lyapunov-type condition (CD2) in [36] are mean ergodic (Theorem 5.1). Then we show that our savanna model PDMPs are such T-processes (Theorem 5.3) which implies Theorem 4.1. In section 6 we provide the proof of Theorem 5.1. The paper concludes with a short discussion.

2. A basic model of savanna dynamics with seasonality. We start with adding seasonality into a simple model to grasp the actual problem with such a modeling approach without intricacies of extended models rich in details and parameters. Basically as our minimal model we continue our work from [31] based on [4] and modify the model presented there. It is a simple competition model between trees and grasses referred to as their biomass amounts (denoted as W and G, respectively) in the system of differential equations:

$$\begin{cases} \frac{dW}{dt} = r_w W\left(1 - \frac{W}{K_w}\right), \\ \frac{dG}{dt} = r_g G\left(1 - \frac{G}{K_g} - \frac{W}{K_w}\right), \end{cases}$$

where r_w and r_g are the respective growth rates, while the carrying capacities for the biomass amounts are K_w and K_g. We normalize both "amount of biomass" variables to lie in $[0, 1]$ by the change of variables

$$w(t) = \frac{W(t)}{K_w}, \quad g(t) = \frac{G(t)}{K_g},$$

and hence the model has the form

$$\begin{cases} \frac{dw}{dt} = r_w w\left(1 - w\right), \\ \frac{dg}{dt} = r_g g\left(1 - g - w\right). \end{cases} \tag{2.1}$$

Observe that (2.1) has three stationary solutions $(1,0)$, $(0,0)$, and $(0,1)$ and that the point $(1,0)$ is asymptotically stable.

We add fires to this model and assume that they occur randomly with

$$\Pr\big(\text{occurrence of fire in } (t,t+\Delta t) \,\big|\, w(t)=w, g(t)=g\big) = \lambda(w,g)\Delta t + o(\Delta t),$$

where the function $\lambda\colon [0,1]^2 \to \mathbb{R}_+$ is continuous. We denote the consecutive moments of fire events by $t_1, t_2, \ldots$. The impact of fire in the model is implemented as the appropriate biomass losses according to

$$\begin{cases} w(t_n) = w(t_n^-) - M_w\, w(t_n^-), \\ g(t_n) = g(t_n^-) - M_g\, g(t_n^-), \end{cases} \tag{2.2}$$

where $M_w, M_g \in (0,1)$ are constants and $v(t^-) = \lim_{s\to t^-} v(s)$ for $v \in \{w,g\}$. When fires occur at fixed deterministic times $t_{n+1} = t_n + \tau$, where τ is a constant, one obtains impulsive systems (see, e.g., [55] or [26] with $\alpha = 1$).

The assumption that the impact of fires is described discretely via constant biomass losses can be improved by a more general setting of random losses. To this end we replace the constants M_w and M_g with random variables. Their distribution can depend on the current biomass amounts. Moreover such a setup can be extended even more by including the seasonality. Thus we introduce two savanna seasons (wet and dry) and code them with variable i, where $i=0$ refers to the dry season, while $i=1$ refers to the wet one. Some model parameters change between seasons. Thus, e.g., r_w^i and r_g^i denote the growth rates in the ith season. The seasons are time intervals changing alternately, and to include this fact in the model we add a new clock variable ζ describing how long the current season lasts, which hence schedules the moments when variable i switches its value. The length of the ith season will be denoted by the constant value ζ_m^i. Additionally, by introducing a 2-dimensional variable ξ for biomass amounts, the differential equation in the ith season takes the final form

$$\begin{cases} \frac{d\xi}{dt} = b^i(\xi), \\ \frac{d\zeta}{dt} = 1, \end{cases} \qquad \text{where} \quad \xi = \begin{pmatrix} w \\ g \end{pmatrix} \quad \text{and} \quad b^i(\xi) = \begin{pmatrix} r_w^i w\,(1-w) \\ r_g^i g\,(1-g-w) \end{pmatrix}. \tag{2.3}$$

Each time ζ reaches its maximal value ζ_m^i, the present season ends, and hence we reset the "duration of stay in a season" that is the value of ζ to 0 and swap the model dynamics by changing all the affected parameters (via switching i to $1-i$ everywhere). Note that the long time behavior of ξ is the same as for (2.1).

Accordingly, the introduction of seasons changes the fire events description to

$$\begin{aligned} \Pr\big(\text{occurrence of fire in } (t,t+\Delta t) \,\big|\, \xi(t)=\xi, \zeta(t)=\zeta, i(t)=i\big) \\ = \lambda^i(\xi,\zeta)\Delta t + o(\Delta t), \end{aligned} \tag{2.4}$$

where λ^i is a positive continuous function. We assume that in the ith season for each ξ and ζ there exists a probability measure $\mathcal{P}^i(\xi,\zeta,A)$ describing both biomass changes due to random fire events

$$\Pr\big(\xi(t_n) \in A \,\big|\, \xi(t_n^-) = \xi, \zeta(t_n^-) = \zeta, i(t_n^-) = i\big) = \mathcal{P}^i(\xi,\zeta,A) \tag{2.5}$$

for any Borel subset A of $\mathbb{R}^2$. In particular, we consider

$$\mathcal{P}^i(\xi,\zeta,A) = \int_\Theta \mathbf{1}_A\big(S_\theta^i(\xi)\big) p_\theta^i(\xi,\zeta)\nu^i(d\theta), \tag{2.6}$$

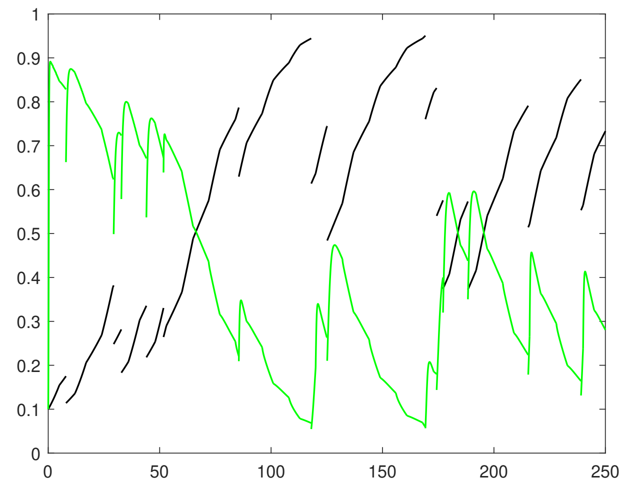

FIG. 1. *Sample trajectories of the stochastic process in* (2.3)–(2.5) *with parameters for the dry season* $r_w^0 = 0.05$, $r_g^0 = 2.5$, $M_w^0 = 0.35$, $M_g^0 = 0.2$, $\lambda^0(w,g,\zeta) = 0.09g + 0.01$, $\zeta_m^0 = 7$ *and for the wet season* $r_w^1 = 0.1$, $r_g^1 = 10.75$, $M_w^1 = 0.2$, $M_g^1 = 0.05$, $\lambda^1(w,g,\zeta) = 0.001g + 0.02$, $\zeta_m^1 = 5$. *The green line represents the graph of the grass biomass amount over time* $t \mapsto g(t)$, *and the black line refers to the wood biomass* $t \mapsto w(t)$.

where $\Theta = (0,1)^2$, ν^i is a Borel measure on Θ, and $(\theta,\xi,\zeta) \to p_\theta^i(\xi,\zeta)$ is a continuous function such that

$$\int_\Theta p_\theta^i(\xi,\zeta)\nu^i(d\theta) = 1. \tag{2.7}$$

The transformation S_θ^i describes the biomass loss due to fire, and to simplify presentation we take

$$S_\theta^i(\xi) = \big((1-\theta_w)w, (1-\theta_g)g\big), \quad \xi = (w,g) \in (0,1) \times (0,1], \quad \theta = (\theta_w, \theta_g). \tag{2.8}$$

Assuming that these losses are constant fractions of available amounts before the fire incident we have $p_\theta^i(\xi,\zeta) \equiv 1$ and $\nu^i(d\theta) = \delta_{(M_w^i, M_g^i)}(d\theta)$, where $M_w^i, M_g^i \in (0,1)$ are constants and δ_M is the Dirac measure at the point $M = (M_w^i, M_g^i)$. On the other hand when these losses are random we can take as ν^i the usual Lebesgue measure on the unit square $(0,1)^2$. Then for each (ξ,ζ) the function $\theta \mapsto p_\theta^i(\xi,\zeta)$ describes the density of the distribution of biomass losses due to fire. In Figure 1 we display sample graphs of wood and grass biomasses in time, including losses due to random fires and changes of seasons.

3. A savanna model featuring herbivores and seasonality. We extend the model from the previous section by adding populations of herbivores depending on the food availability (grass for grazers and trees for browsers). We start with introduction of the population dynamics model that we later complete by adding random fire events and seasonality. The differential equations describing the dynamics of tree and grass biomasses contain additional terms referring to the presence of herbivores:

$$\begin{cases} \frac{dW}{dt} = r_w W\left(1 - \frac{W}{K_w}\right) - c_W H_B W, \\ \frac{dG}{dt} = r_g G\left(1 - \frac{G}{K_g} - \frac{W}{K_w}\right) - c_G H_G G, \end{cases}$$

where H_G, H_B are populations of grazers and browsers and c_W, c_G denote consumption coefficients of woody/grass biomass by browsers/grazers, accordingly. We describe the population dynamics of herbivores as in [50] by

$$\begin{cases} \frac{dH_G}{dt} = e_G H_G G - d_G H_G^2, \\ \frac{dH_B}{dt} = e_W H_B W - d_B H_B^2, \end{cases}$$

where e_W, e_G are consumption and conversion efficiency coefficients of woody/grass biomass by browsers/grazers and d_B, d_G denote death rates of browsers and grazers, respectively.

Similarly to the model from section 2 we normalize biomass amounts and additionally redefine the herbivore population variables by

$$w(t) = \frac{W(t)}{K_w}, \quad g(t) = \frac{G(t)}{K_g}, \quad h_G(t) = \frac{d_G H_G(t)}{e_G K_g}, \quad h_B(t) = \frac{d_B H_B(t)}{e_W K_w},$$

which enforces us to change the parameters as well:

$$c_w \equiv c_W \frac{e_g}{d_G}, \quad c_g \equiv c_G \frac{e_w}{d_B}, \quad e_w \equiv e_W K_W, \quad e_g \equiv e_G K_G.$$

These modifications lead to the simpler system of differential equations:

$$\begin{cases} \frac{dw}{dt} = r_w w\,(1-w) - c_w h_B w, \\ \frac{dg}{dt} = r_g g\,(1-g-w) - c_g h_G g, \\ \frac{dh_G}{dt} = e_g h_G\,(g - h_G)\,, \\ \frac{dh_B}{dt} = e_w h_B\,(w - h_B)\,. \end{cases} \tag{3.1}$$

This system has a unique positive stationary point

$$w = \frac{r_w}{r_w + c_w}, \quad g = \frac{r_g}{r_g + c_g} \frac{c_w}{r_w + c_w}, \quad h_G = g, \quad h_B = w,$$

and it is asymptotically stable. Again, we add alternating seasons, dry ($i = 0$) and wet ($i = 1$), by changing the plant growth rates r_w^i, r_g^i along with them. We illustrate the long time behavior of this system in Figure 2. A typical periodicity of seasonal models is clearly visible in this figure.

Finally we may incorporate the fire events into this model in analogy to the basic no-herbivore model. Now we have a 4-dimensional vector $\xi = (w, g, h_G, h_B)$, and the dynamics is given by (2.3) with the values for $b^i(\xi)$ taken from system (3.1). Fire-related probabilities, (2.4) and (2.5), remain unchanged, while the transformation S_θ^i takes the form

$$S_\theta^i(\xi) = \big((1-\theta_w)w, (1-\theta_g)g, h_G, h_B\big), \quad \xi = (w, g, h_G, h_B), \quad \theta = (\theta_w, \theta_g). \tag{3.2}$$

A sample trajectory of the main model containing all the stochastic effects is presented in Figure 3.

4. PDMPs and seasonality. In this section we recognize introduced savanna models as PDMPs with the aim to show that such processes can be used to study seasonality in ecological/population models. After a brief introduction of the theory basics we formulate one of the main results of this paper concerning the long term behavior of savanna models. For general background on PDMPs we refer the reader to [15, 42].

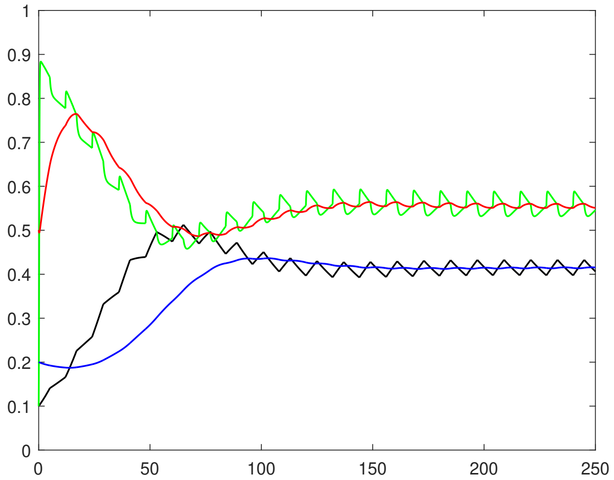

FIG. 2. *Deterministic trajectories for system* (3.1) *with alternating seasons and initial condition* $w = g = 0.1$, $h_G = 0.5$, $h_B = 0.2$. *We used the same color references and parameters as in Figure* 1 *and additionally* $c_w = e_w = 0.1$, $c_g = e_g = 0.2$. *The red line represents the graph of the population of grazers over time* $t \mapsto h_G(t)$, *while the blue line refers to the population of browsers* $t \mapsto h_B(t)$.

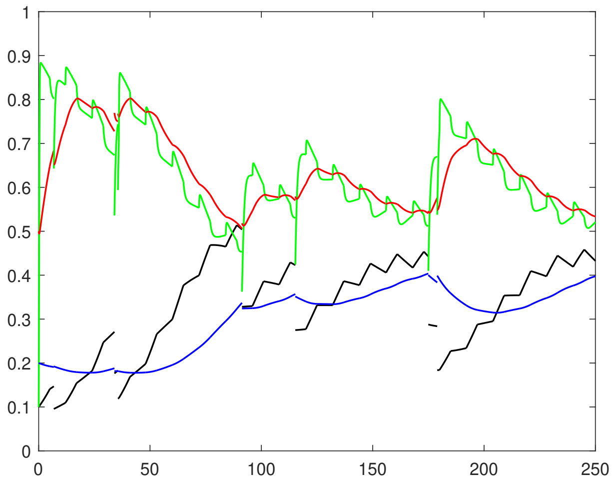

FIG. 3. *Sample trajectories for the stochastic model of savanna vegetation dynamics with herbivores, random fires, and seasonality. The parameters and colors are the same as in Figure* 2.

We consider two flows that arise as solutions of ordinary differential equations

$$\xi'(t) = b^i\big(\xi(t)\big), \tag{4.1}$$

where $b^i \colon \mathbb{R}^d \to \mathbb{R}^d$ is a (locally) Lipschitz continuous mapping. We assume that X_i is a Borel subset of $\mathbb{R}^d$ such that for each $\xi_0 \in X_i$ the solution $\xi(t)$ of (4.1) with initial condition $\xi(0) = \xi_0$ exists and $\xi(t) \in X_i$ for all $t \geq 0$. We denote this solution by $\varphi_t^i(\xi_0)$, $i = 0, 1$. We also introduce the clock variable ζ and the season variable i. Thus, the variable $x = (\xi, \zeta, i)$ changes in time according to the flow

$$\phi_t(x) = \phi_t(\xi, \zeta, i) = \big(\varphi_t^i(\xi), \zeta + t, i\big). \tag{4.2}$$

If we consider the 2-dimensional model from section 2 (no herbivores) then (4.1) and (4.2) introducing the flow ϕ_t correspond to (2.3) with $\xi = (w, g) \in X_i$, where $X_i = (0, 1) \times (0, 1]$ and $i = 0, 1$, while for the 4-dimensional model from section 3 (with grazers and browsers) we have $\xi = (w, g, h_G, h_B) \in X_i$ with $X_i = (0, 1) \times (0, 1] \times (0, \infty)^2$.

Our state space is

$$X = \bigcup_i X_i \times [0, \zeta_m^i) \times \{i\},$$

where ζ_m^i is the length of the ith season. The flow $\{\phi_t\}$ can exit the set X in a finite positive time through a boundary Γ of X. Under our assumptions we have

$$\Gamma = \bigcup_i X_i \times \{\zeta_m^i\} \times \{i\},$$

and the *hitting time* of the boundary Γ is given by

$$t_*(x) = \inf\{t > 0 : \phi_t(x) \in \Gamma\} = \zeta_m^i - \zeta \quad \text{for } x = (\xi, \zeta, i) \in X. \tag{4.3}$$

If the state of the process at the end of a given season is represented by the point (ξ, ζ_m^i, i) from the boundary Γ, then the process moves to the point $(\xi, 0, 1 - i)$ at the beginning of the next season. Thus, jumps are described by a stochastic kernel P defined by

$$P(x, B) = \int_\Theta \mathbf{1}_B\big(\mathbf{S}(x, \theta)\big)\nu(x, d\theta), \quad x \in X \cup \Gamma, B \in \mathcal{B},$$

where $\mathbf{S}\colon (X \cup \Gamma) \times \Theta \to X$ is a measurable transformation and $\nu(x, \cdot)$ is a stochastic kernel. In reference to (2.6), we consider

$$\mathbf{S}(x, \theta) = \mathbf{S}(\xi, \zeta, i, \theta) = \begin{cases} \big(S_\theta^i(\xi), \zeta, i\big) & \text{if } \zeta < \zeta_m^i, \\ (\xi, 0, 1 - i) & \text{if } \zeta = \zeta_m^i, \end{cases} \tag{4.4}$$

and

$$\nu(x, d\theta) = \begin{cases} p_\theta^i(\xi, \zeta)\nu^i(d\theta) & \text{if } \zeta < \zeta_m^i, \\ \nu^i(d\theta) & \text{if } \zeta = \zeta_m^i. \end{cases} \tag{4.5}$$

Finally, let the jump rate function be defined by $q(\xi, \zeta, i) = \lambda^i(\xi, \zeta)$ for $(\xi, \zeta, i) \in X$. For each $x \in X$ we define

$$F_x(t) = \mathbf{1}_{[0, t_*(x))}(t) \exp\left\{-\int_0^t q\big(\phi_r(x)\big)dr\right\}, \quad t \geq 0, \tag{4.6}$$

where ϕ is as in (4.2). If we start at the point $\Psi_0 = (\xi_0, \zeta_0, i_0)$ at time τ_0, then we follow the path $t \mapsto \phi_{t-\tau_0}(\Psi_0)$ up to the occurrence of either the fire or the next season, whichever comes first. Thus the next jump time τ_1 is chosen according to the distribution

$$\mathbb{P}(\tau_1 - \tau_0 > t \,|\, \Psi_0 = x) = F_x(t).$$

Then we define

$$\Phi(t) = \phi_{t-\tau_0}(\Psi_0), \quad \Phi_1 = \phi_{\tau_1 - \tau_0}(\Psi_0), \quad \Psi_1 = \mathbf{S}(\Phi_1, \vartheta_1),$$

where ϑ_1 is a random variable with distribution $\nu(\Phi_1,\cdot)$, and we restart the process from the point Ψ_1. In this way we define a sequence Ψ_n of X-valued random variables and jump-times τ_n such that the process $\Phi=\{\Phi(t):t\geq 0\}$ is defined by

$$\Phi(t)=\phi_{t-\tau_n}(\Psi_n) \quad \text{for } \tau_n\leq t<\tau_{n+1}, \tag{4.7}$$

where

$$\Psi_n=\mathbf{S}\big(\phi_{\sigma_n}(\Psi_n),\vartheta_n\big), \quad \sigma_n=\tau_n-\tau_{n-1}, \tag{4.8}$$

and ϑ_n is a Θ-valued random variable with distribution $\nu(\phi_{\sigma_n}(\Psi_n),\cdot)$, $n\in\mathbb{N}$.

We conclude the section with the main theorem of this paper concerning each of the Markov processes $\Phi=\{\Phi(t):t\geq 0\}$ representing the models from sections 2 and 3. Let $\mathbb{P}_x$ denote the law of the process Φ with initial condition $\Phi(0)=x$, $x\in X$.

We assume that the functions λ^i and p^i_θ satisfy the following:

(i) their values depend only on w, g, and ζ in each case (there is no direct influence of herbivores on fire ignition nor severity);
(ii) λ^i is strictly positive in each season (fires should be always possible but of course much more probable during the dry season);
(iii) there are $a_w,a_g\in(0,1]$ and $\varepsilon_w,\varepsilon_g>0$ such that

$$\lambda^i(w,g,\zeta)\int_\Theta\left[\frac{1}{(1-\theta_w)^{a_w}}-1\right]p^i_\theta(w,g,\zeta)\nu_i(d\theta)-a_w r^i_w\leq-\varepsilon_w \tag{4.9}$$

for all $\zeta\in[0,\zeta^i_m)$, $g\in(0,1]$ and w from a neighborhood of 0, and

$$\begin{aligned}\lambda^i(w,g,\zeta)\int_\Theta\left[\frac{1}{(1-\theta_g)^{a_g}}-1+g^{a_g}\ln\frac{1-w}{1-(1-\theta_w)w}\right]p^i_\theta(w,g,\zeta)\nu_i(d\theta)&\\ -a_g r^i_g(1-w)\leq-\varepsilon_g&\end{aligned} \tag{4.10}$$

for all $\zeta\in[0,\zeta^i_m)$, $w\in(0,1)$, and g from a neighborhood of 0;
(iv) for $a=(a_w,a_g)$ as in (iii) we have

$$\int_0^1\left[\frac{1}{(1-\theta_w)^{a_w}}+\frac{1}{(1-\theta_g)^{a_g}}-\ln(1-(1-\theta_w)w)\right]p^i_\theta(w,g,\zeta)\nu_i(d\theta)<\infty$$

for all $(w,g)\in(0,1)\times(0,1]$, $\zeta\in[0,\zeta^i_m)$.

Conditions (iii)–(iv) are technical assumptions allowing the construction of a Lyapunov function controlling survival of woods and grasses (the behavior of the process when w or g are close to zero). In particular, conditions (4.9) and (4.10) prevent the total loss of wood and grass biomasses, respectively.

THEOREM 4.1. *Suppose that* (i)–(iv) *hold. Then for each* $x=(\xi,\zeta,i)\in X$ *there exists a probability measure* $\Pi(x,\cdot)$ *on* X *such that*

$$\lim_{t\to\infty}\frac{1}{t}\int_0^t\mathbb{P}_x(\Phi(s)\in B)ds=\Pi(x,B) \quad \text{for all } B\in\mathcal{B},$$

and for any bounded Borel measurable f *we have*

$$\mathbb{P}_x\left(\lim_{t\to\infty}\frac{1}{t}\int_0^t f(\Phi(s))ds=\int f d\tilde{\Pi}\right)=1$$

for a random measure $\tilde{\Pi}$ *satisfying* $\Pi(x,B)=\mathbb{E}_x\tilde{\Pi}(B)$, $B\in\mathcal{B}$, $x\in X$.

The proof of Theorem 4.1 will be given in the next section. In fact we will show that the convergence in Theorem 4.1 is uniform with respect to all sets B and that our savanna models are T-processes satisfying a Foster–Lyapunov-type condition (see Theorem 5.3).

We finish the section with the conclusion regarding the model from [31] extended by inclusion of seasonality and (possibly) herbivore activity.

COROLLARY 4.2. *Suppose that the losses are constant fractions* (M_w^i, M_g^i) *of the tree/grass biomass and that* $\lambda^i(w,g,\zeta)=\lambda_0^i g$ *with* $\lambda_0^i>0$, $i=0,1$. *If*

$$r_w^i + \lambda_0^i \ln(1-M_w^i) > 0, \quad i=0,1, \tag{4.11}$$

then Theorem 4.1 *holds.*

Proof. From condition (4.11) it follows that there exists $a_w \in (0,1]$ such that

$$\lambda_0^i \left[\frac{1}{(1-M_w^i)^{a_w}} - 1\right] - a_w r_w^i < 0, \quad i=0,1,$$

implying condition (4.9). Now observe that the left-hand side of (4.10) is of the form

$$\lambda_0^i g \left[\frac{1}{(1-M_g^i)^{a_g}} - 1 + g^{a_g} \ln \frac{1-w}{1-(1-M_w^i)w}\right] - a_g r_g^i (1-w),$$

and for $w \in (0,1)$ and g from a neighborhood of 0, it is always negative. Consequently, assumptions (i)–(iv) are satisfied. ∎

Remark 4.3. In the simplest model as in Corollary 4.2 note that condition (4.11) implies that $r_w^i + \lambda_0^i g \ln(1-M_w^i) > 0$ for all $g \in (0,1]$, $i=0,1$. Thus the mean growth rate of wood biomass is positive in the limit $w \to 0$ in both seasons allowing wood-grass coexistence (in the presence of random fires).

5. Mean ergodic Markov processes. Following [35, 36, 37], we summarize briefly necessary concepts to study the long time behavior of Markov processes. Let X be a locally compact separable metric space, and let $\mathcal{B}$ denote the Borel subsets of X. A function $T\colon X \times \mathcal{B} \to [0,1]$ is called a *(substochastic) kernel* on X if for $B \in \mathcal{B}$ the function $T(\cdot,B)$ is measurable and $T(x,\cdot)$ is a measure on $\mathcal{B}$ (satisfying $T(x,X) \le 1$ for each $x \in X$). The kernel is called *nontrivial* if $T(x,X)>0$ for all $x \in X$ and *stochastic* if $T(x,X)=1$ for all x. A substochastic kernel T defines a linear operator on the space of finite signed measures $\mathcal{M}(X)$ on $\mathcal{B}$. For $\mu \in \mathcal{M}(X)$ we define a new signed measure μT by

$$\mu T(B) = \int_X T(x,B)\mu(dx).$$

If K and T are two kernels their product KT is defined as

$$KT(x,B) = \int_X T(y,B)K(x,dy), \quad x \in X, B \in \mathcal{B}.$$

A kernel T is called a *continuous component* of a kernel K on X if it satisfies $K(x,B) \ge T(x,B)$ for all $x \in X$, $B \in \mathcal{B}$ and the function $T(\cdot,B)$ is *lower semicontinuous*, i.e.,

$$\liminf_{y \to x} T(y,B) \ge T(x,B), \quad x \in X.$$

Let $\Phi = \{\Phi(t) : t \geq 0\}$ be a continuous-time Markov process with state space X, and let $\mathbb{P}_x$ denote the law of the process Φ with initial condition $\Phi(0) = x$, $x \in X$. We assume that Φ is strong Markov and has right-continuous sample paths with left limits. For each $t \geq 0$ the transition probability of the process is

$$P^t(x, B) = \mathbb{P}_x\big(\Phi(t) \in B\big), \quad x \in X, B \in \mathcal{B},$$

and if the process is nonexplosive, then P^t is a stochastic kernel. Recall that the process Φ is *nonexplosive* if there is an increasing sequence of open precompact sets O_n such that $X = \bigcup_n O_n$, and for each $x \in X$ we have

$$\mathbb{P}_x\left(\lim_{n\to\infty} \inf\{t \geq 0 : \Phi(t) \notin O_n\} = \infty\right) = 1.$$

An operator $\mathcal{L}$ is called the *extended generator* of the Markov process Φ (see [15]) if its domain $\mathcal{D}(\mathcal{L})$ consists of those measurable $V : X \to \mathbb{R}$ for which there exists a measurable $W : X \to \mathbb{R}$ such that the function $t \mapsto W(\Phi(t))$ is integrable $\mathbb{P}_x$-a.s. for each $x \in X$ with the process

$$t \mapsto V\big(\Phi(t)\big) - V(x) - \int_0^t W\big(\Phi(s)\big)\, ds$$

being a $\mathbb{P}_x$-local martingale, and we define $\mathcal{L}V = W$. A function $V : X \to [0, \infty]$ is said to be *norm-like* if the sets $\{x \in X : V(x) \leq r\}$ are precompact for all sufficiently large $r > 0$. It follows from [37, Theorem 2.1] that if there exists a norm-like function $V \in \mathcal{D}(\mathcal{L})$ and constants $c, d \geq 0$ such that

$$\mathcal{L}V(x) \leq cV(x) + d, \quad x \in X, \tag{5.1}$$

then the process Φ is nonexplosive.

For any $\mu \in \mathcal{M}(X)$ we define the norm

$$\|\mu\| = \sup_{B\in\mathcal{B}} |\mu(B)|, \quad \mu \in \mathcal{M}(X).$$

It is equivalent to the total variation norm since we have $\|\mu\| \leq \|\mu\|_{TV} \leq 2\|\mu\|$. The process Φ is called *Cesáro-ergodic* (or *mean ergodic*) if for each probability measure μ there exists a measure $\mu\Pi \in \mathcal{M}(X)$ such that

$$\lim_{t\to\infty} \left\| \frac{1}{t} \int_0^t \mu P^s(\cdot) ds - \mu\Pi \right\| = 0. \tag{5.2}$$

In that case we define

$$\Pi(x, B) = \delta_x \Pi(B), \quad B \in \mathcal{B}, x \in X,$$

where δ_x is the Dirac delta. Recall that a probability measure π is called *invariant for the process* Φ if $\pi = \pi P^t$ for all t. In particular, each limiting measure $\mu\Pi$ in (5.2) is invariant for the process Φ. Finally, the process Φ is called a T*-process* if for some probability measure a on $\mathbb{R}_+$ the kernel K_a defined by

$$K_a(x, B) = \int_0^\infty P^t(x, B) a(dt) \tag{5.3}$$

has a nontrivial continuous component.

We now impose a Foster–Lyapunov-type condition corresponding to condition (CD2) in [37]:

(V) there exist a nonnegative norm-like $V \in \mathcal{D}(\mathcal{L})$, a measurable $f\colon X \to [1,\infty)$, a compact set C, and positive constants c, d such that

$$\mathcal{L}V(x) \le -cf(x) + d\mathbf{1}_C(x), \quad x \in X. \tag{5.4}$$

THEOREM 5.1. *Suppose that condition* (V) *holds and that the process* Φ *is a* T*-process. Then* Φ *is mean ergodic, and we have*

$$\mathbb{P}_x\left(\lim_{t\to\infty}\frac{1}{t}\int_0^t f(\Phi(s))ds = \int f d\tilde{\Pi}\right) = 1$$

for any bounded Borel measurable f *and for a random measure* $\tilde{\Pi}$ *satisfying* $\Pi(x,B) = \mathbb{E}_x\tilde{\Pi}(B)$, $B \in \mathcal{B}$, $x \in X$.

The proof of Theorem 5.1 is given in section 6. We have the following direct consequence of Theorem 5.1.

COROLLARY 5.2. *Suppose that condition* (V) *holds and that the process* Φ *is a* T*-process with a unique invariant probability measure* π. *Then*

$$\lim_{t\to\infty}\sup_{B\in\mathcal{B}}\left|\frac{1}{t}\int_0^t P^s(x,B)ds - \pi(B)\right| = 0$$

and

$$\mathbb{P}_x\left(\lim_{t\to\infty}\frac{1}{t}\int_0^t f(\Phi(s))ds = \int f d\pi\right) = 1$$

for all $x \in X$ *and all bounded Borel measurable* f.

Our next result, along with Theorem 5.1, implies Theorem 4.1 and shows that savanna models from sections 2 and 3 are mean ergodic.

THEOREM 5.3. *Under assumptions* (i)–(iv) *the Markov processes from sections* 2 *and* 3 *satisfy condition* (V) *and are* T*-processes.*

Proof. We start by showing how condition (V) can be checked for our PDMP models. Let $M(X)$ be the set of all measurable real-valued functions on X. We define as in [15]

$$M_\Gamma(X) = \{V \in M(X) : V(x) = \lim_{t\downarrow 0} V\big(\phi_{-t}(x)\big) \text{ for } x \in \Gamma\}.$$

It can be shown as in the proof of [15, Theorem 26.14] and [28, Theorem 18] that the domain $\mathcal{D}(\mathcal{L})$ of the extended generator $\mathcal{L}$ contains those functions $V \in M_\Gamma(X)$ that satisfy the following:

1. the function $t \mapsto V(\phi_t(x))$ is absolutely continuous on $[0, t_*(x))$ for $x \in X$;
2. V satisfies the boundary condition

$$V(x) = \int_X V(y)P(x,dy), \quad x \in \Gamma;$$

3. for each $x \in X$ and $t < t_*(x)$

$$\int_0^t\int_X \big|V(y) - V\big(\phi_s(x)\big)\big|P\big(\phi_s(x),dy\big)q\big(\phi_s(x)\big)ds < \infty.$$

The formula for the extended generator $\mathcal{L}$ is

$$\mathcal{L}V(x) = \mathcal{L}_0 V(x) + q(x)\int_X \big(V(y) - V(x)\big)P(x,dy),$$

where

$$\mathcal{L}_0 V(x) = \lim_{t\downarrow 0} \frac{V\big(\phi_t(x)\big) - V(x)}{t}.$$

For $V \in \mathcal{D}(\mathcal{L})$ that is a smooth function of variables ξ and ζ we have

$$\mathcal{L}V(\xi,\zeta,i) = \mathcal{L}_0 V(\xi,\zeta,i) + \lambda^i(\xi,\zeta)\int_\Theta \big(V\big(S^i_\theta(\xi),\zeta,i\big) - V(\xi,\zeta,i)\big)p^i_\theta(\xi,\zeta)\nu^i(d\theta),$$

where

$$\mathcal{L}_0 V(\xi,\zeta,i) = \sum_{j=1}^d b^i_j(\xi)\frac{\partial V}{\partial \xi_j}(\xi,\zeta,i) + \frac{\partial V}{\partial \zeta}(\xi,\zeta,i), \quad \xi \in X_i, \zeta \in [0,\zeta^i_m), i = 0,1,$$

and the boundary condition is of the form

$$V(\xi,\zeta^i_m,i) = V(\xi,0,1-i), \quad \xi \in X_i, i = 0,1.$$

For $d = 2$ and $\xi = (w,g)$ we take

$$V_1(w,g,\zeta,i) = \frac{1}{w^{a_w}} + \frac{1}{g^{a_g}} - \ln(1-w) + \zeta\sqrt{\zeta^i_m - \zeta},$$

while for $d = 4$ and $\xi = (w,g,h_G,h_B)$ we consider

$$V_2(w,g,h_G,h_B,\zeta,i) = V_1(w,g,\zeta,i) + \frac{1}{h_G} + \ln(1+h_G) + \frac{1}{h_B} + \ln(1+h_B).$$

It is easily seen that both functions are in the domain of the corresponding extended generator. Note that for $V = V_1$ and $V = V_2$ we have

$$\begin{aligned} V(S^i_\theta(\xi),\zeta,i) - V(\xi,\zeta,i) = {} & \frac{1}{w^{a_w}}\left[\frac{1}{(1-\theta_w)^{a_w}} - 1\right] + \frac{1}{g^{a_g}}\left[\frac{1}{(1-\theta_g)^{a_g}} - 1\right] \\ & + \ln(1-w) - \ln(1-(1-\theta_w)w). \end{aligned}$$

Thus condition (V) holds, since $\mathcal{L}V(\xi,\zeta,i) \to -\infty$ when ξ tends to the boundary of X_i or $\zeta \to \zeta^i_m$, by assumptions (i) and (iii).

Now we prove that the process $\Phi = \{\Phi(t) : t \geq 0\}$ as in (4.7) is a T-process. Since its probability transition function is given by

$$\begin{aligned} P^t(x,B) = \mathbb{P}_x\big(\Phi(t) \in B\big) &= \sum_{n=0}^\infty \mathbb{P}_x\big(\Phi(t) \in B, \tau_n \leq t < \tau_{n+1}\big) \\ &= \sum_{n=0}^\infty \mathbb{P}\left(\phi_{t-\tau_n}(\Psi_n) \in B, \tau_n \leq t < \tau_{n+1}\right) \end{aligned}$$

for $x \in X$, $B \in \mathcal{B}$, it is enough to show that for each $x_0 \in X$ there exist a constant $c_{x_0} > 0$, an open set U_{x_0} containing x_0, and an open set V_{x_0} such that

$$\int_0^\infty P^t(x,B)e^{-t}dt \geq c_{x_0}\mathbf{1}_{U_{x_0}}(x)m(B \cap V_{x_0}), \quad B \in \mathcal{B}, x \in X, \tag{5.5}$$

where m is the product of the $(d+1)$-dimensional Lebesgue measure and the counting measure on $\{0,1\}$. The kernel $T_{x_0}(x,B) = c_{x_0}\mathbf{1}_{U_{x_0}}(x)m(B\cap V_{x_0})$ is a continuous component nontrivial at x_0 for K_a with a being the exponential distribution on $\mathbb{R}_+$. By taking a sequence of points (x_k) such that $X = \bigcup_k U_{x_k}$ we can define the kernel $T = \sum_{k=1}^{\infty} 2^{-k} T_{x_k}$ and conclude that T is a continuous component nontrivial at every $x \in X$. It implies that Φ is a T-process.

We have for any n

$$\int_0^\infty P^t(x,B)e^{-t}dt \ge \int_0^\infty \mathbb{P}_x\big(\phi_{t-\tau_n}(\Psi_n) \in B, \tau_n \le t < \tau_{n+1}\big)e^{-t}dt. \tag{5.6}$$

We will show that we can pick an n such that the measure in the right-hand side of (5.6) has a lower bound as in (5.5). To this end we apply [6, Lemma 6.3] to the $(d+1)$-dimensional component of X.

Assume first that $d=2$, and take $n=2$ in (5.6). It follows from (4.7) and (4.8) that

$$\phi_{t-\tau_2}(\Psi_2) = \phi_{t-(\sigma_2+\sigma_1)}(\Psi_2), \quad \Psi_2 = \mathbf{S}\big(\phi_{\sigma_2}(\Psi_1), \vartheta_2\big), \quad \Psi_1 = \mathbf{S}\big(\phi_{\sigma_1}(x), \vartheta_1\big),$$

where ϑ_k is random variables with distribution $\nu(\phi_{\sigma_k}(\Psi_{k-1}),\cdot)$, $k=1,2$, while $\mathbf{S}$ and ν are as in (4.4) and (4.5). Let σ be an exponentially distributed random variable independent of all other random variables. Then the right-hand side of (5.6) is equal to

$$\mathbb{P}_x\big(\phi_{\sigma-(\sigma_1+\sigma_2)}(\Psi_2) \in B, \sigma_1+\sigma_2 \le \sigma < \sigma_1+\sigma_2+\sigma_3\big). \tag{5.7}$$

Let $x_0 = (\xi_0, \zeta_0, i_0)$ with $\xi_0 \in (0,1)\times(0,1]$, $\zeta_0 \in [0, \zeta_m^{i_0})$, and $i_0 \in \{0,1\}$. We take two fire occurrences in a single season and the third jump to be the exit time from the given season. We define $i = i_0$, $\xi_1 = S^i_{\theta_1}(\xi_0)$, and $\xi_2 = S^i_{\theta_2}(\xi_1)$, where $\theta_1 \in (0,1)^2$ and $\theta_2 \in (0,1)^2$ are such that $p^i_{\theta_1}(\xi_0,\zeta_0) > 0$ and $p^i_{\theta_2}(\xi_1,\zeta_0) > 0$. We can always choose such θ_1 and θ_2 by (2.7). Recall that the functions p^i are continuous and that the jump rate function q, given by $q(x) = \lambda^i(\xi,\zeta)$, is also continuous. This, together with (4.6) and (4.5), implies that there is a neighborhood of x_0 such that the distribution of the random variable $(\sigma_1,\sigma_2,\sigma)$ has an absolutely continuous part with respect to the 3-dimensional Lebesgue measure and with density being bounded below by a positive constant in a neighborhood of $(0,0,0)$. Let us introduce on $\Delta_t = \{(t_1,t_2) : t_1,t_2 > 0, t_1+t_2 < t\}$ the following mapping:

$$\psi^i_{(t,\xi,\boldsymbol{\theta})}(\mathbf{t}) = \varphi^i_{t-(t_1+t_2)} \circ S^i_{\theta_2} \circ \varphi^i_{t_2} \circ S^i_{\theta_1} \circ \varphi^i_{t_1}(\xi) \quad \text{for } \mathbf{t} = (t_1,t_2) \in \Delta_t,$$

where $t>0$, $\boldsymbol{\theta} = (\theta_1,\theta_2) \in (0,1)^2\times(0,1)^2$, $\xi = (w,g) \in (0,1)\times(0,1]$. To estimate (5.7) from below it is enough by [6, Lemma 6.3] to show that the mapping

$$(\boldsymbol{t}, t) \mapsto \big(\psi^i_{(t,\xi,\boldsymbol{\theta})}(\mathbf{t}), \zeta+t\big)$$

has the derivative of full rank 3 for small t in a neighborhood of (ξ_0,ζ_0).

Observe that

$$\lim_{\xi\to\xi_0,\, t\to 0} \frac{d\psi^i_{(t,\xi,\boldsymbol{\theta})}(\mathbf{t})}{d\mathbf{t}} = A, \tag{5.8}$$

where A is the matrix with columns v_1, v_2 given by

$$v_1 = DS^i_{\theta_2}(\xi_1)DS^i_{\theta_1}(\xi_0)b^i(\xi_0) - b^i(\xi_2), \quad v_2 = DS^i_{\theta_2}(\xi_1)b^i(\xi_1) - b^i(\xi_2),$$

D denotes the derivative with respect to ξ, and b^i is as in (2.3). Now we show that the vectors v_1 and v_2 are linearly independent. The transformation S^i_θ is linear; thus $DS^i_\theta = S^i_\theta$. Let $S_1 = S^i_{\theta_1}$, $S_2 = S^i_{\theta_2}$, and to simplify calculations, let $S_j(w,g) = (\alpha_j w, \beta_j g)$, where $(1-\alpha_j, 1-\beta_j) = \theta_j$ by (2.8). Then we have

$$A = \begin{pmatrix} \alpha_2\alpha_1(\alpha_2\alpha_1 - 1) r^i_w w^2 & \alpha_2(\alpha_2 - 1)\alpha_1^2 r^i_w w^2 \\ \beta_2\beta_1 r^i_g g\big[(\alpha_2\alpha_1 - 1)w + (\beta_2\beta_1 - 1)g\big] & \beta_2\beta_1 r^i_g g\big[(\alpha_2 - 1)\alpha_1 w + (\beta_2 - 1)\beta_1 g\big] \end{pmatrix}.$$

We see that $\det A = 0$ if and only if

$$\frac{\alpha_1}{\beta_1}\frac{1-\alpha_2}{1-\beta_2} = \frac{1-\alpha_1\alpha_2}{1-\beta_1\beta_2}. \tag{5.9}$$

We conclude that

$$\det\left[\frac{d\psi^i_{(t,\xi,\boldsymbol{\theta})}(\mathbf{t})}{d\mathbf{t}}\right] \neq 0$$

for ξ close to ξ_0, sufficiently small t, and suitably chosen $\boldsymbol{\theta}$.

Now for the case of $d = 4$ we take $n = 5$ (two fire occurrences in each season and a switch between the seasons) in (5.6). Let $\Delta_t = \{(t_1,t_2,t_3,t_4) : t_1,t_2,t_3,t_4 > 0, t_1+t_2+t_3+t_4 < t\}$ and

$$\psi^i_{(t,\xi,\zeta,\boldsymbol{\theta})}(\mathbf{t}) = \varphi^{1-i}_{t-(t_3+t_4+\zeta^i_m-\zeta)} \circ S^{1-i}_{\theta_4} \circ \varphi^{1-i}_{t_4} \circ S^{1-i}_{\theta_3} \circ \varphi^{1-i}_{t_3} \circ \varphi^i_{\zeta^i_m-\zeta-(t_1+t_2)} \circ S^i_{\theta_2} \circ \varphi^i_{t_2} \circ S^i_{\theta_1} \circ \varphi^i_{t_1}(\xi)$$

for $\mathbf{t} = (t_1,t_2,t_3,t_4) \in \Delta_t$, $t > 0$, $\boldsymbol{\theta} = (\theta_1,\theta_2,\theta_3,\theta_4)$ with each $\theta_j \in (0,1)^2$, and $\xi = (w,g,h_G,h_B) \in (0,1)\times(0,1]\times(0,\infty)^2$. We take arbitrary $x_0 = (\xi_0,\zeta_0,i_0)$ with $\xi_0 \in (0,1)\times(0,1]\times(0,\infty)^2$, $\zeta_0 \in [0,\zeta^{i_0}_m)$, and $i_0 \in \{0,1\}$. We define $i = i_0$,

$$\xi_1 = \varphi^i_{\zeta^i_m-\zeta_0}(\xi_0), \quad \xi_2 = S^i_{\theta_1}(\xi_1), \quad \xi_3 = S^i_{\theta_2}(\xi_2), \quad \xi_4 = S^{1-i}_{\theta_3}(\xi_3), \quad \xi_5 = S^{1-i}_{\theta_4}(\xi_4),$$

where $\theta_1,\theta_2,\theta_3,\theta_4 \in (0,1)^2$ are such that $p^i_{\theta_j}(\xi_j,\zeta^i_m-\zeta_0) > 0$ for $j = 1,2$ and $p^{1-i}_{\theta_j}(\xi_j,0) > 0$ for $j = 3,4$. Similarly as for $d = 2$ by [6, Lemma 6.3] it is enough to show that the mapping

$$(\boldsymbol{t},t) \mapsto \Big(\psi^i_{(t,\xi,\zeta,\boldsymbol{\theta})}(\mathbf{t}), t-(\zeta^i_m-\zeta)\Big)$$

has the derivative of full rank 5 for a short time of staying in the season $1-i$, i.e., as $t \downarrow \zeta^i_m - \zeta_0$, and in a neighborhood of (ξ_0,ζ_0). It is easily seen that

$$\lim_{\substack{\xi\to\xi_0,\,\zeta\to\zeta_0,\\ t,t_1\to\zeta^i_m-\zeta_0,\,t_2\to 0}} \frac{d\psi^i_{(t,\xi,\zeta,\boldsymbol{\theta})}(\mathbf{t})}{d\mathbf{t}} = A, \tag{5.10}$$

where now A is the matrix with columns v_1,v_2,v_3,v_4 given by

$$\begin{aligned}
v_1 &= DS^{1-i}_{\theta_4}(\xi_4)DS^{1-i}_{\theta_3}(\xi_3)(DS^i_{\theta_2}(\xi_2)DS^i_{\theta_1}(\xi_1)b^i(\xi_1) - b^i(\xi_3)),\\
v_2 &= DS^{1-i}_{\theta_4}(\xi_4)DS^{1-i}_{\theta_3}(\xi_3)(DS^i_{\theta_2}(\xi_2)b^i(\xi_2) - b^i(\xi_3)),\\
v_3 &= DS^{1-i}_{\theta_4}(\xi_4)DS^{1-i}_{\theta_3}(\xi_3)b^{1-i}(\xi_3) - b^{1-i}(\xi_5),\\
v_4 &= DS^{1-i}_{\theta_4}(\xi_4)b^{1-i}(\xi_4) - b^{1-i}(\xi_5).
\end{aligned}$$

By using the formula for $b(\xi)$ given by the right-hand side of (3.1) with $\xi=(w,g,h_G,h_B)$ and by taking $S(\xi)=(\alpha w,\beta g,h_G,h_B)$ for the corresponding S^i_θ as in (2.8), we obtain

$$S\big(b(\xi)\big)-b\big(S(\xi)\big)=\begin{pmatrix}\alpha(\alpha-1)r_w w^2\\ \beta r_g g\big[(\alpha-1)w+(\beta-1)g\big]\\ (1-\beta)e_g h_G g\\ (1-\alpha)e_w h_B w\end{pmatrix}\quad\text{for } \xi=(w,g,h_G,h_B). \tag{5.11}$$

Let us take $S_j=S^i_{\theta_j}$ for $j=1,2$ and $S_j=S^{1-i}_{\theta_j}$ for $j=3,4$ so that $S_j(w,g,h_G,h_B)=(\alpha_j w,\beta_j g,h_G,h_B)$ with $(1-\alpha_j,1-\beta_j)=\theta_j$. Applying (5.11) with $r_w=r^i_w$ and $r_g=r^i_g$ and appropriate α,β, the vector v_1 with $\xi_1=(w,g,h_G,h_B)$ is of the form

$$v_1=\begin{pmatrix}\alpha_4\alpha_3\alpha_2\alpha_1(\alpha_2\alpha_1-1)r^i_w w^2\\ \beta_4\beta_3\beta_2\beta_1 r^i_g g\big[(\alpha_2\alpha_1-1)w+(\beta_2\beta_1-1)g\big]\\ (1-\beta_2\beta_1)e_g h_G g\\ (1-\alpha_2\alpha_1)e_w h_B w\end{pmatrix}.$$

Similarly, we obtain

$$v_2=\begin{pmatrix}\alpha_4\alpha_3\alpha_2\alpha_1^2(\alpha_2-1)r^i_w w^2\\ \beta_4\beta_3\beta_2\beta_1 r^i_g g\big[(\alpha_2-1)\alpha_1 w+(\beta_2-1)\beta_1 g\big]\\ (1-\beta_2)\beta_1 e_g h_G g\\ (1-\alpha_2)\alpha_1 e_w h_B w\end{pmatrix}.$$

Next observe that

$$v_3=\begin{pmatrix}\alpha_4\alpha_3(\alpha_4\alpha_3-1)\alpha_2^2\alpha_1^2 r^{1-i}_w w^2\\ \beta_4\beta_3\beta_2\beta_1 r^{1-i}_g g\big[(\alpha_4\alpha_3-1)\alpha_2\alpha_1 w+(\beta_4\beta_3-1)\beta_2\beta_1 g\big]\\ (1-\beta_4\beta_3)\beta_2\beta_1 e_g h_G g\\ (1-\alpha_4\alpha_3)\alpha_2\alpha_1 e_w h_B w\end{pmatrix}$$

and

$$v_4=\begin{pmatrix}\alpha_4(\alpha_4-1)\alpha_3^2\alpha_2^2\alpha_1^2 r^{1-i}_w w^2\\ \beta_4\beta_3\beta_2\beta_1 r^{1-i}_g g\big[(\alpha_4-1)\alpha_3\alpha_2\alpha_1 w+(\beta_4-1)\beta_3\beta_2\beta_1 g\big]\\ (1-\beta_4)\beta_3\beta_2\beta_1 e_g h_G g\\ (1-\alpha_4)\alpha_3\alpha_2\alpha_1 e_w h_B w\end{pmatrix}.$$

Using Gaussian elimination it is easily seen that the first two coordinates of v_1 and v_2 can be made zero and hence $\det A=0$ if and only if (5.9) holds or

$$\frac{\alpha_3}{\beta_3}\frac{1-\alpha_4}{1-\beta_4}=\frac{1-\alpha_3\alpha_4}{1-\beta_3\beta_4}. \tag{5.12}$$

Consequently, we can find $\theta_j=(1-\alpha_j,1-\beta_j)$, $j=1,2,3,4$, such that both (5.9) and (5.12) do not hold implying that

$$\det\frac{d\psi^i_{(t,\xi,\zeta,\boldsymbol{\theta})}(\mathbf{t})}{d\mathbf{t}}\neq 0$$

for t close to $\zeta^{i_0}_m-\zeta_0$ and (ξ,ζ) in a neighborhood of (ξ_0,ζ_0). ∎

6. Proof of Theorem 5.1. The resolvent kernel $R\colon X\times\mathcal{B}\to[0,1]$ is defined as

$$R(x,B)=\int_0^\infty e^{-t}P^t(x,B)dt.$$

The kernel R is the transition probability for the discrete-time Markov chain $\breve{\Phi}$ that is defined by observing the process Φ at jump-times of a Poisson process with intensity 1 that is independent of the process Φ. We call this chain the *R-chain*. We say that the R-chain is a *T-chain* if there is a probability distribution $b = (b_k)$ on $\mathbb{Z}_+$ and a nontrivial continuous component for the kernel

$$R_b(x, B) = \sum_{n=0}^{\infty} b_n R^n(x, B).$$

Following [35] and [36] we say that a trajectory converges to infinity if it visits each compact set only finitely many times, and we write $\{\breve{\Phi} \to \infty\}$ for the R-chain and $\{\Phi \to \infty\}$ for the process Φ.

LEMMA 6.1. *If the R-chain $\breve{\Phi}$ is a T-chain, then Φ is a T-process and*

$$\mathbb{P}_x\{\breve{\Phi} \to \infty\} = \mathbb{P}_x\{\Phi \to \infty\}, \quad x \in X. \tag{6.1}$$

If $\mathbb{P}_x\{\Phi \to \infty\} < 1$ for all $x \in X$ and Φ is a T-process, then the R-chain is a T-chain.

Proof. Since the nth jump of the Poisson process has the Erlang distribution, we have

$$R^n(x, B) = \int_0^{\infty} e^{-t} \frac{t^{n-1}}{(n-1)!} P^t(x, B) dt.$$

If we consider the probability measure

$$a(dt) = \sum_{n=0}^{\infty} b_n e^{-t} \frac{t^n}{n!} dt$$

on $\mathbb{R}_+$, where $b = (b_n)$ is a probability measure on $\mathbb{Z}_+$, then the kernel K_a has the same continuous component as R_b. The equality in (6.1) follows from [36, Proposition 3.2]. The converse statement is [36, Theorem 4.1(iii)]. ∎

The R-chain is called a *mean ergodic* chain on X if for each probability measure $\mu \in \mathcal{M}(X)$ there exists a measure $\mu\Pi \in \mathcal{M}(X)$ such that

$$\lim_{n \to \infty} \left\| \frac{1}{n} \sum_{k=0}^{n-1} \mu R^k - \mu\Pi \right\| = 0. \tag{6.2}$$

Observe that the measure $\pi = \mu\Pi$ in condition (6.2) is invariant for the R-chain, i.e., $\pi R = \pi$. It is known (see [2]) that a measure π is invariant for the process Φ if and only if it is invariant for the R-chain. We now show that the convergence in (6.2) is equivalent to the one in (5.2).

LEMMA 6.2. *The process Φ is mean ergodic if and only if the R-chain is mean ergodic on X. Moreover, for any bounded Borel measurable f we have*

$$\lim_{t \to \infty} \frac{1}{t} \int_0^t f\big(\Phi(s)\big) ds = \lim_{n \to \infty} \frac{1}{n} \sum_{k=1}^{n} f(\breve{\Phi}_k)$$

if any of the pointwise limits exist.

Proof. For any probability measure μ on $\mathcal{B}$ we define the resolvent operator of P^t by

$$\mu U_\alpha(B)=\int_0^\infty e^{-\alpha t}\mu P^t(B)dt, \quad \alpha>0, B\in\mathcal{B}.$$

We have $\mu U_1=\mu R$ and

$$\mu U_\alpha(B)=\sum_{k=1}^\infty(1-\alpha)^{k-1}\mu R^k(B), \quad B\in\mathcal{B}. \tag{6.3}$$

First observe that the Cesáro convergence in (6.2) implies the Abel convergence

$$\lim_{\alpha\to 0^+}\alpha\sum_{k=1}^\infty(1-\alpha)^{k-1}\mu R^k=\mu\Pi,$$

(see, e.g., [33, Theorem 2.1]) and leads to

$$\lim_{\alpha\to 0^+}\|\alpha\mu U_\alpha-\mu\Pi\|=0. \tag{6.4}$$

Condition (6.4) implies (6.2) by [17, Theorem 3.1] and (5.2) by [17, Theorem 3.3]. Finally, the implication leading from (5.2) to (6.4) follows by using standard arguments. The second part follows from [9, Theorem 5.1.1]. ☐

We need to introduce more notation. The following notions will be presented only for the continuous-time process Φ, but analogous definitions are valid for the discrete-time R-chain $\check{\Phi}=\{\check{\Phi}_k\}$. We refer to [38] for the general theory of discrete-time Markov chains.

Given a measurable set B we define the first hitting time of the set B and the number of visits to B, respectively, by

$$\tau_B=\inf\{t>0:\Phi(t)\in B\} \quad\text{and}\quad \eta_B=\int_0^\infty \mathbf{1}\{\Phi(t)\in B\}dt.$$

A set B is called (stochastically) *closed* for the process if $B\neq\emptyset$ and $\mathbb{P}_x\{\Phi(t)\in B \text{ for all } t\geq 0\}=1$ for $x\in B$. A closed set B is said to be *maximal* if $x\in B\iff \mathbb{P}_x\{\eta_B=\infty\}=1$. A set H is called a *Harris set* for the process Φ if it is closed and if there exists some σ-finite measure ψ such that $\mathbb{P}_x\{\eta_B=\infty\}=1$ for all $x\in H$ and all $B\in\mathcal{B}$ with $\psi(B)>0$. A set H is called a *maximal Harris set* if it is a Harris set and a maximal closed set. The process restricted to a maximal Harris set H has an essentially unique invariant measure on H. If the measure is finite, then it can be normalized, and the process has a unique invariant probability measure on H. In that case the set H is called a *positive Harris set*.

LEMMA 6.3. *Suppose that condition* (V) *holds. Then* $\mathbb{P}_x\{\Phi\to\infty\}=0$ *for all* $x\in X$. *If the process* Φ *is a* T*-process, then the space* X *has the decomposition into disjoint sets*

$$X=\bigcup_{i=1}^N H_i\cup E=H\cup E,$$

where each H_i *is a positive Harris set and* $\mathbb{P}_x\{\eta_H=\infty\}=1$ *for all* $x\in X$. *Moreover, the* R*-chain is mean ergodic on* X.

Proof. The function V in condition (V) is norm-like and satisfies $\mathcal{L}V(x) \le d\mathbf{1}_C(x)$ for all $x \in X$. Thus condition (CD1) of [36] holds, and [36, Theorem 3.1] implies that $\mathbb{P}_x\{\Phi \to \infty\} = 0$ for all $x \in X$. The Doeblin decomposition [36, Theorem 4.1] and [37, Theorem 4.6] show that the space X has the required decomposition. It follows from [36, Theorem 2.1] that

$$\mathbb{P}_x\{\check{\tau}_H < \infty\} = \mathbb{E}_x\big(1 - \exp(-\eta_H)\big), \quad x \in X,$$

where $\check{\tau}_H = \inf\{k \ge 1 : \check{\Phi}_k \in H\}$ is the first hitting time of H by the R-chain. Consequently, $\mathbb{P}_x\{\check{\tau}_H < \infty\} = 1$ for all $x \in X$.

From [47, Theorem 2.1] extended in [11] to the case of Borel right process it follows that a set is a maximal Harris set for the process Φ if and only if it is a maximal Harris set for the R-chain. Hence, the R-chain restricted to the set H_i is a positive Harris recurrent chain with the unique invariant probability measure π_i. By [25, Theorem 1.2] for each $x \in H_i$ we have

$$\lim_{n\to\infty} \frac{1}{n} \sum_{k=0}^{n-1} R^k(x, \cdot) = \pi_i,$$

where the convergence is in the total variation norm on $\mathcal{M}(H_i)$. Thus the R-chain is mean ergodic on each set H_i. The rest of the proof is similar to the proof of part (i) of [35, Theorem 7.1]. ∎

Remark 6.4. It should be noted that the limiting measure $\mu\Pi$ in (6.2) is of the form

$$\mu\Pi(B) = \int_X \Pi(x, B)\mu(dx),$$

where the kernel Π is given by [35, Theorem 7.1]

$$\Pi(x, B) = \sum_{i=1}^{N} \pi_i(B \cap H_i)\mathbb{P}_x\{\check{\tau}_{H_i} < \infty\}, \quad x \in X, B \in \mathcal{B}, \tag{6.5}$$

and π_i, $i = 1, \dots N$, are invariant probability measures. Moreover, as in the proof of [35, Theorem 7.1] we obtain that for any bounded Borel measurable f

$$\mathbb{P}_x\left(\lim_{n\to\infty} \frac{1}{n} \sum_{k=1}^{n} f(\check{\Phi}_k) = \int f d\tilde{\Pi}\right) = 1, \quad x \in X,$$

where the random measure $\tilde{\Pi}$ is defined as

$$\tilde{\Pi}(B) = \sum_{i=1}^{N} \mathbf{1}(\check{\tau}_{H_i} < \infty)\pi_i(B \cap H_i).$$

Theorem 5.1 is a direct consequence of Lemmas 6.2 and 6.3 together with Remark 6.4.

7. Discussion. In the present paper we propose a novel approach to the study of seasonal dynamics. It can be applied to stochastic models in population dynamics that underlie periodic changes to its parameters. Especially we provide sufficient conditions for the coexistence of competing species. As a model we introduce two PDMPs describing behavior in each season as the system switches between them in given constant periods of time (season lengths). This may be generalized to more seasons than two. Such description needs an additional time variable to keep track of the duration of stay in the present season, leading to time-homogeneous Markov processes. Therefore one cannot use the usual approach to study convergence of distributions. We explore the time averages instead and provide sufficient conditions for their convergence.

The common way to study the effects of seasonality on the dynamics of populations modeled with differential equations is to consider periodically forced parameters [12, 13]. Such models are very difficult to treat analytically, although there exist general tools for a study of nonautonomous differential equations with continuous and periodic functions of time [18, 32]. A frequently used numerical approach is bifurcation analysis, first used in this context in [34, 41], where, for simplicity, the forcing is of the form

$$c(t) = c_0(1 + \varepsilon \sin(2\pi t)),$$

with c_0 being any model parameter and ε denoting the forcing amplitude (see [46] and the references therein).

Another attempt to model seasonal effects is related to the so-called (seasonal) succession dynamics [30] or, formally similar, behavior shift [48], in which the model equations change between seasons. A detailed analysis is possible in simple models [27]. By changing growth parameters in (2.1) and (3.1) to piecewise-constant periodic functions of time we get examples of this dynamics, with a particular behavior illustrated as in Figure 2. This approach, in contrary to the situation in the previous paragraph, gives a discontinuous periodic forcing and can simplify the analysis. Including seasonality might still not support the coexistence of species, as in the case of model (2.1), since positive solutions of both systems converge to the same equilibrium $(1, 0)$ representing woodland. Modeling fire impact on vegetation introduces stochasticity into our systems and can have a positive effect on the survival of all species. Especially, adding fire alone or together with herbivores prevents an overgrowth of trees and allows existence of a mixed woodland-grassland ecosystem reflecting savanna.

In general, savanna models incorporate fire disturbances into model equations in a deterministic way [44, 55, 26]. To our knowledge there exists only a discrete-time matrix model [1] that contains both seasonality and fire-vegetation feedback, but it does not provide any analytical insight focusing mainly on simulations. We propose the analytically tractable continuous-time models, although they are less convenient to simulate and limited to discrete losses of the biomass, while it would be more realistic to model impact of fire in a spatially explicit way.

We were not studying sufficient conditions for the uniqueness of invariant distributions in our models and leave it to a future work. Once uniqueness is obtained then the law of large numbers from Theorem 4.1 implies automatically stochastic persistence [5, 7, 22, 19] of considered populations. It would be also interesting to study extinction [7, 22, 39]. Our approach can be used to extend other stochastic models like [22] by adding seasonal effects.

REFERENCES

[1] F. Accatino and C. De Michele, *Humid savanna-forest dynamics: A matrix model with vegetation-fire interactions and seasonality*, Ecol. Model., 265 (2013), pp. 170–179, https://doi.org/10.1016/j.ecolmodel.2013.05.022.

[2] J. Azéma, M. Kaplan-Duflo, and D. Revuz, *Mesure invariante sur les classes récurrentes des processus de Markov*, Z. Wahrscheinlichkeit., 8 (1967), pp. 157–181, https://doi.org/10.1007/BF00531519.

[3] M. Baudena, F. D'Andrea, and A. Provenzale, *An idealized model for tree-grass coexistence in savannas: The role of life stage structure and fire disturbances*, J. Ecol., 98 (2010), pp. 74–80, https://doi.org/10.1111/j.1365-2745.2009.01588.x.

[4] B. Beckage, L. J. Gross, and W. J. Platt, *Grass feedbacks on fire stabilize savannas*, Ecol. Model., 222 (2011), pp. 2227–2233, https://doi.org/10.1016/j.ecolmodel.2011.01.015.

[5] M. Benaïm, *Stochastic Persistence*, preprint, arXiv:1806.08450, 2018.

[6] M. Benaïm, S. Le Borgne, F. Malrieu, and P.-A. Zitt, *Qualitative properties of certain piecewise deterministic Markov processes*, Ann. Inst. Henri Poincaré Probab. Stat., 51 (2015), pp. 1040–1075, https://doi.org/10.1214/14-AIHP619.

[7] M. Benaïm and C. Lobry, *Lotka–Volterra with randomly fluctuating environments or "how switching between beneficial environments can make survival harder"*, Ann. Appl. Probab., 26 (2016), pp. 3754–3785, https://doi.org/10.1214/16-AAP1192.

[8] M. Benaïm and E. Strickler, *Random switching between vector fields having a common zero*, Ann. Appl. Probab., 29 (2019), pp. 326–375, https://doi.org/10.1214/18-AAP1418.

[9] P. Brémaud, R. Kannurpatti, and R. Mazumdar, *Event and time averages: A review*, Adv. Appl. Probab., 24 (1992), pp. 377–411, https://doi.org/10.2307/1427697.

[10] B. Cloez, R. Dessalles, A. Genadot, F. Malrieu, A. Marguet, and R. Yvinec, *Probabilistic and piecewise deterministic models in biology*, in Journées MAS 2016 de la SMAI—Phénomènes complexes et hétérogènes, ESAIM Proc. Surveys 60, EDP Sciences, Les Ulis, France, 2017, pp. 225–245, https://doi.org/10.1051/proc/201760225.

[11] O. L. V. Costa and F. Dufour, *Ergodic properties and ergodic decompositions of continuous-time Markov processes*, J. Appl. Probab., 43 (2006), pp. 767–781, https://doi.org/10.1239/jap/1158784945.

[12] J. M. Cushing, *Periodic time-dependent predator-prey systems*, SIAM J. Appl. Math., 32 (1977), pp. 82–95, https://doi.org/10.1137/0132006.

[13] J. M. Cushing, *Two species competition in a periodic environment*, J. Math. Biol., 10 (1980), pp. 385–400, https://doi.org/10.1007/BF00276097.

[14] M. H. A. Davis, *Piecewise-deterministic Markov processes: A general class of nondiffusion stochastic models*, J. Roy. Statist. Soc. Ser. B, 46 (1984), pp. 353–388, https://doi.org/10.1111/j.2517-6161.1984.tb01308.x.

[15] M. H. A. Davis, *Markov Models and Optimizations*, Monogr. Statist. Appl. Probab. 49, Chapman & Hall, London, 1993, https://doi.org/10.1201/9780203748039.

[16] P. D'Odorico, F. Laio, and L. Ridolfi, *A probabilistic analysis of fire-induced tree-grass coexistence in savannas*, Am. Nat., 167 (2006), pp. E79–E87, https://doi.org/10.1086/500617.

[17] R. Émilion, *Mean-bounded operators and mean ergodic theorems*, J. Funct. Anal., 61 (1985), pp. 1–14, https://doi.org/10.1016/0022-1236(85)90037-0.

[18] J. Guckenheimer and P. Holmes, *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields*, Appl. Math. Sci. 42, Springer, New York, 1990, https://doi.org/10.1007/978-1-4612-1140-2.

[19] A. Guillin, A. Personne, and E. Strickler, *Persistence in the Moran Model with Random Switching*, preprint, arXiv:1911.01108, 2019.

[20] A. Hening and Y. Li, *Stationary distributions of persistent ecological systems*, J. Math. Biol., 82 (2021), 64, https://doi.org/10.1007/s00285-021-01613-2.

[21] A. Hening, D. Nguyen, N. Nguyen, and H. Watts, *Random Switching in an Ecosystem with Two Prey and One Predator*, preprint, arXiv:2111.12750, 2021.

[22] A. Hening and D. H. Nguyen, *Coexistence and extinction for stochastic Kolmogorov systems*, Ann. Appl. Probab., 28 (2018), pp. 1893–1942, https://doi.org/10.1214/17-AAP1347.

[23] A. Hening and D. H. Nguyen, *The competitive exclusion principle in stochastic environments*, J. Math. Biol., 80 (2020), pp. 1323–1351, https://doi.org/10.1007/s00285-019-01464-y.

[24] A. Hening and E. Strickler, *On a predator-prey system with random switching that never converges to its equilibrium*, SIAM J. Math. Anal., 51 (2019), pp. 3625–3640, https://doi.org/10.1137/18M1196042.

[25] O. Hernández-Lerma and J. B. Lasserre, *Further criteria for positive Harris recurrence of Markov chains*, Proc. Amer. Math. Soc., 129 (2001), pp. 1521–1524, https://doi.org/10.1090/S0002-9939-00-05672-0.

[26] A. Hoyer-Leitzel and S. Iams, *Impulsive fire disturbance in a savanna model: Tree–grass coexistence states, multiple stable system states, and resilience*, Bull. Math. Biol., 83 (2021), 113, https://doi.org/10.1007/s11538-021-00944-x.

[27] S.-B. Hsu and X.-Q. Zhao, *A Lotka–Volterra competition model with seasonal succession*, J. Math. Biol., 64 (2012), pp. 109–130, https://doi.org/10.1007/s00285-011-0408-6.

[28] J. Jacod and A. V. Skorokhod, *Jumping Markov processes*, Ann. Inst. Henri Poincaré Probab. Stat., 32 (1996), pp. 11–67.
[29] C. A. Klausmeier, *Floquet theory: A useful tool for understanding nonequilibrium dynamics*, Theor. Ecol., 1 (2008), pp. 153–161, https://doi.org/10.1007/s12080-008-0016-2.
[30] C. A. Klausmeier, *Successional state dynamics: A novel approach to modeling nonequilibrium foodweb dynamics*, J. Theoret. Biol., 262 (2010), pp. 584–595, https://doi.org/10.1016/j.jtbi.2009.10.018.
[31] P. Klimasara and M. Tyran-Kamińska, *A model for random fire induced tree-grass coexistence in savannas*, Math. Appl. (Warsaw), 46 (2018), pp. 87–96, https://doi.org/10.14708/ma.v46i1.6382.
[32] P. E. Kloeden and M. Rasmussen, *Nonautonomous Dynamical Systems*, Math. Surveys Monogr. 176, American Mathematical Society, Providence, RI, 2011, https://doi.org/10.1090/surv/176.
[33] U. Krengel, *Ergodic Theorems*, De Gruyter Stud. Math. 6, De Gruyter, Berlin, 1985, https://doi.org/10.1515/9783110844641.
[34] Y. A. Kuznetsov, S. Muratori, and S. Rinaldi, *Bifurcations and chaos in a periodic predator-prey model*, Internat. J. Bifur. Chaos Appl. Sci. Engrg., 2 (1992), pp. 117–128, https://doi.org/10.1142/S0218127492000112.
[35] S. P. Meyn and R. L. Tweedie, *Stability of Markovian processes* I*: Criteria for discrete-time chains*, Adv. Appl. Probab., 24 (1992), pp. 542–574, https://doi.org/10.2307/1427479.
[36] S. P. Meyn and R. L. Tweedie, *Stability of Markovian processes* II*: Continuous-time processes and sampled chains*, Adv. Appl. Probab., 25 (1993), pp. 487–517, https://doi.org/10.2307/1427521.
[37] S. P. Meyn and R. L. Tweedie, *Stability of Markovian processes* III*: Foster–Lyapunov criteria for continuous-time processes*, Adv. Appl. Probab., 25 (1993), pp. 518–548, https://doi.org/10.2307/1427522.
[38] S. P. Meyn and R. L. Tweedie, *Markov Chains and Stochastic Stability*, 2nd ed., Cambridge University Press, Cambridge, UK, 2009, https://doi.org/10.1017/CBO9780511626630.
[39] D. H. Nguyen and E. Strickler, *A method to deal with the critical case in stochastic population dynamics*, SIAM J. Appl. Math., 80 (2020), pp. 1567–1589, https://doi.org/10.1137/20M131134X.
[40] A. B. N'dri, T. D. Soro, J. Gignoux, K. Dosso, M. Koné, J. K. N'dri, N. A. Koné, and S. Barot, *Season affects fire behavior in annually burned humid savanna of West Africa*, Fire Ecol., 14 (2018), 5, https://doi.org/10.1186/s42408-018-0005-9.
[41] S. Rinaldi, S. Muratori, and Y. Kuznetsov, *Multiple attractors, catastrophes and chaos in seasonally perturbed predator-prey communities*, Bull. Math. Biol., 55 (1993), pp. 15–35, https://doi.org/10.1007/BF02460293.
[42] R. Rudnicki and M. Tyran-Kamińska, *Piecewise Deterministic Processes in Biological Models*, SpringerBriefs Appl. Sci. Technol., Springer, Cham, 2017, https://doi.org/10.1007/978-3-319-61295-9.
[43] R. Scholes and S. Archer, *Tree-grass interactions in savannas*, Ann. Rev. Ecol. Syst., 28 (1997), pp. 517–544, https://doi.org/10.1146/annurev.ecolsys.28.1.517.
[44] A. C. Staver, S. Archibald, and S. Levin, *Tree cover in sub-Saharan Africa: Rainfall and fire constrain forest and savanna as alternative stable states*, Ecology, 92 (2011), pp. 1063–1072, https://doi.org/10.1890/10-1684.1.
[45] A. D. Synodinos, B. Tietjen, D. Lohmann, and F. Jeltsch, *The impact of inter-annual rainfall variability on African savannas changes with mean rainfall*, J. Theoret. Biol., 437 (2018), pp. 92–100, https://doi.org/10.1016/j.jtbi.2017.10.019.
[46] R. A. Taylor, J. A. Sherratt, and A. White, *Seasonal forcing and multi-year cycles in interacting populations: Lessons from a predator-prey model*, J. Math. Biol., 67 (2013), pp. 1741–1764, https://doi.org/10.1007/s00285-012-0612-z.
[47] P. Tuominen and R. L. Tweedie, *The recurrence structure of general Markov processes*, Proc. London Math. Soc. (3), 39 (1979), pp. 554–576, https://doi.org/10.1112/plms/s3-39.3.554.
[48] R. Tyson and F. Lutscher, *Seasonally varying predation behavior and climate shifts are predicted to affect predator-prey cycles*, Am. Nat., 188 (2016), pp. 539–553, https://doi.org/10.1086/688665.
[49] F. Van Langevelde, C. A. D. M. Van De Vijver, L. Kumar, J. Van De Koppel, N. De Ridder, J. Van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, H. H. T. Prins, and M. Rietkerk, *Effects of fire and herbivory on the stability of savanna ecosystems*, Ecology, 84 (2003), pp. 337–350, https://doi.org/10.1890/0012-9658(2003)084[0337:EOFAHO]2.0.CO;2.

[50] F. van Langevelde, C. A. D. M. van de Vijver, H. H. T. Prins, and T. A. Groen, *Effects of grazing and browsing on tropical savanna vegetation*, in The Ecology of Browsing and Grazing II, I. J. Gordon and H. H. T. Prins, eds., Springer, Cham, 2019, pp. 237–257, https://doi.org/10.1007/978-3-030-25865-8_10.

[51] P. A. Werner, *Growth of juvenile and sapling trees differs with both fire season and understorey type: Trade-offs and transitions out of the fire trap in an Australian savanna*, Austral Ecol., 37 (2012), pp. 644–657, https://doi.org/10.1111/j.1442-9993.2011.02333.x.

[52] E. R. White and A. Hastings, *Seasonality in ecology: Progress and prospects in theory*, Ecol. Complex., 44 (2020), 100867, https://doi.org/10.1016/j.ecocom.2020.100867.

[53] R. J. Williams, G. D. Cook, A. M. Gill, and P. H. R. Moore, *Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia*, Austral Ecol., 24 (1999), pp. 50–59, https://doi.org/10.1046/j.1442-9993.1999.00946.x.

[54] I. V. Yatat Djeumen, Y. Dumont, A. Doizy, and P. Couteron, *A minimalistic model of vegetation physiognomies in the savanna biome*, Ecol. Model., 440 (2021), 109381, https://doi.org/10.1016/j.ecolmodel.2020.109381.

[55] I. V. Yatat Djeumen, A. Tchuinté Tamen, Y. Dumont, and P. Couteron, *A tribute to the use of minimalistic spatially-implicit models of savanna vegetation dynamics to address broad spatial scales in spite of scarce data*, Biomath, 7 (2018), 1812167, https://doi.org/10.11145/j.biomath.2018.12.167.

IV

Randomly switching evolution equations

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Randomly switching evolution equations[☆]

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ABSTRACT

We present an investigation of stochastic evolution in which a family of evolution equations in L^1 are driven by continuous-time Markov processes. These are examples of so-called piecewise deterministic Markov processes (PDMP's) on the space of integrable functions. We derive equations for the first moment and correlations (of any order) of such processes. We also introduce the mean of the process at large time and describe its behaviour. The results are illustrated by some simple, yet generic, biological examples characterized by different one-parameter types of bifurcations.

1. Introduction

The theory of piecewise deterministic Markov processes (PDMP's) has generated considerable interest in the scientific community over the past three decades, having been first introduced in [1]. From the point of view of modelling in natural sciences the class of PDMP's is a very broad family of stochastic models covering most of the applications, omitting mainly diffusion related phenomena. A recent monograph [2] surveys the applicability of PDMP's to problems in the biological sciences.

Briefly, a PDMP is a continuous-time Markov process with values in some metric space. The process evolves deterministically between the so-called jump times that form an increasing sequence of random times. Usually deterministic evolution is described by ordinary differential equations (ODE's) inducing dynamical systems (or flows). However, in a PDMP at the jump times one considers a different type of behaviour such that there is an actual jump to a different point in the phase space *or* a change of the dynamics. The latter are referred to as randomly switching dynamical systems or switching ODE's.

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The class of PDMP's is widely used in many areas of science, especially in biology [2,3], and these include the applications of randomly switching dynamical systems. A prototype of PDMP's is the telegraph process first studied by Goldstein [4] and Kac [5] in connection with the telegraph equation where a particle moves on a real line with constant velocity alternating between two opposite values according to a Poisson process. An extension of such a process is a velocity jump process where an individual moves in a space with constant velocity and at the jump times a new velocity is chosen randomly [6,7]. Another example is a multi-state gene network where the gene switches between its active and inactive state at the jump times [8–10].

Existing models usually describe the underlying phenomena for some population from the point of view of a single individual. In physics this is often known as a particle perspective [11]. That means that the dynamics of every single individual is driven by separate stochastic laws depending on a variety of factors, e.g. its mass or energy. However, there are alternative situations in which the entire population is affected by randomly switching environmental conditions, e.g. particles driven by a common environmental noise [11] or the response of a metabolic or gene regulatory system to an environmental stimulus [12]. This is known as a population perspective [11], and is the approach that we use in this paper since we consider one common source of randomness which affects all individuals in a population.

Here we treat the evolution of the density of a population distribution in the situation where every individual has its own deterministic dynamics but the whole population is affected by some continuous-time Markov process with finite state space that changes the current state of all individuals. In this approach, a state is represented by a population density — an element of an infinite dimensional space. It is particularly difficult to study the evolution of such densities and thus we investigate their moments and correlations of all orders. These infinite dimensional processes are dual to the class of PDMP's known as random evolutions introduced earlier by Griego and Hersh [13], motivated by the work of Goldstein [4] and Kac [5], see [14]. (For an amusing and non-technical account of this history see [15] and [16].) They are particular examples of models governed by so-called switching Partial Differential Equations (PDEs) that recently have a growing interest in the literature [17–21]. Most of these papers focus on applications in biological sciences. From the mathematical point of view they are based on diffusion processes and PDEs of parabolic type.

In [17,22] the authors provide the moment and correlation equations in the case of diffusion processes. The current study is a generalization of their work by giving moment and correlation equations for a broader class of processes. The main result of our paper is that the mean of a process described by randomly switching PDEs can be viewed as an appropriate stochastic semigroup (see Theorem 5.1 and Corollary 5.3). This has further important consequences, especially that the mean of random density in the population perspective can be seen as identical to a density from the individual perspective (see Section 6). We study the mean of the process at large time for a variety of examples that are biological applications. It allows us to investigate the asymptotic behaviour for the mean of the process in the cases of fold, transcritical, pitchfork, and Hopf bifurcations. We also provide numerical simulations for the mean of the process which were prepared by using FiPy [23].

This paper is organized as follows. In Section 2 we provide some basic material from the theory of stochastic semigroups on L^1. Section 3 briefly reviews randomly switching dynamical systems in Euclidean state spaces. In Section 4 we introduce randomly switching semigroups with the state space being the set of densities leading to a stochastic evolution equation in an L^1 space. We study the first moment of its solutions in Section 5 where we stress the correspondence between this moment equation and the Fokker–Planck type equations from Section 4. Section 5 contains the main results of this paper, namely Theorem 5.1 and Corollary 5.3. The behaviour of the mean at large time is considered in Section 6, where we also give examples of applications of our results to situations in which the underlying dynamics display a variety of bifurcations. In Section 7 we study second order correlations of solutions of the stochastic evolution equation. We conclude in Section 8 with a brief summary. The appendix contains relevant concepts from the theory of tensor products that are used in Section 7.

2. Preliminaries

In this section we collect some preliminary material. We begin with the notion of stochastic (Markov) semigroups and provide examples of such semigroups.

Let a triple $(E, \mathcal{E}, m)$ be a σ-finite measure space and let $L^1 = L^1(E, \mathcal{E}, m)$. We define the set of densities $D \subset L^1$ by

$$D = \{f \in L^1 : f \geq 0, \|f\| = 1\}.$$

A *stochastic (Markov) operator* is any linear mapping $P: L^1 \to L^1$ such that $P(D) \subset D$ [24]. A family of linear operators $\{P(t)\}_{t\geq 0}$ on L^1 is called a *stochastic semigroup* if each operator $P(t)$ is stochastic and $\{P(t)\}_{t\geq 0}$ is a C_0-*semigroup*, i.e. the following conditions hold:

1. $P(0) = \mathrm{Id}$,
2. $P(t+s) = P(t)P(s)$ for all $t, s \geq 0$,
3. for every f the function $t \to P(t)f$ is continuous.

The infinitesimal *generator* of $\{P(t)\}_{t\geq 0}$ is, by definition, the operator A with domain $\mathcal{D}(A) \subset L^1$ defined as

$$\mathcal{D}(A) = \{f \in L^1 : \lim_{t\downarrow 0} \frac{1}{t}(P(t)f - f) \text{ exists}\},$$

$$Af = \lim_{t\downarrow 0} \frac{1}{t}(P(t)f - f), \quad f \in \mathcal{D}(A).$$

We will use stochastic semigroups to represent solutions of evolution equations. One of the simplest examples of such equations is the deterministic Liouville equation which has a simple interpretation [25]. Consider the movement of particles in the phase space $\mathbb{R}^d$, $d \geq 1$, described by a differential equation:

$$x'(t) = b(x(t)), \tag{2.1}$$

where $b(x)$ is a d-dimensional vector. Then the Liouville equation describes the evolution of the density of the distribution of particles, i.e. if $x(t)$ has a density $u(t, x)$, then u is the solution of the following equation:

$$\frac{\partial u(t,x)}{\partial t} = -\operatorname{div}(b(x)u(t,x)). \tag{2.2}$$

Let, for any $x_0 \in \mathbb{R}^d$, Eq. (2.1) with initial condition $x(0) = x_0$ have a solution for all t, which we denote by $\pi(t, x_0)$, and let the mapping $x_0 \mapsto \pi(t, x_0)$ be *non-singular* with respect to the Lebesgue measure Leb on $\mathbb{R}^d$, i.e. $\mathrm{Leb}(\{x \in \mathbb{R}^d : \pi(t,x) \in B\}) = 0$ for all Borel sets B with $\mathrm{Leb}(B) = 0$. If $f\colon \mathbb{R}^d \to [0, +\infty)$ is the density of the $\mathbb{R}^d$-valued random vector ξ_0, then the density of $\pi(t, \xi_0)$ is given by

$$P(t)f(x) = f(\pi(-t,x)) \det[\frac{d}{dx}\pi(-t,x)].$$

The family of operators $\{P(t)\}_{t\geq 0}$ forms a stochastic semigroup on the space $L^1(\mathbb{R}^d)$ and $u(t,x) = P(t)f(x)$ is the solution of (2.2) with initial condition $u(0,x) = f(x)$.

3. Randomly switching dynamics

In this section we recall a classical setting of PDMP based models seen from the perspective of individual units and taking place in a finite dimensional space. This well-known situation will be contrasted in the following sections with a population perspective approach, thus moving the analysis to infinite dimensional space. See [11, Figure 1] for a nice pictorial distinction between the individual and populational perspectives.

Consider sufficiently smooth vector fields b_i, $i \in I = \{0, 1, \dots, k\}$, $k \in \mathbb{N}$, defined on an open subset G of $\mathbb{R}^d$. Let $E \subset G$ be a Borel set with non-empty interior and with boundary of Lebesgue measure zero. We assume that for each i and $x_0 \in E$ the equation

$$x'(t) = b_i(x(t)), \tag{3.1}$$

with initial condition $x(0) = x_0$, has a solution $\pi_i(t, x_0)$ for all $t > 0$ in the set E. The mapping $(t, x_0) \mapsto \pi_i(t, x_0)$ is continuous. We assume that each $\pi_i(t, \cdot)$ is non-singular with respect to the Lebesgue measure on E. Now let $f\colon E \to [0, +\infty)$ be a density of an E-valued random vector ξ_0. Then the density of $\pi_i(t, \xi_0)$ is given by

$$P_i(t)f(x) = \mathbf{1}_E(\pi_i(-t,x)) f(\pi_i(-t,x)) \det[\frac{d}{dx}\pi_i(-t,x)]. \tag{3.2}$$

For every $i \in I$ the family of operators $\{P_i(t)\}_{t\geq 0}$ forms a stochastic semigroup on $L^1(E)$ called a Frobenius–Perron semigroup [24, Section 7.4].

A randomly switching dynamics is a Markov process $\xi(t) = (x(t), i(t))$ on the state space $E \times I$ such that the dynamics of $x(t)$ is given by the solution of the equation

$$x'(t) = b_{i(t)}\big(x(t)\big), \tag{3.3}$$

and $i(t)$ is a continuous-time Markov chain with values in I and intensity matrix $[q_{ij}]$. If the system initially is at time t_0 at the state (x_0, i) then $x(t)$ changes in time according to Eq. (3.1) as long as $i(t) = i$ and $\xi(t) = (\pi_i(t - t_0, x_0), i)$. If $i(t)$ changes its value to some j with intensity q_{ij}, i.e. the probability of switching from i to j after time Δt is $q_{ij}\Delta t + o(\Delta t)$, $j \in I, j \neq i$, then we choose the vector field b_j and we start afresh. Let t_1 be the moment of switching from i to j and $x_1 = \pi_i(t_1 - t_0, x_0)$. Then we have $\xi(t) = (\pi_j(t - t_1, x_1), j)$ until the next change of the state of the process $\{i(t)\}_{t\geq 0}$. This construction repeats indefinitely. We set

$$q_i = \sum_{j\neq i} q_{ij} \quad \text{and} \quad q_{ii} = -q_i, \quad i \in I. \tag{3.4}$$

Note that if $k = 1$, then we have $q_{10} = -q_{11} = q_1$ and $q_{01} = -q_{00} = q_0$.

For each $i \in I$, let $\{P_i(t)\}_{t\geq 0}$ be the stochastic semigroup as in (3.2) and let $(A_i, \mathcal{D}(A_i))$ be its generator. If $f = (f_i)_{i\in I}$ is a column vector consisting of functions f_i such that $f_i \in \mathcal{D}(A_i)$, we set $Af = (A_i f_i)_{i\in I}$ which is also a column vector. We denote the matrix $[q_{ij}]$ by Q and its transpose $[q_{ji}]$ by Q^T. Then the operator $A + Q^T$ is the infinitesimal generator of a stochastic semigroup $\{P(t)\}_{t\geq 0}$ on the space $L^1(E \times I) = L^1(E \times I, \mathcal{B}(E \times I), \mu)$. Here $\mathcal{B}(E \times I)$ is the σ-algebra of Borel subsets of $E \times I$ and μ is the product of the d-dimensional Lebesgue measure and the counting measure on I.

Thus if we define $u(t) = P(t)f$, then u satisfies the evolution equation

$$\begin{cases} u'(t) = Au(t) + Q^T u(t), \\ u(0) = f. \end{cases} \tag{3.5}$$

Now using the notation $f = (f_i)_{i\in I}$ and $u(t) = (u_i(t))_{i\in I}$, we can rewrite (3.5) as

$$\begin{cases} u_i'(t) = A_i u_i(t) + \sum_{j\in I} q_{ji} u_j(t), \\ u_i(0) = f_i, \quad i \in I. \end{cases} \tag{3.6}$$

Moreover, the process $\xi(t) = (x(t), i(t))$ induces the stochastic semigroup $\{P(t)\}_{t\geq 0}$ (see [2, Section 4.2]), i.e. if f is the density of $\xi(0)$ then $P(t)f$ is the density of $\xi(t)$ and

$$\mathbb{P}(x(t) \in B, i(t) = i) = \int_{B\times\{i\}} P(t)f d\mu = \int_B u_i(t,x)\,dx, \quad i \in I.$$

4. Randomly switching densities

In this section we look at the role of stochasticity in explaining biological phenomena from the point of view of the *whole population* in an environment affected by some random disturbances. We illustrate this approach using two examples, namely a population model with two different birth rates [26], and a model of inducible gene expression with positive feedback on gene transcription [27].

Example 4.1 (*Population Model with Two Different Birth Rates*)**.** Consider a population of size $x \geq 0$, a death rate μ and birth rate $\beta - cx$ with β changing in time between two possible values β_0 and β_1 in response to some environmental disturbance. The growth of the population is assumed to be determined by the differential equation (3.1) with

$$b_0(x) = (\beta_0 - cx)x - \mu x \quad \text{and} \quad b_1(x) = (\beta_1 - cx)x - \mu x. \tag{4.1}$$

For each value of i, Eq. (3.1) induces a stochastic semigroup $\{P_i(t)\}_{t\geq 0}$ given by Eq. (3.2). If the population initially grows with birth rate related to a value $i \in \{0, 1\}$ and has a distribution density g, then after time $t > 0$ the population distribution density is given by $P_i(t)g$. We consider the switching between the semigroups $\{P_0(t)\}_{t\geq 0}$ and $\{P_1(t)\}_{t\geq 0}$ according to a Markov chain $i(t) \in \{0, 1\}$ and obtain a stochastic Liouville equation (as introduced by Bressloff in [11]):

$$\frac{\partial u(t,x)}{\partial t} = -\frac{\partial\left(b_{i(t)}(x)u(t,x)\right)}{\partial x}, \tag{4.2}$$

where $u(t, x) = P_i(t)g(x)$ for $i(t) = i$ is the population density. This is an infinite dimensional version of Eq. (3.3).

Example 4.2 (*One Dimensional Inducible Goodwin Model with Positive Feedback on Gene Transcription*)**.** We consider the inducible operon model [27] which describes the expression of genes driven by positive feedback control of gene transcription. This provides an effective mechanism by which a protein can maintain the expression of its own gene as well as switch between two levels of expression (un-induced and induced). We look at a cluster of identical copies of a selected gene, e.g. the cluster of multiple copies of the same gene in the case of bacteria, where one of these genes is 16S ribosomal RNA — the component of prokaryotic ribosome [28]. We denote the concentration level at time t by $x(t) \geq 0$ and assume the degradation rate is changing with constant intensities between two values γ_0 and γ_1 driven by environmental noise.

For a given $i \in \{0, 1\}$ the concentration level is assumed to evolve according to the nonlinear differential equation:

$$x'(t) = \frac{x^n(t)}{1 + x^n(t)} - \gamma_i x(t), \tag{4.3}$$

where n is a natural number. This equation induces a semigroup $\{P_i(t)\}_{t\geq 0}$ as in formula (3.2). If the gene cluster initially has a degradation rate γ_i and a distribution density g then after time $t > 0$ the population distribution density is given by $P_i(t)g$. By taking $b_i(x)$ equal to the right-hand side of Eq. (4.3) we obtain the stochastic Liouville equation (4.2) as in the previous example.

We next consider the general case of a population of individuals living in an environment with random disturbances. This situation with a population of particles affected by a common environmental noise was considered from a statistical physics viewpoint by Bressloff in [11]. The dynamics of a population is described by Eq. (3.1) with a state space being some Borel subset of $\mathbb{R}^d$ and i taking values from a given finite set I. The environmental disturbances correspond to switching between different values of i. Thus the total population density $u(t, x)$ is described by the equation:

$$\frac{\partial u(t,x)}{\partial t} = -\operatorname{div}(b_{i(t)}(x)u(t,x)), \tag{4.4}$$

where $i(t)$ is a Markov chain on a discrete state space I. We supplement equation (4.4) with an initial condition $u(0, x) = g(x)$. Note that Eq. (4.4) is a more general case of the stochastic Liouville equation (4.2). Randomly switching environments have also been analysed in the case of diffusion processes [22]. In such situations the stochastic Liouville equation is replaced by an appropriate parabolic equation. We may generalize all these cases by looking at a general scheme for randomly switching stochastic semigroups.

Let $L^1(E) = L^1(E, \mathcal{B}(E), m)$, where (E, ρ) is a separable metric space and m is a σ-finite measure, and let $I = \{0, 1, \ldots, k\}$, $k \in \mathbb{N}$. For every $i \in I$, consider a linear operator $(A_i, \mathcal{D}(A_i))$ which is the generator of a stochastic semigroup $\{P_i(t)\}_{t\geq 0}$ on $L^1(E)$. We assume that the stochastic process $\{i(t)\}_{t\geq 0}$ is a continuous time Markov chain with state space I and constant intensities q_{ij}, $i, j \in I$. We consider the following stochastic evolution equation:

$$\begin{cases} u'(t) = A_{i(t)}u(t), \\ u(0) = g. \end{cases} \tag{4.5}$$

Eq. (4.5) generates a well-defined PDMP [2, p. 32]

$$X(t) = (u(t), i(t)), \quad t \geq 0, \tag{4.6}$$

with values in the space $L^1(E) \times I$.

Now we derive the solution $u(t)$ of (4.5). Let $t_0 = 0$ and for each $n \in \mathbb{N}$ let t_n be the nth jump time of the Markov process $i(t)$ so that

$$\mathbb{P}(t_{n+1} - t_n > t | i(t_n) = i) = e^{-q_i t}, \quad n \geq 0.$$

Let $\mathbb{P}_j$ be the probability measure defined on sample paths ω of the process $\{i(t)\}_{t\geq 0}$ with $i(0) = j$. Denote integration with respect to the measure $\mathbb{P}_j$ by $\mathbb{E}_j$, set $U(t_0) = U(0) = \mathrm{Id}$ and define

$$U(t) = P_{i(t_n)}(t - t_n) \circ U(t_n) \quad \text{for } t \in [t_n, t_{n+1}), n \geq 0,$$

where

$$U(t_n) = P_{i(t_{n-1})}(t_n - t_{n-1}) \circ \ldots \circ P_{i(t_1)}(t_2 - t_1) \circ P_{i(0)}(t_1).$$

Further, let

$$N(t) = \max\{n \geq 0 : t_n \leq t\} \tag{4.7}$$

be the number of jumps of the process $\{i(t)\}_{t\geq 0}$ up to time t. Using $N(t)$ we can write

$$U(t) = P_{i(t_{N(t)})}(t - t_{N(t)})U(t_{N(t)}), \quad t \geq 0. \tag{4.8}$$

Then $u(t) = U(t)g$ for $g \in L^1(E)$ is the solution of (4.5). Note that $U(t)$ depends on ω. For each $t > 0$, $g \in L^1(E)$, and ω, if $t \in [t_n(\omega), t_{n+1}(\omega))$ for some $n = n(\omega)$ then for $i = i(t_n(\omega))$ we have

$$U(t, \omega)g = P_i(t - t_n(\omega))U(t_n(\omega))g,$$

and $U(t, \omega)$ is a composition of a finite number of stochastic operators. Thus

$$\|U(t, \omega)g\| = \int_E |U(t, \omega)g(x)|m(dx) \leq \int_E |g(x)|m(dx) = \|g\|$$

and $U(t)g$ can be regarded as a random variable with values in $L^1(E)$. It is, in fact, a Bochner integrable $L^1(E)$-valued random variable, by [29, Theorem 3.7.4]. Furthermore, for each $j \in I$, $\mathbb{E}_j(U(t)g)$ is represented by the a.e. finite function $\mathbb{E}_j(u(t, x))$ where $u(t, x) = U(t)g(x)$, i.e. for any $h \in L^\infty(E, \mathcal{B}(E), m)$

$$\int_E \mathbb{E}_j(U(t)g)(x)h(x)m(dx) = \int_E \mathbb{E}_j(u(t, x))h(x)m(dx).$$

In the next sections we derive equations for the moments of $u(t, x)$ and compare them to the evolution equation (3.5) from Section 3.

5. First moment equations

We continue with the general setting from Section 4 and study the first moment of the solution $u(t)$ of (4.5). Recall that $u(t, x) = U(t)g(x)$, where $U(t)$ is given by (4.8). Using a simple decomposition, the first moment of $u(t, x)$ can be written as

$$V(t, x) = \mathbb{E}(u(t, x)) = \sum_{j\in I} \mathbb{E}_j(u(t, x)) = \sum_{j\in I}\sum_{i\in I} \mathbb{E}_j(\mathbf{1}_{\{i(t)=i\}}u(t, x)), \quad x \in E, t \geq 0,$$

where $\mathbb{E}$ denotes the expectation and $\mathbf{1}_F$ is the indicator function of an event F. If we take

$$V_i(t, x) = \sum_{j\in I} \mathbb{E}_j(\mathbf{1}_{\{i(t)=i\}}u(t, x)), \tag{5.1}$$

then

$$V(t,x)=\sum_{i\in I}V_i(t,x),\quad x\in E, t\geq 0. \tag{5.2}$$

We will show that:

$$\frac{\partial}{\partial t}V_i=A_iV_i+\sum_j q_{ji}V_j,\quad i\in I. \tag{5.3}$$

It will turn out that $(V_i)_{i\in I}$ can be represented as a stochastic semigroup.

Let $L^1(E\times I)=L^1(E\times I,\mathcal{B}(E\times I),\mu)$, where μ is the product of the measure m on E and the counting measure on I. We denote elements of the space $L^1(E\times I)$ by $f:=(f_i)_{i\in I}\in L^1(E\times I)$, where $f_i\in L^1(E)$, $i\in I$, and define the family of operators $\{P(t)\}_{t\geq 0}$ on the space $L^1(E\times I)$ by

$$(P(t)f)_i=\sum_{j\in I}\mathbb{E}_j(\mathbf{1}_{\{i(t)=i\}}U(t)f_j),\quad i\in I. \tag{5.4}$$

We impose the following conditions:

(I) There exist a Banach space B, a set of Borel measurable functions $\mathcal{H}\subseteq B$, and a family $\mathcal{C}$ of Borel subsets of E that is closed under intersections and generates the Borel σ-algebra $\mathcal{B}(E)$ such that for each set $F\in\mathcal{C}$ there is a nonincreasing sequence of function $h_n\in\mathcal{H}$ satisfying

$$\lim_{n\to\infty}h_n(x)=\mathbf{1}_F(x),\quad x\in E. \tag{5.5}$$

(II) Let $\{P_i(t)\}_{t\geq 0}$ be a stochastic semigroup on $L^1(E)$ with generator $(A_i,\mathcal{D}(A_i))$, $i\in I$. For each $i\in I$ there is a C_0-semigroup $\{T_i(t)\}_{t\geq 0}$ on B such that

$$\langle P_i(t)g,h\rangle=\langle g,T_i(t)h\rangle,\quad g\in L^1(E), h\in B, t\geq 0. \tag{5.6}$$

Here, the scalar product of two functions g,h with their domain E is defined by $\langle g,h\rangle:=\int_E g(x)h(x)m(dx)$.

Now we state and prove one of the main results of this paper.

Theorem 5.1. *Assume conditions (I) and (II). Then the family of operators $\{P(t)\}_{t\geq 0}$ defined in (5.4) is a stochastic semigroup on $L^1(E\times I)$. Moreover, the infinitesimal generator of the semigroup $\{P(t)\}_{t\geq 0}$ is the operator $A+Q^T$ where $Af=(A_if_i)_{i\in I}$ and $Q^Tf=(\sum_j q_{ji}f_j)_{i\in I}$ for $f=(f_i)_{i\in I}$ with $f_i\in\mathcal{D}(A_i)$, $i\in I$.*

Proof. Given B and $\{T_i(t)\}_{t\geq 0}$, $i\in I$, as in conditions (I) and (II), we define the random evolution family $\{M(t), t\geq 0\}$ of operators on the space B by [13]

$$M(t)=T_{i(0)}(t_1)T_{i(t_1)}(t_2-t_1)\cdots T_{i(t_{N(t)})}(t-t_{N(t)}),$$

where $N(t)$ is as in (4.7). Consider the product space $B\times B\times\cdots\times B=B^{k+1}$, where $k+1$ denotes the number of elements of the set I, and for any $h:=(h_i)_{i\in I}\in B^{k+1}$, $i\in I$ define

$$(T(t)h)_i=\mathbb{E}_i(M(t)h_{i(t)}). \tag{5.7}$$

Griego and Hersh [13] showed that the family $\{T(t)\}_{t\geq 0}$ forms a strongly continuous semigroup of bounded linear operators on B^{k+1}. The integral in (5.7) with respect to $\mathbb{P}_i$ is understood in the sense of Bochner. Observe that $M(t)$ depends on ω and that $\omega\mapsto M(t,\omega)h_{i(t)(\omega)}$ is $\mathbb{P}_j$-Bochner integrable for each $j\in I$ (see [13, Lemma 2]). By Hille's lemma for the Bochner integral [29, Theorem 3.7.12] in B we obtain

$$\langle\mathbb{E}_j(M(t)h_{i(t)}),g\rangle=\mathbb{E}_j(\langle M(t)h_{i(t)},g\rangle),\quad j\in I, g\in L^1(E), h\in B^{k+1}, \tag{5.8}$$

where the integral on the right-hand side of (5.8) is in the sense of Lebesgue.

For $f\in L^1(E\times I)$ and $h\in B^{k+1}$, set

$$\langle f,h\rangle=\sum_{j\in I}\langle f_j,h_j\rangle=\sum_{j\in I}\int_E f_j(x)h_j(x)m(dx).$$

We first show that

$$\langle T(t)h,f\rangle=\langle h,P(t)f\rangle. \tag{5.9}$$

It follows from (5.8) that

$$\langle T(t)h,f\rangle=\sum_{j\in I}\langle\mathbb{E}_j(M(t)h_{i(t)}),f_j\rangle=\sum_{j\in I}\mathbb{E}_j(\langle M(t)h_{i(t)},f_j\rangle).$$

Using (5.6) it is easily seen that

$$\langle M(t)h_{i(t)}, f_j\rangle = \langle h_{i(t)}, U(t)f_j\rangle, \quad t \geq 0.$$

Hence

$$\langle T(t)h, f\rangle = \sum_{j\in I} \mathbb{E}_j(\langle h_{i(t)}, U(t)f_j\rangle) = \sum_{j,i\in I} \mathbb{E}_j(\langle h_i, \mathbf{1}_{\{i(t)=i\}}U(t)f_j\rangle).$$

Using Hille's lemma for Bochner integrals in $L^1(E)$, we see that

$$\langle T(t)h, f\rangle = \sum_{i\in I}\langle h_i, \sum_{j\in I} \mathbb{E}_j(\mathbf{1}_{\{i(t)=i\}}U(t)f_j)\rangle = \langle h, P(t)f\rangle,$$

as claimed.

Now, we check the semigroup property $P(t+s)f = P(t)\circ P(s)f$ for $t, s \geq 0, f \in L^1(E \times I)$. Since $\{T(t)\}_{t\geq 0}$ is a semigroup, it follows from (5.9) that

$$\langle T(t) \circ T(s)h, f\rangle = \langle T(t+s)h, f\rangle = \langle h, P(t+s)f\rangle$$

for any $t, s \geq 0$ and $f \in L^1(E \times I)$, $h \in B^{k+1}$. This together with (5.9) gives

$$\langle h, P(t+s)f\rangle = \langle T(s)h, P(t)f\rangle = \langle h, P(s)\circ P(t)f\rangle,$$

implying that for each $i \in I$ and $h \in \mathcal{H}$ we have

$$\int_E h(P(t+s)f)_i dm = \int_E h(P(s)\circ P(t)f)_i dm. \tag{5.10}$$

Since for each i the semigroup $\{P_i(t)\}_{t\geq 0}$ is stochastic, we see that each operator $P(t)$ is stochastic on $L^1(E \times I)$. Thus decomposing an arbitrary f into its positive and negative parts, we can assume that $f \in L^1(E \times I)$ is nonnegative. Since (5.10) holds for each h_n, the Lebesgue convergence theorem implies that (5.10) holds for $\mathbf{1}_F$, showing that

$$\int_F (P(t+s)f)_i dm = \int_F (P(t)\circ P(s)f)_i dm \tag{5.11}$$

for all sets $F \in \mathcal{C}$. The family $\mathcal{C}$ is a π-system, i.e., $F_1 \cap F_2 \in \mathcal{C}$ for $F_1, F_2 \in \mathcal{C}$, and equality (5.11) holds for all $F \in \mathcal{C}\cup\{E\}$. Hence we conclude that (5.11) holds for all Borel subsets of E. Consequently, $(P(t+s)f)_i = (P(t)\circ P(s)f)_i$ for all $t, s \geq 0$ and $i \in I$. Since almost all sample paths of the stochastic switching process $i(t)$ are right-continuous functions, we conclude that $\{P(t)\}_{t\geq 0}$ is a C_0-semigroup, completing the proof that $\{P(t)\}_{t\geq 0}$ is a stochastic semigroup.

Finally, it was shown in [13] that the generator $\mathcal{L}$ of the semigroup $\{T(t)\}_{t\geq 0}$ is given by

$$(\mathcal{L}h)_i = \mathcal{L}_i h_i + \sum_{j\in I} q_{ij}h_j$$

for $h = (h_i)_{i\in I} \in B^{k+1}$ with $h_i \in \mathcal{D}(\mathcal{L}_i)$, $i \in I$, where $(\mathcal{L}_i, \mathcal{D}(\mathcal{L}_i))$ is the generator of the semigroup $\{T_i(t)\}_{t\geq 0}$ on B, $i \in I$. Observe that

$$\langle f, \mathcal{L}h\rangle = \sum_{i\in I}\langle f_i, \mathcal{L}_i h_i + \sum_{j\in I} q_{ij}h_j\rangle = \sum_{i\in I}\langle f_i, \mathcal{L}_i h_i\rangle + \sum_{i\in I}\sum_{j\in I}\langle f_i, q_{ij}h_j\rangle$$

for $f = (f_i)_{i\in I}$ with $f_i \in \mathcal{D}(A_i)$, $i \in I$. Since we have

$$\langle f_i, \mathcal{L}_i h_i\rangle = \langle A_i f_i, h_i\rangle, \quad i \in I,$$

by assumption (II), we conclude that

$$\langle f, \mathcal{L}h\rangle = \sum_{i\in I}\langle A_i f_i, h_i\rangle + \sum_{j\in I}\langle \sum_{i\in I} q_{ij}f_i, h_j\rangle = \langle (A + Q^T)f, h\rangle,$$

implying the form of the generator of the semigroup $\{P(t)\}_{t\geq 0}$. □

We next show that Theorem 5.1 can be applied to semigroups of Frobenius–Perron operators given by (3.2).

Corollary 5.2. *Let E be a Borel subset of $\mathbb{R}^d$ and for each $i \in I$ let $\{P_i(t)\}_{t\geq 0}$ be given by (3.2). Then conditions (I) and (II) hold, and Theorem 5.1 does also.*

Proof. Let B be the space $C(E)$ of continuous functions on E if E is compact or the space $C_0(E)$ of continuous functions on E which vanish at infinity, otherwise. Recall that the σ-algebra of Borel subsets of E is generated by the family of compact sets. For each compact set F the function h_n defined by

$$h_n(x) = \max\{1 - n\rho(x, F), 0\},$$

where $\rho(x, F)$ denotes the distance of the point x from the set F, is globally Lipschitz. Since h_n belongs to B and satisfies (5.5), we conclude that condition (I) holds. We define $T_i(t)\colon B \to B$ by $T_i(t)h(x) = h(\pi_i(t, x))$, $t \geq 0$, $x \in E$, $h \in B$. Note that $T_i(t)$ is a C_0-semigroup on B, see [30, Section B-II] and condition (5.6) holds, see [24, Section 7.4]. □

Using Theorem 5.1 we obtain the following, which is the second main result of this paper:

Corollary 5.3. *Assume conditions (I) and (II). Let $\{P(t)\}_{t\geq 0}$ be given by (5.4) and $u(t)$ by (4.5). For each $g \in L^1(E)$ and $l \in I$ such that $u(0) = g$ and $i(0) = l$ we have $V_i(t, x) = (P(t)f)_i(x)$, where V_i is as in (5.1) and $f = (f_j)_{j\in I}$ is of the form*

$$f_j = \begin{cases} g, & j = l, \\ 0, & j \neq l. \end{cases}$$

In particular, the mean of the process in (4.6) is given by

$$V(t, x) = \mathbb{E}(u(t, x)) = \sum_{i\in I}(P(t)f)_i(x). \tag{5.12}$$

6. Mean of the process at large time

We consider the relationship between Fokker–Planck type systems (3.5) for a distribution of processes in $\mathbb{R}^d$ space, and the first moment equation (5.3). The latter has the same form as (3.6) and $P(t)f$ is the solution of the evolution equation (3.5) with initial condition f. Hence, if $(u_0, u_1, u_2, \dots, u_k)$ is a solution of (3.6) and for each $i \in I$ there exists $f_i^* \in L^1(E)$ such that

$$\lim_{t\to\infty} \int_E \left|u_i(t, x) - f_i^*(x)\right| m(dx) = 0, \tag{6.1}$$

then, by Corollary 5.3, we have

$$\lim_{t\to\infty} \int_E \left|V_i(t, x) - f_i^*(x)\right| m(dx) = 0$$

and, by Eq. (5.2),

$$\lim_{t\to\infty} \int_E \left|V(t, x) - V^*(x)\right| m(dx) = 0 \tag{6.2}$$

where $V^*(x) = \sum_{i\in I} f_i^*(x)$. The function V^* is called the *mean of the process at large time*. In particular, condition (6.1) holds if the semigroup $\{P(t)\}_{t\geq 0}$ is *asymptotically stable*, i.e. there exists $f^* \in L^1(E \times I)$ such that for each density $f \in L^1(E \times I)$

$$\lim_{t\to\infty} \|P(t)f - f^*\| = 0 \tag{6.3}$$

Note that f^* in (6.3) is an *invariant density* for $\{P(t)\}_{t\geq 0}$, i.e. $P(t)f^* = f^*$ for all $t \geq 0$.

On the other hand, if the semigroup $\{P(t)\}_{t\geq 0}$ is *sweeping from compact subsets of* $E \times I$, i.e. for each compact subset F of E, any $f \in L^1(E \times I)$ and $i \in I$ we have

$$\lim_{t\to\infty} \int_F (P(t)f)_i(x)m(dx) = 0,$$

then the mean of the process in (4.6) at large time is equal to zero, since for any compact subset F of E we have

$$\lim_{t\to\infty} \int_F V(t, x)m(dx) = 0. \tag{6.4}$$

We now provide sufficient conditions for asymptotic behaviour of the stochastic semigroup $\{P(t)\}_{t\geq 0}$ induced by the randomly switching dynamics $\xi(t) = (x(t), i(t))$ with $x(t)$ satisfying (3.3) as described in Section 3 with $E \subseteq \mathbb{R}^d$. We follow the work of [31,32] and [2,26].

Recall that the Lie bracket of two sufficiently smooth vector fields b_i and b_j is defined by

$$[b_i, b_j](x) = Db_j(x)b_i(x) - Db_i(x)b_j(x)$$

where $Db(x)$ is the derivative of the vector field b at point x. Given vector fields $b_0, \dots, b_k$ sufficiently smooth in a neighbourhood of x we say that *Hörmander's condition holds at* x if the vectors

$$b_1(x) - b_0(x), \dots, b_k(x) - b_0(x),\ [b_i, b_j](x)_{0\leq i,j\leq k},\ [b_i, [b_j, b_l]](x)_{0\leq i,j,l\leq k}, \dots$$

span the space $\mathbb{R}^d$. This condition is called the hypo-ellipticity condition A in [31] and the strong bracket condition in [32].

From [31, Theorem 2] (see also [32, Theorem 4.4]) and [2, Corollary 5.3] we obtain the following

Corollary 6.1. *Suppose that Hörmander's condition holds at every $x \in E$. If the semigroup $\{P(t)\}_{t\geq 0}$ has no invariant density, then it is sweeping from compact subsets of $E \times I$.*

A point $x \in E$ is called *reachable from* y if we can find $n \in \mathbb{N}$, indices $i_1, \dots, i_n \in I$ and times $s_1, \dots, s_n$ such that $x = \pi_{i_n}(s_n, \dots, \pi_{i_1}(s_1, y))$, where for each i the function $t \mapsto \pi_i(t, x_0)$ is the solution of (3.1) with initial condition $x(0) = x_0$. Finally, a point x is called *accessible from* y if each neighbourhood of x contains a point reachable from y. Now, combining [31, Theorem 1] with [32, Theorem 4.6] we have

Corollary 6.2. *Suppose that the semigroup $\{P(t)\}_{t\geq 0}$ has an invariant density. If Hörmander's condition holds at a point $x \in E$ that is accessible from any point in E then the semigroup $\{P(t)\}_{t\geq 0}$ is asymptotically stable.*

We illustrate the behaviour of the mean of the process at large time for some simple examples exhibiting bifurcations in their trajectory dynamics [33]. Note that in [34] direct bifurcations of the heat equation with randomly switching boundary conditions were studied. We will use the results from [35] and [26], and we start by recalling some notions from them.

We consider $E \subset (0, \infty)$ and $I = \{0, 1\}$ so that we have a switching between b_0 and b_1 leading to a Markov process $\xi(t) = (x(t), i(t))$, $t \geq 0$ on the state space $E \times \{0, 1\}$. By $q_i = q_{i(1-i)}$, $i = 0, 1$, (see (3.4)) we denote constant positive intensities of switching from b_i to b_{1-i}. Additionally we assume that $b_0(0) = b_1(0) = 0$ and that either b_0 or b_1 has one more stationary point a that is accessible from any point in E. Hörmander's condition holds at x if $b_1(x) - b_0(x) \neq 0$. Let

$$r(x) = \frac{q_0}{b_0(x)} + \frac{q_1}{b_1(x)} \quad \text{and} \quad R(x) = \int_{x_0}^{x} r(s)ds,$$

where $x_0 \in (0, a)$. Then the functions given by

$$f_0(x) = \frac{e^{-R(x)}}{|b_0(x)|} \quad \text{and} \quad f_1(x) = \frac{e^{-R(x)}}{|b_1(x)|}$$

are stationary solutions of the corresponding Fokker–Planck equation (3.6). Now if

$$\kappa = \int_0^a \big(f_0(x) + f_1(x)\big)dx < \infty, \tag{6.5}$$

then the semigroup $\{P(t)\}_{t\geq 0}$ is asymptotically stable and the mean at large time is given by

$$V^*(x) = \kappa^{-1}(f_0(x) + f_1(x))\mathbf{1}_{(0,a)}(x). \tag{6.6}$$

If $b_0'(0)b_1'(0) \neq 0$ then condition (6.5) holds for $\lambda > 0$ where this parameter depends on the form of the functions b_0, b_1 and is defined by

$$\lambda = p_0 b_0'(0) + p_1 b_1'(0) \tag{6.7}$$

with

$$p_0 = \frac{q_1}{q_0 + q_1} \quad \text{and} \quad p_1 = \frac{q_0}{q_0 + q_1}$$

representing the probability of choosing the function b_0 and b_1, respectively. In the opposite situation with $\lambda < 0$ this semigroup is sweeping from the family of all compact subsets of the state space implying that the mean at large time is zero. The parameter λ turns out to be the mean growth rate if the population is small [26].

Example 6.1 (*Transcritical Bifurcation*)**.** Transcritical bifurcations appear in many biological models, c.f [36–39], and we thus re-consider Example 4.1. The functions b_0 and b_1 are given by (4.1) with $\beta_0 < \mu$ and $\beta_1 > \mu$. Thus, (3.1) with $i = 0$ has the form $x' = (\beta_0 - cx)x - \mu x$ and there are two stationary points, 0 and $a_0 = (\beta_0 - \mu)/c$, where the first one is stable and the second is unstable. However, for $i = 1$ the quantitative character of the stationary points of $x' = (\beta_1 - cx)x - \mu x$ is exchanged. That is, 0 is an unstable stationary point while $a_1 = (\beta_1 - \mu)/c$ is stable. Hence, we have a transcritical bifurcation. We take $a = a_1$. Again, we look at the value of the parameter λ in (6.7). For $\lambda < 0$ the mean of the process at large time is 0, while for $\lambda > 0$ the mean is positive and given by the corresponding V^* with f_i, $i = 0, 1$ given, up to a multiplicative constant, by

$$f_i(x) = \frac{1}{x|x - a_i|} x^{-\left(\frac{q_0}{ca_0} + \frac{q_1}{ca_1}\right)} (x - a_0)^{\frac{q_0}{ca_0}} (a_1 - x)^{\frac{q_1}{ca_1}} \mathbf{1}_{(0,a_1)}(x). \tag{6.8}$$

We illustrate the behaviour of the mean $V(t, x)$ as in (5.12) for chosen times and parameters in Figs. 1 and 2(a). Fig. 1 shows convergence of V to the mean at large time V^* for $\lambda > 0$ while Fig. 2(a) presents sweeping to 0 for $\lambda < 0$.

Example 6.2 (*Fold Bifurcation*)**.** We next go back to the inducible operon model of Example 4.2. Consider the following nonlinear differential equation

$$x'(t) = \frac{x^n(t)}{1 + x^n(t)} - \gamma x(t), \tag{6.9}$$

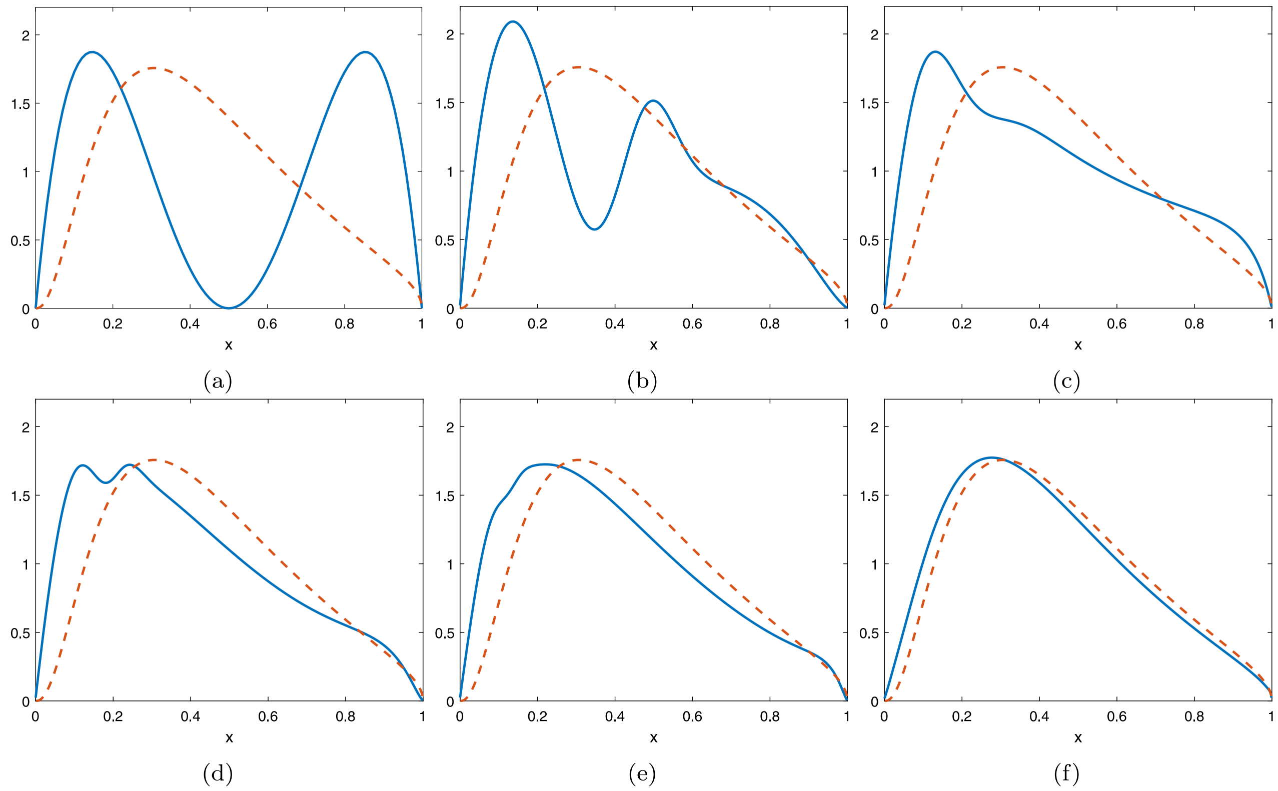

Fig. 1. Numerical simulations of the mean $V(t, x)$ (solid line) in Example 6.1. The initial density is shown in (a). The dashed line represents the graph of the mean in large time $V^*(x)$. Consecutive times are $t = 0.25$ (b), $t = 0.5$ (c), $t = 0.7$ (d), $t = 1$ (e), and $t = 2.5$ (f). The values of parameters used in this example are: $q_0 = 5$, $q_1 = 3$, $\beta_0 = 1$, $\beta_1 = 4$, $c = 2$, $\mu = 2$.

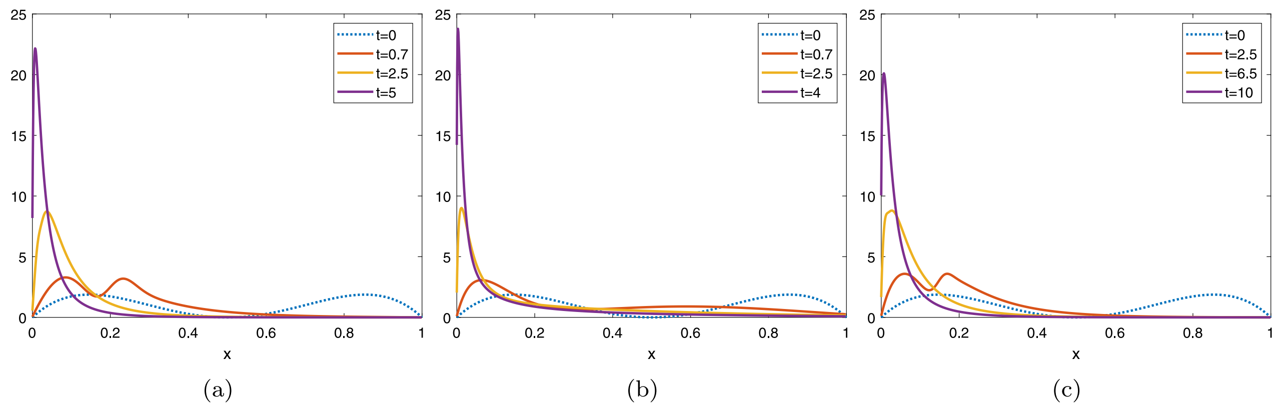

Fig. 2. Numerical simulations of $V(t, x)$ when the mean at large time is 0: (a) Example 6.1 with parameters: $q_0 = 2$, $q_1 = 6$, $\beta_0 = 1$, $\beta_1 = 4$, $c = 2$, $\mu = 2$, (b) Example 4.2 with parameters: $q_0 = 6$, $q_1 = 2$, $\gamma_0 = 2$, $\gamma_1 = 0.25$, (c) Example 6.3 with parameters: $q_0 = 4$, $q_1 = 2$, $\alpha_0 = -0.5$, $\alpha_1 = 1$.

where $x(t) > 0$ denotes the concentration level of protein molecules at time t, γ is a degradation rate and $n > 1$. It is known (see [27]) that if the parameters satisfy the condition

$$n^n \gamma^n > (n-1)^{n-1}, \tag{6.10}$$

then 0 is the only stationary point of Eq. (6.9) and it is stable. In the opposite case to (6.10), there are also two additional stationary points of this equation; one of them is stable and the other one is unstable. Hence, we choose the values of the parameters γ_0 and γ_1 in such way that a fold bifurcation occurs. Thus we take γ_0 such that $n^n \gamma_0^n > (n-1)^{n-1}$ and γ_1 such that $n^n \gamma_1^n < (n-1)^{n-1}$. By using the same type of argument as in the proof of [35, Theorem 4.2] together with the properties of the dynamics $x(t)$, we see that $x(t)$ reaches a neighbourhood of 0 in finite time and hence we deduce that the semigroup $\{P(t)\}_{t \ge 0}$ is sweeping from the family of all compact subsets of $(0, +\infty) \times \{0, 1\}$. Consequently, the mean at large time is equal to zero. This behaviour is illustrated in Fig. 2(b).

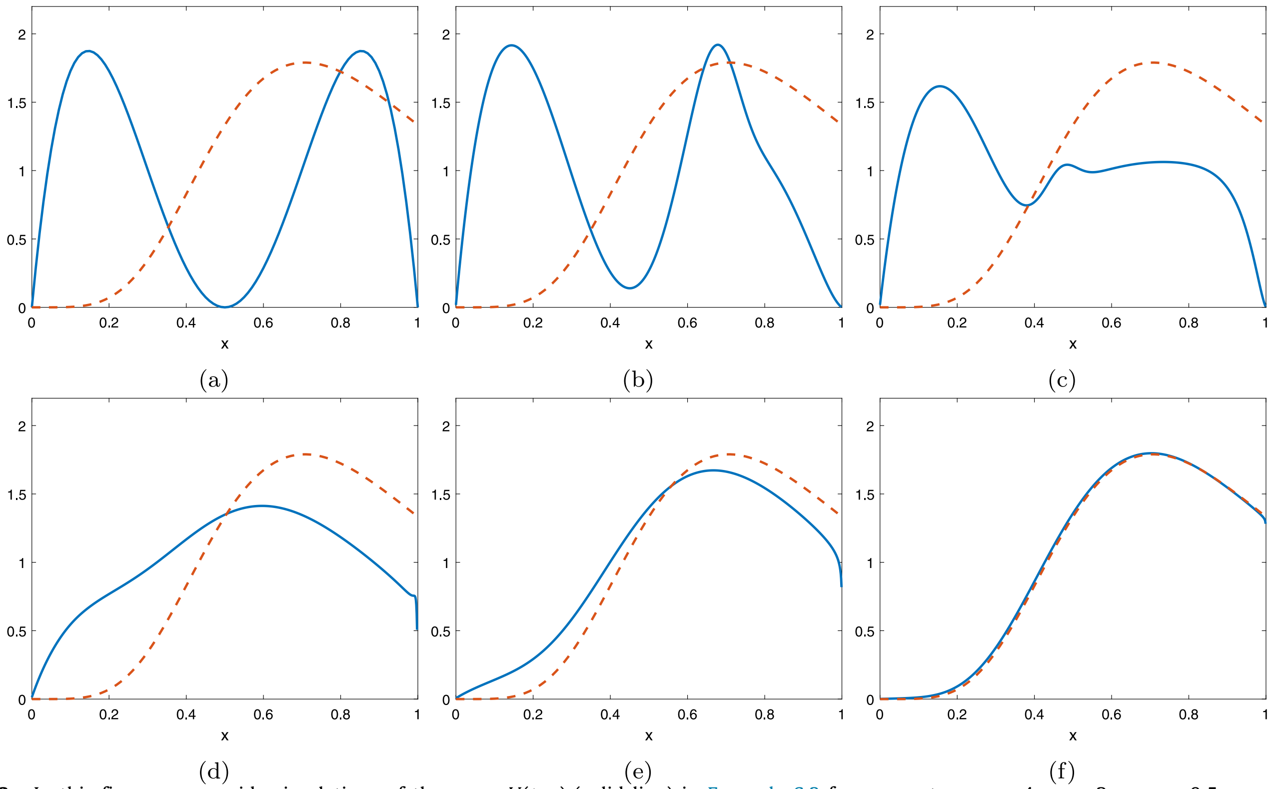

Fig. 3. In this figure we provide simulations of the mean $V(t,x)$ (solid line) in Example 6.3 for parameters $q_0=4$, $q_1=2$, $\alpha_0=-0.5$, $\alpha_1=1$ at times $t=0$ (a), $t=0.25$ (b), $t=0.7$ (c), $t=2.5$ (d), $t=5$ (e), and $t=10$ (f). The dashed line graph represents the mean at large time $V^*(x)$.

Example 6.3 (*Pitchfork Bifurcation*)**.** The normal form for a supercritical pitchfork bifurcation is

$$x'(t)=\alpha x(t)-x^3(t). \tag{6.11}$$

For $\alpha<0$ there is a single stationary point $x_*=0$ while for $\alpha>0$ there is an unstable stationary point at 0 and two stationary points $x_\pm=\pm\sqrt{\alpha}$ that are locally stable. Now let $\alpha_0<0$ and $\alpha_1>0$ be two fixed parameters. We consider equation (6.11) with $\alpha=\alpha_i$. Thus we have $b_0(x)=\alpha_0 x-x^3$ and $b_1(x)=\alpha_1 x-x^3$.

First we take $E=(0,\infty)$ and $a=\sqrt{\alpha_1}$. Then for positive λ from (6.7) we have a positive mean at large time with f_i given by

$$f_i(x)=\frac{1}{x|\alpha_i-x^2|}x^{-\frac{q_0}{\alpha_0}-\frac{q_1}{\alpha_1}}(x^2-\alpha_0)^{\frac{q_0}{2\alpha_0}}(\alpha_1-x^2)^{\frac{q_1}{2\alpha_1}}1_{(0,\sqrt{\alpha_1})}(x),\ \ i\in\{0,1\}, \tag{6.12}$$

while for $\lambda<0$ the mean of the process at large time is equal to 0. The situation with $E=(-\infty,0)$ is analogous to stationary solutions of the corresponding Fokker–Planck equation given by $f_i(-x)$, $x<0$ where this function is as in (6.12). The behaviour of the mean $V(t,x)$ in this example is shown in Figs. 3 and 2(c). The convergence of V to the mean at large time V^* for $\lambda>0$ is illustrated in Fig. 3 while sweeping to 0 for $\lambda<0$ is presented in Fig. 2(c).

Our last example treats the normal form of a supercritical Hopf bifurcation, see also [35].

Example 6.4 (*Hopf Bifurcation*)**.** Another commonly reported class of models in biology is one which exhibits a Hopf bifurcation. The normal form for a supercritical Hopf bifurcation, after changing to polar coordinates (θ,r), is

$$\begin{cases}\theta'(t)=\omega+br^2(t),\\ r'(t)=\mu r(t)-r^3(t).\end{cases} \tag{6.13}$$

For $\mu<0$ there is a single steady state $(\theta_*,r_*)=(0,0)$ while for $\mu>0$ there is an unstable steady state at $(0,0)$ and a co-existing limit cycle with $r=\sqrt{\mu}$. In analogy to the previous cases, we take $\omega=\omega_i$ and $\mu=\mu_i$, $i=0,1$, in (6.13) with $\mu_0<0$ and $\mu_1>0$. Let $E=\mathbb{S}^1\times(0,\infty)$, where $\mathbb{S}^1$ is the unit circle in $\mathbb{R}^2$. To simplify the analysis we assume that $b=0$. If $\omega_0\neq\omega_1$ then the Hörmander condition holds at every point $(\theta,r)\in E$. Note that the point $(0,\sqrt{\mu_1})$ is accessible from any point in E. The asymptotic behaviour of the mean given by (5.12) again depends on the sign of the parameter λ in (6.7) with $b_i'(0)=\mu_i$, $i=0,1$. If λ is positive then the mean at large time is equal to

$$V^*(\theta,r)=\frac{1}{2\pi\kappa}\big(f_0(r)+f_1(r)\big)\mathbf{1}_{\mathbb{S}^1}(\theta),$$

where f_i has the form as in (6.12) with $\alpha_i=\mu_i$. On the other hand for $\lambda<0$ the mean of the process at large time is zero.

If $\omega = \omega_0 = \omega_1$ then the angular variable θ is independent of the radial variable r and it satisfies the same equation $\theta'(t) = \omega$ for each i. Thus, the process $(\theta(t), r(t), i(t))$ can be decomposed into two independent processes: $\theta(t)$ that is deterministic and $(r(t), i(t))$ that behaves as the process in Example 6.3.

The asymptotic behaviour of the process in (4.6) is now different when $\lambda > 0$. If we take the initial g in (4.6) as the product of two marginal densities $g(\theta, r) = g_1(\theta)g_2(r)$ then the mean V satisfies

$$\lim_{t\to\infty} \int_E |V(t,\theta,r) - \frac{1}{\kappa} g_1(\theta - \omega t)\big(f_0(r) + f_1(r)\big)| d\theta dr = 0,$$

where f_0 and f_1 are as above.

7. Second and higher order correlations

In this section we continue the study of the stochastic process (4.6) by looking at equations for correlations. These are extensions of the moment equations considered in Section 5. We provide the full analysis only for second order correlations, but higher order cases are straightforward and can be easily obtained by similar considerations. We use some notation from the theory of tensor products, and for a brief summary of standard definitions used here see Appendix.

We start with the definition of second order correlations:

$$C_i(t,x,y) = \mathbb{E}(\mathbf{1}_{\{i(t)=i\}} u(t,x)u(t,y)), \quad x, y \in E, \ i \in I, \ t \ge 0. \tag{7.1}$$

We will show that the following equation holds:

$$\frac{\partial}{\partial t} C_i = (A_i \otimes \mathrm{Id})C_i + (\mathrm{Id} \otimes A_i)C_i + \sum_{j\in I} q_{ji} C_j, \quad i \in I, \tag{7.2}$$

where $A_i \otimes \mathrm{Id}$ and $\mathrm{Id} \otimes A_i$ are defined on functions $(x, y) \mapsto f(x, y)$ with $f \in L^1(E^2)$ as tensor products of operators A_i and Id. Especially, if $A_i f(x) = -\operatorname{div}(b_i(x)f(x))$ then we have

$$(A_i \otimes \mathrm{Id})f(x,y) = -\operatorname{div}(b_i(x)f(x,y)), \tag{7.3}$$

$$(\mathrm{Id} \otimes A_i)f(x,y) = -\operatorname{div}(b_i(y)f(x,y)). \tag{7.4}$$

We consider equation (7.2) in the space $L^1(E^2 \times I) = L^1(E^2 \times I, \mathcal{B}(E^2 \times I), \mu^2)$, where μ^2 is the product of two copies of the measure m on E and the counting measure on I. We define the family of operators on $L^1(E^2 \times I)$ by

$$(S(t)f)_i = \sum_{j\in I} \mathbb{E}_j(\mathbf{1}_{\{i(t)=i\}} U(t) \otimes U(t) f_j), \quad i \in I, \tag{7.5}$$

for $f = (f_j)_{j\in I} \in L^1(E^2 \times I)$, $f_j \in L^1(E^2)$, $j \in I$, and where $U(t)$ is as in (4.8).

Theorem 7.1. *Assume conditions (I) and (II). Then the family of operators $\{S(t)\}_{t\ge0}$ defined in (7.5) is a stochastic semigroup on $L^1(E^2 \times I)$. The infinitesimal generator of this semigroup is the operator $A + Q^T$, where*

$$A(f_i)_{i\in I} = \big((A_i \otimes Id)f_i + (Id \otimes A_i)f_i\big)_{i\in I} \quad \text{and} \quad Q^T(f_i)_{i\in I} = (\sum_{j\in I} q_{ji} f_j)_{i\in I}, \tag{7.6}$$

with $f_i \in \mathcal{D}(A_i) \otimes \mathcal{D}(A_i)$, $i \in I$.

Proof. Observe that

$$U(t) \otimes U(t) = (P_{i(t_{N(t)})}(t - t_{N(t)}) \otimes P_{i(t_{N(t)})}(t - t_{N(t)})) \circ (U(t_{N(t)}) \otimes U(t_{N(t)})), \quad t \ge 0.$$

Let $i \in I$. Since $\{P_i(t)\}_{t\ge0}$ is a stochastic semigroup on $L^1(E)$, we see that $P_i(t) \otimes P_i(t)$ is a stochastic semigroup on $L^1(E^2)$, see Corollary A.2. Taking the injective tensor product space $B\check{\otimes}B$ (see Appendix for the notation), we see that $T_i(t) \otimes T_i(t)$ is a C_0-semigroup on $B\check{\otimes}B$ satisfying

$$\langle P_i(t) \otimes P_i(t)(f_1 \otimes f_2), h_1 \otimes h_2\rangle = \langle f_1 \otimes f_2, T_i(t) \otimes T_i(t)(h_1 \otimes h_2)\rangle, \tag{7.7}$$

where $f_1 \otimes f_2 \in L^1(E) \otimes L^1(E)$, $h_1 \otimes h_2 \in B \otimes B$, $t \ge 0$. Thus we have

$$\langle (P_i(t) \otimes P_i(t))f, h\rangle = \langle f, (T_i(t) \otimes T_i(t))h\rangle, \quad t \ge 0, \tag{7.8}$$

for all $f \in L^1(E) \otimes L^1(E)$ and $h \in B \otimes B$. Since $L^1(E) \otimes L^1(E)$ is dense in $L^1(E^2)$ and $B \otimes B$ is dense in $B\check{\otimes}B$, we conclude that (7.8) holds for all $f \in L^1(E^2)$ and $h \in B\check{\otimes}B$.

The σ-algebra $\mathcal{B}(E^2)$ is generated by the π-system of sets $\mathcal{C} \times \mathcal{C} = \{F_1 \times F_2 : F_1, F_2 \in \mathcal{C}\}$. Given the set $F = F_1 \times F_2$ we consider the sequence $h_n(x_1, x_2) = h_{1,n}(x_1)h_{2,n}(x_2)$, where $h_{1,n}$ and $h_{2,n}$ are sequences approximating the functions $\mathbf{1}_{F_1}$ and $\mathbf{1}_{F_2}$. Since h_n converges to $\mathbf{1}_F$, we see that condition (I) holds. Consequently, Theorem 5.1 implies that $\{S(t)\}_{t\ge0}$ is a stochastic semigroup on $L^1(E^2 \times I)$. It follows from Proposition A.1 that for each $i \in I$ the generator of the semigroup

$P_i(t) \otimes P_i(t)$ is the closure of the operator $A_i \otimes \mathrm{Id} + \mathrm{Id} \otimes A_i$ defined on the core $\mathcal{D}(A_i) \otimes \mathcal{D}(A_i)$. Thus the closure of the operator A defined in (7.6) is the generator of the stochastic semigroup $(P_i(t) \otimes P_i(t))_{i\in I}$. Hence, Theorem 5.1 implies that the generator of the semigroup $\{S(t)\}_{t\geq 0}$ is the operator $A + Q^T$. □

Using Theorem 7.1 we obtain the following:

Corollary 7.2. *Assume conditions (I) and (II). Let $S(t)$ be given by (7.5) and u by (4.5). For each $g \in L^1(E^2)$ and $l \in I$ such that $u(0) = g$ and $i(0) = l$ we have $C_i(t, x, y) = (S(t)f)_i(x, y)$, where C_i is as in (7.1) and $f = (f_j)_{j\in I}$ is of the form*

$$f_j = \begin{cases} g, & j = l, \\ 0, & j \neq l. \end{cases}$$

Remark 7.3. If for each $i \in I$ the semigroup $\{P_i(t)\}_{t\geq 0}$ is as in (3.2) then the operator $A + Q^T$ from Theorem 7.1 is also the generator of a stochastic semigroup induced by the stochastic process $(x(t), y(t), i(t))$, where $(x(t), y(t))$ satisfies the system of equations:

$$\begin{cases} x'(t) = b_{i(t)}(x(t)), \\ y'(t) = b_{i(t)}(y(t)). \end{cases}$$

8. Conclusion

In this paper we introduced the concept of randomly switching stochastic semigroups. We investigated a stochastic evolution equation in L^1 space. Such a regime could explain the source of stochasticity when observing the evolution of some population driven by a common environmental stimulus. Next, we studied the first moment of the stochastic evolution equation solutions and found the correspondence between this moment equation and a deterministic system of Fokker–Planck type equations for the distributions of the process in Euclidean state space. We concluded that the mean of the process at large time can be expressed by the stationary solutions of a Fokker–Planck type system providing that they exist. Similarly, we connected the mean of the process at large time with sweeping property. We gave then some examples of the application of our results to biological models in which the underlying dynamics display a variety of bifurcations and provided numerical simulations for them. Finally, we studied second order correlations of solutions of the stochastic evolution equation and we provided a rigorous way to extend our considerations to correlations of higher order. Thus, this paper extends and justifies analytically the numerical results of Bressloff [11].

The next step would be to show convergence in distribution of the infinite dimensional process $(u(t), i(t))$ to a stationary distribution. In particular examples connected with diffusion processes such convergence is known, see [18,40]. However, the results of [18,40] are not applicable to our stochastic semigroups $\{P_i(t)\}_{t\geq 0}$ on L^1 spaces because we have preservation of the norm while in these papers strict contraction on average was required. We hope to find in the future yet another approach that could be used for stochastic semigroups.

One possible future extension of this work is connected with addition of switching to stochastic PDEs driven by Gaussian noise or, more generally, by Lévy noise, see [41]. Another one could be related to randomly occurring phenomena in more complex systems like networks subjected to Markovian switching topology appearing in filtering problems as in [42] and [43]. More careful recognition of these relations require further research.

CRediT authorship contribution statement

Paweł Klimasara: Conceptualization, Methodology, Writing and editing of the manuscript. **Michael C. Mackey:** Conceptualization, Methodology, Writing and editing of the manuscript. **Andrzej Tomski:** Conceptualization, Methodology, Writing and editing of the manuscript. **Marta Tyran-Kamińska:** Conceptualization, Methodology, Writing and editing of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix. Tensor products

We recall some standard notation from the theory of tensor products [44]. Let $\mathcal{X}_1$ and $\mathcal{X}_2$ be two Banach spaces of functions, i.e., either $\mathcal{X}_i$ is an L^1 space or it is a subspace of the space of all bounded measurable functions defined on a given set and equipped with the supremum norm. For $f_1 \in \mathcal{X}_1$ and $f_2 \in \mathcal{X}_2$ we identify the function $(x_1, x_2) \mapsto f_1(x_1)f_2(x_2)$ with the tensor $f_1 \otimes f_2$. We define the tensor product space $\mathcal{X}_1 \otimes \mathcal{X}_2$ as the set of all linear combinations of such tensors. The completion of the linear space $\mathcal{X}_1 \otimes \mathcal{X}_2$ when equipped with the projective norm

$$\|h\|_\pi = \inf\{\sum_{k=1}^{n} \|f_k\| \|g_k\| : f_k \in \mathcal{X}_1, g_k \in \mathcal{X}_2, h = \sum_{k=1}^{n} f_k \otimes g_k\}$$

is called the *projective tensor product* of the spaces $\mathcal{X}_1$ and $\mathcal{X}_2$ and will be denoted by $\mathcal{X}_1 \hat{\otimes} \mathcal{X}_2$.

It is known [44, Chapter 2] that $L^1(E_1, \mathcal{E}_1, m_1)\hat{\otimes}L^1(E_2, \mathcal{E}_2, m_2)$ is isometrically isomorphic with $L^1(E_1 \times E_2, \mathcal{E}_1 \times \mathcal{E}_2, m_1 \times m_2)$. If instead we consider $\mathcal{X}_1 \otimes \mathcal{X}_2$ with the injective norm

$$\|h\|_\varepsilon = \sup\{|(\gamma_1 \otimes \gamma_2)(h)| : \gamma_i \in \mathcal{X}_i^*, \|\gamma_i\| \le 1\},$$

where $\mathcal{X}_i^*$ is the dual of $\mathcal{X}_i$ and

$$(\gamma_1 \otimes \gamma_2)(h) = \sum_{k=1}^{n} \gamma_1(f_k)\gamma_2(g_k) \quad \text{for } h = \sum_{k=1}^{n} f_k \otimes g_k,$$

then the completion of $\mathcal{X}_1 \otimes \mathcal{X}_2$ is called the *injective tensor product* and it will be denoted by $\mathcal{X}_1 \check{\otimes} \mathcal{X}_2$. In particular, if $C(E_i)$ is the space of continuous functions on a compact space E_i then $C(E_1)\check{\otimes}C(E_2)$ is the space $C(E_1 \times E_2)$, by [44, Section 3.2]. Note that if $\mathcal{Y}_i$ is a closed linear subspace of the Banach space $\mathcal{X}_i$ then $\mathcal{Y}_1\check{\otimes}\mathcal{X}_2$ and $\mathcal{X}_1\check{\otimes}\mathcal{Y}_2$ are closed linear subspaces of $\mathcal{X}_1\check{\otimes}\mathcal{X}_2$.

Given two linear and bounded operators $S_i\colon \mathcal{X}_i \to \mathcal{X}_i$ the linear mapping $S_1 \otimes S_2\colon \mathcal{X}_1 \otimes \mathcal{X}_2 \to \mathcal{X}_1 \otimes \mathcal{X}_2$ defined by

$$(S_1 \otimes S_2)(f_1 \otimes f_2) = S_1(f_1) \otimes S_2(f_2)$$

has a continuous extension to tensor product spaces. We will use the following result from [30, Section A-I.3, Proposition]:

Proposition A.1. *Let $\{S_1(t)\}_{t\ge 0}$ and $\{S_2(t)\}_{t\ge 0}$ be C_0-semigroups on some Banach spaces $\mathcal{X}_1$, $\mathcal{X}_2$ and let the operators $(A_1, \mathcal{D}(A_1))$, $(A_2, \mathcal{D}(A_2))$ be their generators. Then the family*

$$\{S_1(t) \otimes S_2(t)\}_{t\ge 0} \tag{A.1}$$

is a C_0-semigroup on both projective and injective tensor products of $\mathcal{X}_1$ and $\mathcal{X}_2$. The closure of

$$A_1 \otimes \mathrm{Id} + \mathrm{Id} \otimes A_2, \tag{A.2}$$

defined on the core $\mathcal{D}(A_1) \otimes \mathcal{D}(A_2)$, is its generator.

Corollary A.2. *If $\{S_1(t)\}_{t\ge 0}$ and $\{S_2(t)\}_{t\ge 0}$ are stochastic semigroups on the spaces $L^1(E_1, \mathcal{E}_1, m_1)$ and $L^1(E_2, \mathcal{E}_2, m_2)$, respectively, then $\{S_1(t) \otimes S_2(t)\}_{t\ge 0}$ is a stochastic semigroup on $L^1(E_1 \times E_2, \mathcal{E}_1 \times \mathcal{E}_2, m_1 \times m_2)$.*

Proof. For $f_i \in L^1(E_i, \mathcal{E}_i, m_i)$ we have

$$\int_{E_1\times E_2} (S_1(t) \otimes S_2(t))(f_1 \otimes f_2)d(m_1 \times m_2) = \int_{E_1} S_1(t)f_1 dm_1 \int_{E_2} S_2(t)f_2 dm_2.$$

This implies that the operator $S_1(t) \otimes S_2(t)$ preserves the integral. It is easy to see that $S_1(t) \otimes S_2(t)$ is a positive operator, completing the proof. □

References

[1] M.H.A. Davis, Piecewise-deterministic Markov processes: a general class of nondiffusion stochastic models, J. R. Stat. Soc. Ser. B Stat. Methodol. 46 (3) (1984) 353–388.

[2] R. Rudnicki, M. Tyran-Kamińska, Piecewise deterministic processes in biological models, in: SpringerBriefs in Applied Sciences and Technology, Springer, Cham, 2017, SpringerBriefs in Mathematical Methods.

[3] P.C. Bressloff, Stochastic switching in biology: From genotype to phenotype, J. Phys. A 50 (13) (2017) 133001.

[4] S. Goldstein, On diffusion by discontinuous movements, and on the telegraph equation, Quart. J. Mech. Appl. Math. 4 (1951) 129–156.

[5] M. Kac, A stochastic model related to the telegrapher's equation, Rocky Mountain J. Math. 4 (1974) 497–509.

[6] T. Hillen, K.P. Hadeler, Hyperbolic systems and transport equations in mathematical biology, in: Analysis and Numerics for Conservation Laws, Springer, Berlin, 2005, pp. 257–279.

[7] D.W. Stroock, Some stochastic processes which arise from a model of the motion of a bacterium, Z. Wahrscheinlichkeitstheor. Verwandte Geb. 28 (1974) 303–315.

[8] A. Bobrowski, T. Lipniacki, K. Pichór, R. Rudnicki, Asymptotic behavior of distributions of mRNA and protein levels in a model of stochastic gene expression, J. Math. Anal. Appl. 333 (2) (2007) 753–769.
[9] A. Tomski, The dynamics of enzyme inhibition controlled by piece-wise deterministic Markov process, in: Semigroups of Operators - Theory and Applications, in: Springer Proceedings in Mathematics & Statistics, vol. 113, Springer, New York, 2015, pp. 299–316.
[10] S. Zeiser, U. Franz, V. Liebscher, Autocatalytic genetic networks modeled by piecewise-deterministic Markov processes, J. Math. Biol. 60 (2) (2010) 207–246.
[11] P.C. Bressloff, Stochastic Liouville equation for particles driven by dichotomous environmental noise, Phys. Rev. E 95 (1) (2017) 012124.
[12] A. Belle, A. Tanay, L. Bitincka, R. Shamir, E.K. O'Shea, Quantification of protein half-lives in the budding yeast proteome, Proc. Natl. Acad. Sci. USA 103 (35) (2006) 13004–13009.
[13] R. Griego, R. Hersh, Theory of random evolutions with applications to partial differential equations, Trans. Amer. Math. Soc. 156 (1971) 405–418.
[14] M.A. Pinsky, Lectures on RandOm Evolution, World Scientific Publishing Co., Inc., River Edge, NJ, 1991.
[15] R. Hersh, R.J. Griego, Brownian motion and potential theory, Sci. Am. 220 (3) (1969) 66–77.
[16] R. Hersh, The birth of random evolutions, Math. Intelligencer 25 (1) (2003) 53–60.
[17] P.C. Bressloff, S.D. Lawley, Moment equations for a piecewise deterministic PDE, J. Phys. A 48 (10) (2015) 105001, 25.
[18] S.D. Lawley, J.C. Mattingly, M.C. Reed, Stochastic switching in infinite dimensions with applications to random parabolic PDE, SIAM J. Math. Anal. 47 (4) (2015) 3035–3063.
[19] S.D. Lawley, J.A. Best, M.C. Reed, Neurotransmitter concentrations in the presence of neural switching in one dimension, Discrete Contin. Dyn. Syst. Ser. B 21 (7) (2016) 2255–2273.
[20] A.M. Berezhkovskii, S.Y. Shvartsman, Diffusive flux in a model of stochastically gated oxygen transport in insect respiration, J. Chem. Phys. 144 (20) (2016) 204101.
[21] P.C. Bressloff, S.D. Lawley, P. Murphy, Effective permeability of a gap junction with age-structured switching, SIAM J. Appl. Math. 80 (1) (2020) 312–337.
[22] S.D. Lawley, Boundary value problem for statistcs of diffusion in randomly switching environment: PDE and SDE perspectives, SIAM J. Appl. Dyn. Syst. 15 (2016) 1410–1433.
[23] J.E. Guyer, D. Wheeler, J.A. Warren, FiPy: Partial differential equations with Python, Comput. Sci. Eng. 11 (3) (2009) 6–15, http://www.ctcms.nist.gov/fipy.
[24] A. Lasota, M.C. Mackey, Chaos, fractals, and noise, in: Applied Mathematical Sciences, vol. 97, Springer-Verlag, New York, 1994.
[25] R. Rudnicki, K. Pichór, M. Tyran-Kamińska, Markov Semigroups and their applications, in: Dynamics of Dissipation, in: Lectures Notes in Physics, 597, Springer, Berlin, 2002, pp. 215–238.
[26] R. Rudnicki, M. Tyran-Kamińska, Piecewise deterministic Markov processes in biological models, in: Semigroups of Operators - Theory and Applications, in: Springer Proceedings in Mathematics & Statistics, vol. 113, Springer, New York, 2015, pp. 235–255.
[27] J. Griffith, Mathematics of cellular control processes II. Positive feedback to one gene, J. Theoret. Biol. 20 (2) (1968) 209–216.
[28] R. Case, Y. Boucher, I. Dahllöf, C. Holmström, W. Doolittle, S. Kjelleberg, Use of 16S rRNA and rpoB genes as molecular markers for microbial ecology studies, Appl. Environ. Microbiol. 73 (1) (2007) 278–288.
[29] E. Hille, R.S. Phillips, Functional Analysis and Semi-Groups, vol. 31, American Mathematical Soc, 1996.
[30] W. Arendt, A. Grabosch, G. Greiner, U. Groh, H.P. Lotz, U. Moustakas, R. Nagel, F. Neubrander, U. Schlotterbeck, One-parameter semigroups of positive operators, in: Lecture Notes in Mathematics, vol. 1184, Springer-Verlag, Berlin, 1986.
[31] Y. Bakhtin, T. Hurth, Invariant densities for dynamical systems with random switching, Nonlinearity 25 (10) (2012) 2937–2952.
[32] M. Benaïm, S. Le Borgne, F. Malrieu, P.-A. Zitt, Qualitative properties of certain piecewise deterministic Markov processes, Ann. Inst. Henri Poincaré Probab. Stat. 51 (3) (2015) 1040–1075.
[33] Y.A. Kuznetsov, Elements of Applied Bifurcation Theory, vol. 112, Springer Science & Business Media, 2013.
[34] S.D. Lawley, Blowup from randomly switching between stable boundary conditions for the heat equation, Commun. Math. Sci. 16 (4) (2018) 1133–1156.
[35] T. Hurth, C. Kuehn, Random switching near bifurcations, Stoch. Dyn. (2019) 2050008.
[36] H. Boudjellaba, T. Sari, Dynamic transcritical bifurcations in a class of slow–fast predator–prey models, J. Differential Equations 246 (6) (2009) 2205–2225.
[37] F. Brauer, C. Kribs, Dynamical Systems for Biological Modelling: An Introduction, second ed., Chapman and Hall / CRC, 2015.
[38] B. Buonomo, A note on the direction of the transcritical bifurcation in epidemic models, Nonlinear Anal. Model. Control 20 (2015) 38–55.
[39] Y. Wang, H. Wang, W. Jiang, Hopf-transcritical bifurcation in toxic phytoplankton–zooplankton model with delay, J. Math. Anal. Appl. 415 (2) (2014) 574–594.
[40] B. Cloez, M. Hairer, Exponential ergodicity for Markov processes with random switching, Bernoulli 21 (1) (2015) 505–536.
[41] S. Peszat, J. Zabczyk, Stochastic partial differential equations with Lévy noise, in: Encyclopedia of Mathematics and its Applications, vol. 113, Cambridge University Press, Cambridge, 2007, An evolution equation approach.
[42] Q. Liu, Z. Wang, X. He, D. Zhou, Event-based distributed filtering over Markovian switching topologies, IEEE Trans. Automat. Control 64 (4) (2018) 1595–1602.
[43] L. Ma, Z. Wang, Y. Liu, F.E. Alsaadi, Distributed filtering for nonlinear time-delay systems over sensor networks subject to multiplicative link noises and switching topology, Internat. J. Robust Nonlinear Control 29 (10) (2019) 2941–2959.
[44] R.A. Ryan, Introduction to tensor products of banach spaces, in: Springer Monographs in Mathematics, Springer-Verlag London, Ltd., London, 2002.