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Eco-hydrology driven fire regime in savanna

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HIGHLIGHTS

- A new eco-hydrological predator–prey model for savanna wildfire is presented.
- Fire frequency arises as an ecosystem property from savanna composition.
- When grass fuel is scarce, fires are more frequent and less destructive.
- Dry and mesic savannas are characterized by different fire regimes.
- The vulnerability of trees to grass fire regulates the shift between the fire regimes.

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ABSTRACT

Fire is an important evolutionary force and ecosystem consumer that shapes savanna composition. However, ecologists have not comprehensively explained the functioning and maintenance of flammable savannas. A new minimal model accounting for the interdependence between soil saturation, biomass growth, fuel availability and fire has been used to predict the increasing tree density and fire frequency along a Mean Annual Rainfall (MAR) gradient for a typical savanna. Cyclic fire recurrence is reproduced using a predator prey approach in which fire is the “predator” and vegetation is the “prey”. For the first time, fire frequency is not defined a priori but rather arises from the composition of vegetation, which determines fuel availability and water limitation. Soil aridity affects fuel production and fuel composition, thus indirectly affecting the ecosystem vulnerability to fire and fire frequency. The model demonstrates that two distinct eco-hydrological states correspond to different fire frequencies: (i) at low MAR, grass is abundant and the impact of fire on the environment is enhanced by the large fuel availability, (ii) at higher MAR, tree density progressively increases and provides less fuel for fire, leading to more frequent and less destructive fires, and (iii) the threshold MAR that determines the transition between the two states and the fire frequency at high MAR are affected by the vulnerability of trees to grass fire.

The eco-hydrology-driven predator–prey model originally predicts that the transition between dry and wet savanna is characterized by a shift in wildfire frequency driven by major differences in soil moisture available for plants and savanna structure. The shift and the role of fire in conserving savanna ecosystems could not have been predicted if fire was considered as an external forcing rather than an intrinsic property of the ecosystem.

1. Introduction

The savanna question Sarmiento (1984) posed concerning the reason trees and grasses coexist in savanna stimulated the formulation of several hypotheses and modeling concepts; however, this ecological issue remains partially unresolved. Recent remotely sensed estimate of tree cover in Africa evidenced an increase of tree cover with MAR up to the threshold MAR $\approx 1000\ \mathrm{mm\ yr^{-1}}$ when tree closure is possible and bimodality of tree cover appears (Staver et al., 2011b). Whether the bimodality of tree density is globally widespread, and associated with a sharp transition between alternative stable states is unclear. Global patterns of tree density (Hirota et al., 2011) as well as fire manipulation experiments (Higgins et al., 2007) may be used to infer the resilience of tropical forest and savanna to critical transitions.

Indeed, whether savannas are intrinsically unstable systems maintained by disturbances such as fire and grazing or whether savannas are stable systems that persist despite these disturbances

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is unclear (Sankaran et al., 2004). Fire, grazing and rainfall may represent chance events for one or the other species (Archer et al., 1995; Bond and Keeley, 2005; Hoffmann et al., 2004; Scholes et al., 2002). Possible determinants of savanna structure include (i) competition and niche differentiation (e.g., root niche separation) with respect to limiting resources (e.g., water) (Walter, 1971; Walker et al., 1981; Walker and Noy-Meir, 1982; Eagleson and Segara, 1985; Fernandez-Illescas and Rodriguez-Iturbe, 2004; van Langevelde et al., 2003) and (ii) demographic bottlenecks to tree seedling germination and establishment (Menaut et al., 1990; Hochberg et al., 1994; Jeltsch et al., 1996, 2000; Higgins et al., 2000; van Wijk and Rodriguez-Iturbe, 2002; Gignoux et al., 2009). Resource based controls are modeled here with soil saturation dependent growth rates and tree carrying capacity, in order to predict the extent to which the niche differentiation between grass and trees may impact fire dynamics.

Fire could be a major cause of these bottlenecks in frequently burned savannas (Archer et al., 1995). However, fire ignites if enough fuel is present and if the fuel is dry (Liedloff and Cook, 2007). Recent catastrophic fire events have “ignited” the debate on the interconnection between climate and fire regime (e.g., Moritz, 2012). The frequency and the influence of fire are affected by climate, species composition and fuel availability. Introduced grasses can alter the fire regime (Gill et al., 2009), and fire suppression may cause species losses and the switch from savanna to forest ecosystems (Peterson and Reich, 2001).

Several minimal models analyze the impact of fire, grazing or climate on the stability of savanna, but none, as far as I know, accounts for the influence of climate on fuel production and, consequently, fire regime. Among others, Staver and Levin (2012) incorporated a positive grass–fire feedback into a simple space implicit model and demonstrated that bistability of tree cover is determined by fire feedbacks at intermediate rainfall, Beckage et al. (2009) developed a fire disturbance model incorporating fire-vegetation feedbacks and demonstrated that positive and negative feedbacks result in a stable savanna state. Beckage et al. (2011) used a stochastic modeling framework to demonstrate that a strong feedback between grass density and fire probability may stabilize savanna. Baudena et al. (2010) demonstrated that stochastic disturbances such as fire widen the parameter range over which tree–grass coexistence is expected. Accatino et al. (2010) showed that the co-existence of trees and grasses could be controlled by fire and rainfall scarcity.

In disturbance models (Accatino et al., 2010; Baudena et al., 2010; Beckage et al., 2009, 2011), fire is an external source of additional vegetation mortality. Using a substantially different approach, Casagrandi and Rinaldi (1999) assumed that fire could ignite via either lightening or human action in any year, provided that sufficient fuel (mainly grass) is present. Because the frequency of fire is not defined a priori, the ecosystem itself dictates the frequency and intensity of fire. Fire is a crucial determinant of tree cover at intermediate *MAR* (Staver et al., 2011a; Staver and Levin, 2012). Positive feedbacks between grass abundance and fire spread, and between tree establishment and rainfall, and a negative feedback between tree establishment and fire, ensure that at very low and high *MAR* tree cover is stable and determined by climate. Previous models accounting for the grass–fire feedback (Casagrandi and Rinaldi, 1999; Staver et al., 2011a; Staver and Levin, 2012) link the fire regime to the ecosystem characterization but neglect the influence of climate on growth of vegetation, fuel production and the environmental conditions for fire ignition that will be evaluated in this study.

Fire has been defined as a “global herbivore” (Bond and Keeley, 2005). In the following sections, the cyclic savanna fire regime is predicted by a predator–prey model, in which burning biomass is the predator and standing biomass is the prey. This new modeling concept is formulated to clarify if the observed increase in fire frequency along a MAR gradient (Sankaran et al., 2007) can be attributed to the interrelation between fuel production and fire-induced mortality of grasses and trees and the extent to which this interrelation is affected by niche competition. The classical predator–prey model, based on a two-species system (Lotka, 1920; Volterra, 1926), considers one predator and one prey in a static environment in which the food for prey is unlimited and exhibits only two types of behavior: static point and limit cycle. The model described in the following section is a two-predator–two-prey model, in which grass and trees are the prey and the burning grass and trees (the predators) feed on both vegetation species. The balance of fuel is not taken explicitly into account, but fuel (the dry biomass) is considered to be proportional to the living biomass. The two-predator–two-prey model can exhibit richer dynamics than the classical Lotka–Volterra model and includes chaos (Casagrandi and Rinaldi, 1999).

To account for the eco-hydrological interaction between climate, soil and vegetation, the model includes an ordinary balance equation for soil moisture in addition to the balance equations for two predators and two prey. The soil moisture balance equation drives the system of two-predator–two-prey to different behaviors as the hydrological forcing changes, including the static point (no fire regime), the limit cycle (with more or less frequent fire occurrence) or chaotic behavior (corresponding to a more complex structure of the fire occurrence), as demonstrated by Ursino and Rulli (2011) for a Mediterranean forest.

The interdependence between moisture, biomass and fire is introduced here for the first time in a minimal modeling framework to predict wildfire frequency in savanna. The minimal model is described in Section 2. The novel modeling framework may be used to evaluate the importance of fire versus resources in shaping the tree–grass composition of savannas, as well as to forecast the resulting wildfire regime in climate change scenarios. This study aims at testing new modeling hypotheses rather than reproducing site-specific behavior, although I also compared literature data with the model outcomes. First, the model equilibrium in the absence of fire was analyzed (Section 3). Second, the impact of soil moisture on the vegetation growth and thus on savanna composition was investigated (Section 4). Third, the model outcome was compared with real data (average tree density and fire frequency) along a MAR gradient (Section 5). The results are discussed in Section 6.

2. Model description

A conceptual implicit-space model describes the dynamics of trees, grass and soil moisture. Fuel load is proportional to vegetation biomass density. Fire ignites any time the fuel load is above a certain threshold then burns a fraction of the trees and grass that cover the soil, before becoming extinguished when the flammable fuel is depleted. The reduction in burning biomass density allows standing biomass to build up again until the following fire ignites after several growing seasons. Scarce moisture availability limits the biomass growth and may be ascribed either to low MAR or to large excess rainfall and low effective rainfall entering the soil, when intense and infrequent rainfall events occur. Here, effective rainfall is modeled as proportional to MAR. Neither the inter-annual variability of dry season length and rainfall abundance nor the daily variability of rainfall, soil moisture, temperature and wind is taken into account, even though they influence plant growth. Thus, the soil moisture variability is strongly interconnected with the fire regime and the changes of biomass density that fire determines. Because of its simplicity, the model allows the analytical calculation of the steady state in the absence of fire and