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Humid savanna–forest dynamics: A matrix model with vegetation–fire interactions and seasonality

Francesco Accatino, Carlo De Michele*

Politecnico di Milano, P.zza L. da Vinci 32, Milano, Italy

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ABSTRACT

Rainfall seasonality and vegetation–fire feedbacks characterize humid savannas and tropical forests dynamics. In these ecosystems fire occurrence is influenced by the amount of grass, and trees respond to fire differently according to their height. Here we present a spatially implicit matrix model of humid savanna–forest dynamics. The state variables are the fraction of space occupied by trees and the grass biomass density. Rainfall seasonality is included using a discrete seasonal time step, distinguishing between wet and dry seasons. The demography of trees is taken into account considering different size classes and describing their dynamics with transition matrices, which depend on the season and presence/absence of fire. The occurrence of fire is represented by a *Bernoulli* variable, whose probability of occurrence is function of grass density. We explore different fire probabilities at the savanna–forest boundary and show different behaviors of the ecosystems. We investigate also the model's behavior with matrices of three *Acacia* species taken from literature.

1. Introduction

Savannas are ecosystems characterized by co-existence of trees and grasses, with a near continuous grassland stratum and a highly variable (between 20% and 80%) tree cover (Scholes and Archer, 1997).

According to the mean annual rainfall, savannas can be split in *arid* and *humid*. In arid savannas tree–grass co-existence is attributed to water scarcity, which limits the tree growth. In humid savannas, fire prevents the closure of the canopy that would be allowed by rainfall abundance. The rainfall threshold between arid and humid savannas is located between 600 mm/year (Sankaran et al., 2005) and 820 mm/year (Higgins et al., 2010). Here we focus on humid savannas and on their possible transitions to and from forests. Recently, extensive analyses using MODIS data (Staver et al., 2011b; Hirota et al., 2011) showed that both humid savannas and forests can occur in a very large range of mean annual rainfall ([650–2500] mm/year), suggesting that they can exist as alternative stable states. This fact is an outcome of many models (e.g., Accatino et al., 2010; De Michele et al., 2011).

In literature many models of savanna vegetation are available. Here we focus only on spatially implicit ones. They can be split in *deterministic* and *stochastic*. Deterministic models (e.g., van Langevelde et al., 2003; Accatino et al., 2010; De Michele et al., 2011; Baudena et al., 2010; Staver et al., 2011a) represent savanna dynamics through a system of ordinary differential equations. For these models the stability map is useful to investigate savanna domain in the parameter space and the bifurcation analysis is useful to study the nature of transitions (whether broad or abrupt) between different steady states. Stochastic models (e.g., D'Odorico et al., 2006; De Michele et al., 2008; Vezzoli et al., 2008) represent savanna dynamics through a system of stochastic differential equations where the drivers (e.g., rainfall or fire) are stochastic variables. In these models steady state probability distributions are found starting from the probability distributions of the drivers. In general these models are parsimonious in parameters, analytically tractable, and are used for analysis of the steady states, yet they are too simplified to reproduce realistic trajectories of the ecosystem state variables. The investigation of the temporal trajectories is fundamental to understand the behavior of the ecosystem, especially the role of transients to reach a steady state, which can be very long with respect to the time horizon of human management. A model which is able to reproduce realistic trajectories is important to make predictions of vegetation dynamics under climate scenarios (Whitlock et al., 2010).

Here we propose a model for reproducing humid savanna–forest dynamics. We take into account the alternation between wet and dry seasons and the vegetation–fire feedbacks. We treat fire occurrence as a stochastic *Bernoulli* variable, whose probability depends on the status of the system. In this way fire is an outcome rather than an external driver. We divide the population into height classes

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* Corresponding author. Tel.: +39 02 23996233; fax: +39 02 23996207.
E-mail addresses: francesco.accatino@mail.polimi.it (F. Accatino), carlo.demichele@polimi.it (C. De Michele).

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to account for their different responses to fire. Tree population is updated with transition matrices which are dependent on the season and on the presence/absence of fire.

With this model we aim to (i) explore the different behaviors of the system in the savanna–forest boundary, investigate how different behaviors can be predicted from the parameters' values, and (ii) simulate the system dynamics with measured matrices of three different *Acacia* species, investigating how different demographic parameters can lead to different dynamics.

In Section 2, we discuss the key factors influencing the behavior of humid savannas, and considered in the model, i.e., rainfall seasonality, and fire–vegetation feedbacks. In Section 3 we describe the model. In Section 4, we give an example of tree demography calibrating the model using the information reported in Staver et al. (2009). In Section 5, we describe the properties of the model, discuss some simulations at the savanna–forest boundary, show some simulations using matrices of three *Acacia* species taken from literature.

2. Rainfall seasonality and fire–vegetation feedbacks

One important consequence of the wet-dry alternation of rainfall regime is the correspondent dynamics of grass. During the wet period the total amount of rainfall determines the density of the grass stratum. In the following dry season the grass biomass dries out (Sarmiento et al., 1985) becoming fuel load for fires (van Wilgen, 2009). In our model we mark the difference between wet and dry periods, where different phenomena determine the dynamics of savanna.

Fires influence the woody structure and vegetation dynamics in humid savannas (Scholes and Archer, 1997; Peterson and Reich, 2001). As shown in field observations and fire exclusion experiments, the woody cover is negatively affected by fire occurrence (see e.g., Frost et al., 1986; Bond and van Wilgen, 1996). Humid savannas can be labeled as *fire-dependent* ecosystems (Bond et al., 2003), since woody cover is maintained low by fire occurrence and cannot reach the canopy closure that would be allowed by climate (Anderson and Brown, 1986; Bond and Keeley, 2005). Fires generally take place at the end of the dry season favored by the accumulation of dead grass (Sarmiento et al., 1985; Scholes and Archer, 1997). The probability of ignition and spreading depends on the density and continuity of the grass stratum in the dry season, therefore fire occurrence is closely linked to the amount of rainfall in the wet season: a high amount of rainfall cause a high amount of dead grass in the dry season and thus a high fire probability. Fire occurrence is not an exogenous variable, with its own return period, it is rather an emergent property of the ecosystem. This fact is widely recognized in literature (see e.g., van Wilgen et al., 2003; Govender et al., 2006), however accounted only in few models (D'Odorico et al., 2006; Beckage et al., 2011). In other savanna models, fire is described as a *Poisson* process (Baudena et al., 2010), or as a deterministic function of grass biomass (Accatino et al., 2010; De Michele et al., 2011; Staver et al., 2011a). In our model we treat fire occurrence as a *Bernoulli* random variable with a probability dependent on the status of the ecosystem, like in Beckage et al. (2011), and we do not refer to managed ecosystems, with a regular fire regime.

Trees are more or less vulnerable to fire depending essentially on their ability to escape the flame zone. In general trees can be easily damaged by fire when they are low, while they are more fire-tolerant once they escape the fire trap. Thus the distinction of trees in height classes is important because it puts in evidence the bottlenecks posed by fire on tree demography (Lehmann et al., 2009). This distinction, suggested by Sankaran et al. (2004) in their review article, has been inserted in some savanna models including Higgins et al. (2007), Staver et al. (2009), and Baudena et al. (2010).

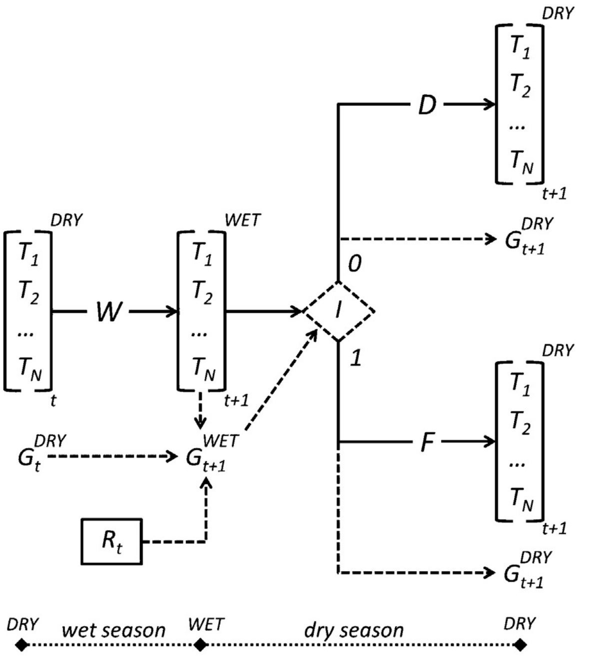

Fig. 1. Scheme of the seasonal model, discrete-time, of humid savanna with trees distinguished in *N* height classes, Eqs. (1)–(4).

3. A seasonal discrete-time model of humid savanna–forest dynamics

The model is time-discrete and spatially implicit. Each time step represents one year, and is partitioned in two sub-time steps representing the two seasons. If X represents the state variable, the notation X_t^S refers to the value of the variable at the end of season S of the year t, where $S \in \{WET, DRY\}$. The year begins with the wet season and the time succession of the variables is $X_{t-1}^{WET}, X_{t-1}^{DRY}, \ldots, X_{t+1}^{WET}, X_{t+1}^{DRY}, \ldots$

Space is accounted implicitly with the same approach of Tilman (1994). We consider a unitary area divided in sites and assume that one site contains one individual tree, regardless of its height class. Let $\mathbf{T} = [T_1, T_2, \ldots, T_N]'$ be the vector containing the fraction of sites occupied by trees belonging respectively to the height class 1, 2, ..., N, and G the total grass biomass density in the area (it is interpreted as *green* biomass in the wet season, and as *dead* biomass in the dry season). All the components of vector $\mathbf{T}$ range between 0 and 1, and their sum must not exceed 1. Components of vector $\mathbf{T}$ are dimensionless, whereas G is expressed in [tons/ha], being the use of different units not relevant. We assume that grass grows also under the canopy of trees, so that even if trees occupy all the sites, the presence of a certain amount of grass is not necessarily precluded.

The dynamics of trees are described by transition matrices (Caswell, 2001; Tuljapurkar and Horvitz, 2006) containing in the generic element (i, j) the proportion of trees of class j that move to class i at the end of the seasonal time step. All the elements of the transition matrices must range between 0 and 1, and the sum of each column must not exceed 1. If the sum of a column j is less than one, a proportion of trees of class j dies.

The conceptual scheme of the model is illustrated as follows (see also Fig. 1): in the wet season trees are updated and the amount of grass is determined by trees and rainfall. In the dry season, grass determines fire probability and trees are updated with different matrices according to the presence or absence of a fire.