



Exploring the tug of war between positive and negative interactions among savanna trees: Competition, dispersal, and protection from fire



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ARTICLE INFO

Article history:

Received 13 May 2013

Received in revised form 12 November 2013

Accepted 25 November 2013

Available online 25 December 2013

Keywords:

Savanna

Tree–tree competition

Tree–grass equilibrium

Individual based model

Clustering

Fire-spread model

ABSTRACT

Savannas are characterized by a discontinuous tree layer superimposed on a continuous layer of grass. Identifying the mechanisms that facilitate this tree–grass coexistence has remained a persistent challenge in ecology and is known as the “savanna problem”. In this work, we propose a model that combines a previous savanna model Calabrese et al., 2010, which includes competitive interactions among trees and dispersal, with the Drossel–Schwabl forest fire model, therefore representing fire in a spatially explicit manner. The model is used to explore how the pattern of fire-spread, coupled with an explicit, fire-vulnerable tree life stage, affects tree density and spatial pattern. Tree density depends strongly on both fire frequency and tree–tree competition although the fire frequency, which induces indirect interactions between trees and between trees and grass, appears to be the crucial factor controlling the tree-extinction transition in which the savanna becomes grassland. Depending on parameters, adult trees may arrange in different regular or clumped patterns, the later of two different types (compact or open). Cluster-size distributions have fat tails but clean power-law behavior is only attained in specific cases.

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1. Introduction

Savanna ecosystems are characterized by the long-term coexistence of trees and grass. The mechanisms allowing for the persistence of both types of vegetation and governing the population dynamics and spatial arrangement of savanna trees are poorly understood (Scholes and Archer, 1997; Bond, 2008). Of the many potential driving mechanisms investigated, local-scale interactions among trees have received increasing attention in recent years (Barot et al., 1999; Wiegand et al., 2006; Meyer et al., 2008, 2007a,b; Scanlon et al., 2007; Calabrese et al., 2010). Such tree–tree interactions can roughly be divided into two classes: facilitative and competitive. Facilitation among trees promotes tree clustering and may be mediated by a variety of direct and indirect mechanisms such as limited-range dispersal, improvement of local resource conditions, and protection from fire (Belsky et al., 1989; Hochberg et al., 1994; Holdo, 2005; Scanlon et al., 2007; Calabrese et al., 2010). Alternatively, competition among trees for water, nutrients, and light may constrain tree density and

favor tree–grass coexistence, as well as promoting spatial separation between trees (Barot et al., 1999; Meyer et al., 2008; Calabrese et al., 2010).

There is evidence for both classes of interactions in the savanna literature. For example, several studies have found evidence consistent with competition in the Kalahari (Skarpe, 1991; Jeltsch et al., 1999; Moustakas et al., 2006, 2008; Meyer et al., 2008), while others have found evidence suggesting facilitation (Caylor et al., 2003; Scanlon et al., 2007). Indeed, one of the key difficulties in understanding the forces structuring savanna tree populations is that both classes of local-scale interactions often occur together and it is not obvious whether the net effect of local interactions on tree population dynamics will be positive or negative (Bond, 2008). Further studies, both empirical and theoretical, are needed to better understand the interplay between these opposing forces. Specifically, studies that focus on a limited number of processes and their interactions should help illuminate the conditions under which positive or negative local interactions structure savanna tree populations.

Semi-arid savannas often feature intense competition among trees, but fires in such systems do not occur frequently enough to play a major role (Sankaran et al., 2005; Bucini and Hanan, 2007). In contrast, fire often limits tree cover in humid savannas, but competition for water is much less intense (Sankaran et al., 2005;

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Bucini and Hanan, 2007). In-between these extremes, mesic savannas that receive 400–800 mm of mean annual precipitation (MAP) are particularly interesting because there is evidence from such systems that both tree–tree competition and fire play important roles (Sankaran et al., 2005; Bucini and Hanan, 2007). Both of these factors can act strongly on juvenile trees and can contribute to a demographic bottleneck through which juvenile trees must pass to recruit into the adult population. In contrast to forest tree species, savanna trees are often more fire resistant (Hoffmann et al., 2003), thus savanna fires effectively burn the grass layer and the young trees included in it, leaving adult trees alive, affecting only tree recruitment and not adult survival (Gignoux et al., 1997). Recent studies highlighting the importance of tree competition and/or fire on savannas are Higgins et al. (2000), Moustakas et al. (2006, 2008), D'Odorico et al. (2006), Hanan et al. (2008), Meyer et al. (2008), or Calabrese et al. (2010). From their results we might expect a kind of tug of war between these forces, the outcome of which affects both the tree–grass balance of the savanna and the spatial arrangement of adult trees.

The role of fire in mesic savannas is two-fold. On the one hand, it provides an indirect way for grass to compete against trees: the higher recovery rates of grasses compared to juvenile trees make grass the dominant form of vegetation shortly after a fire has destroyed both. On the other hand, several studies have suggested that adult trees can protect vulnerable juveniles from fire, thus increasing their chances of survival (Hochberg et al., 1994; Holdo, 2005), but this protection effect has not been intensively studied. However, given the frequent occurrence of fires in many savannas, it seems likely that the protection effect may be one of the most common facilitative interactions among savanna trees, and the dominance of grass after fire could be as important as tree–tree competition in restricting the amount of tree-cover in the savanna.

Recently, Calabrese et al. (2010) studied the interaction between competition and fire in a highly simplified savanna model. They showed that these two forces interact non-linearly with sometimes surprising consequences for tree population density and spatial pattern. However, because Calabrese et al. (2010) treated fire in a non-spatially explicit manner, only the negative impact on trees, and not the protection effect, was included and thus they could not fully tease apart how these contrasting local interactions function in combination.

Here, we focus on a spatially explicit lattice model of savanna tree and grass population dynamics under the influence of competition and fire. The model is an extension of the semi-spatial model studied by Calabrese et al. (2010). Importantly, both competition and fire are spatially explicit processes in the new model. This allows us to study directly how adult trees influence the survival probabilities of nearby juveniles. We treat competition in the same way as in Calabrese et al. (2010) and fire is implemented in a similar manner as in the Drossel–Schwabl forest fire model from statistical physics (Drossel and Schwabl, 1992). In contrast to adult trees in the Drossel–Schwabl model, grasses and juvenile trees are the flammable objects in our case. We highlight the ranges of conditions under which local interactions result in net positive and net negative influences on juvenile tree recruitment, and we demonstrate how these local interactions affect the density and spatial structure of adult-tree populations.

2. Methods

2.1. Spatially explicit fire models

Bak and Chen (1990) introduced a simple forest fire model to demonstrate the emergence of scaling and fractal energy dissipation. Drossel and Schwabl (1992) extended this model by

introducing a lightning or sparking parameter f , and this is the forest fire model we have adapted to study fire spread in savannas. It is one of the best studied examples of non-conservative, self-organized criticality (Bak and Chen, 1990; Grassberger and Kantz, 1991; Drossel and Schwabl, 1992; Clar et al., 1996, 1999; Schenk et al., 2000). The forest fire model is a probabilistic cellular automaton defined on a 2-dimensional lattice of L^2 sites, initialized with a combination of burning trees and live trees, and updated at each time-step with the following four simple rules: (i) a burning tree becomes an empty site. (ii) A live tree becomes a burning tree if at least one of its nearest neighbors is burning. Some immunity can be introduced in this rule, so that a green tree becomes a burning tree with probability $1 - I$ (Clar et al., 1996). (iii) A new tree establishes at an empty site with probability r . (iv) Live trees in the lattice spontaneously (i.e., without the need of a burning neighbor) ignite with probability f . This model displays very rich behavior, and depending on the parameters f and r , it features spiral-like fronts, critical states and phase transitions. Furthermore, while the Drossel–Schwabl model is minimalistic, it produces burn patterns similar to those observed empirically, and is closely related to more detailed wildfire models (Zinck and Grimm, 2009).

2.2. Savanna fire model (SFM)

Our model is run in a square lattice with periodic boundary conditions. We use a lateral size of $L = 200$ sites, so that there are $N = L \times L = 4 \times 10^4$ lattice sites in the simulation domain. Each site represents a savanna square of 5 m on a side. In the previous savanna model (SM) of Calabrese et al. (2010), each site in the lattice could be in one of two states: grass- or tree-occupied. The main parameters in this previous model were (i) the death rate: transition from tree- to grass-occupied state; (ii) dispersal rate: each site within the dispersal neighborhood of a tree receives seeds at this rate; (iii) competition intensity, and (iv) a parameter related to effects of fire on grass biomass appearing in the probability of surviving fire. This last parameter is not included in the new savanna fire model introduced here, since fire is implemented in an explicit way described in the following. The savanna fire model (SFM) introduced here combines the previous SM and the above-described Drossel–Schwabl forest fire model, but with the flammable components being grass and juvenile trees. In this way, fire is included explicitly as a possible state in the dynamics. The SFM considers three new states in addition to the two in the SM so that each site on the lattice can be in one of the following five states: grass (G), juvenile tree (JT), adult tree (AT), burning (B) and ashes (A).

As in the SM model we can distinguish two interaction neighborhoods for each lattice site: the *near* neighborhood consists of the eight sites sharing an edge or a corner with the central one (Moore neighborhood), and we assume this is the spatial scale at which direct competition among trees occurs. The *far* neighborhood consists of the sixteen additional sites surrounding the *near* ones and sharing edges or corners with them. They will be assumed to be the farthest sites to which seeds from a focal tree can arrive.

We note that fire propagation occurs over a much shorter timescale (the spread rate may be around 2 m/s, see Cheney and Gould (1995)) than tree growth, reproduction, death, and other ecological processes. Thus we implement the burning process on top of the previous SM, but acting on a faster scale. Specifically, we detail now our algorithm defining the SMF model: the initial condition is 10% of the sites in the lattice covered by randomly distributed adult trees, the rest of sites being in the grass state. At each time step, time advances by $\Delta t = 0.1$ years, and the whole lattice is scanned in parallel to check for one of the following updates:

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