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Spatial patterns in mesic savannas: The local facilitation limit and the role of demographic stochasticity

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HIGHLIGHTS

- Minimalistic savanna model with long-range competition and fire-induced local facilitation.
- Long-time coexistence of grass and trees. Clustering of trees may appear.
- Patterns in the system are determined by the long-range kernel competition function.
- Study the influence of demographic fluctuations in the patterns.
- Realistic patterns for mesic savannas under demographic noise and parameter constraints.

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ABSTRACT

We propose a model equation for the dynamics of tree density in mesic savannas which considers long-range competition among trees and the effect of fire indirectly acting as a local facilitation mechanism. Despite the fact that we take short-range facilitation to the local-range limit, the standard full spectrum of spatial structures already obtained in self-organization models of vegetation is recovered. Nonlocal competition, in the limit of infinitesimally short facilitation, promotes the clustering of trees. The long time coexistence between trees and grass, and how fires affect the survival of trees as well as the maintenance of the patterns is studied. The influence of demographic noise is analyzed. The stochastic system, under the parameter constraints typical of mesic savannas, shows non-homogeneous patterns characteristic of realistic situations. The coexistence of trees and grass still remains at reasonable noise intensities.

1. Introduction

Savanna ecosystems are characterized by the long-term coexistence between a continuous grass layer and scattered or clustered trees (Sarmiento, 1984). Occurring in many regions of the world, in areas with very different climatic and ecological conditions, the spatial structure, persistence, and resilience of savannas have long intrigued ecologists (Scholes and Archer, 1997; Sankaran et al., 2005; Borgogno et al., 2009; Belsky, 1994). However, despite substantial research, the origin and nature of savannas have not yet been fully resolved considering the diversity of ecological situations that are encompassed via the general concept of savanna.

Savanna tree populations often exhibit pronounced, non-random spatial structures (Skarpe, 1991; Barot et al., 1999; Jeltsch et al., 1999; Caylor et al., 2003; Scanlon et al., 2007). Much research has therefore focused on explaining how some types of spatial patterns observable in mesic savannas may arise (Jeltsch et al., 1996, 1999; Scanlon et al., 2007; Skarpe, 1991; Calabrese et al., 2010; Vázquez et al., 2010). In most natural plant systems both facilitative and competitive processes are simultaneously present (Scholes and Archer, 1997; Vetaas, 1992) and hard to disentangle (Veblen, 2008; Barbier et al., 2008). Some savanna studies have pointed toward the existence of short-distance facilitation (Caylor et al., 2003; Scanlon et al., 2007), while others have demonstrated evidence of competition (Skarpe, 1991; Jeltsch et al., 1999; Barot et al., 1999), with conflicting reports sometimes arriving from the same regions.

Different classes of savannas, which can be characterized by how much rainfall they typically receive, should be affected by different modalities of interactions between facilitation and competition. For example, in semiarid savannas water is extremely

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limited (low mean annual precipitation) and competition among trees, and more generally among all plants, is expected to be strong. However, fire plays little role because there is typically not enough grass biomass to serve as fuel. In contrast, humid savannas should be characterized by weaker competition among trees, but also by frequent and intense fires. In-between these extremes, in mesic savannas, trees likely have to contend with intermediate levels of both competition for water and fire (Calabrese et al., 2010; Sankaran et al., 2005, 2008; Bond et al., 2003; Bond, 2008; Bucini and Hanan, 2007).

Competition among trees is mediated by roots that typically extend well beyond the crown (Borgogno et al., 2009; Barbier et al., 2008). Additionally, fire can lead to local facilitation due to a protection effect, whereby vulnerable juvenile trees placed near adults are protected from fire by them (Holdo, 2005). We are particularly interested in how the interplay between these mechanisms governs the spatial arrangement of trees in mesic savannas, where both mechanisms may operate. On the other side, it has frequently been claimed that pattern formation in arid systems can be explained by a combination of long-distance competition and short-distance facilitation (Klausmeier, 1999; Lefever and Lejeune, 1997; Lefever et al., 2009; Lefever and Turner, 2012; Rietkerk et al., 2002; Hardenberg et al., 2001; D'Odorico et al., 2006a). This combination of mechanisms is also known to produce spatial structures in many other natural systems (Cross and Hohenberg, 1993). Although mesic savannas do not display the same range of highly regular spatial patterns that arise in arid systems (e.g., tiger bush), similar mathematical mechanisms might be at work. Specifically, the interaction between long-range competition and short-range facilitation might still play a role in pattern formation in savanna tree populations, but only for a limited range of parameter values and possibly modulated by demographic stochasticity.

Although the facilitation component has often been thought to be a key component in previous vegetation models (D'Odorico et al., 2006a, 2006b; Rietkerk et al., 2002; Scanlon et al., 2007), Rietkerk and van de Koppel (2008), speculated, but did not show, that pattern formation could occur without short-range facilitation in the particular example of tidal freshwater marsh. In the case of savannas, as stated before, the presence of adult trees favors the establishment of new trees in the area, protecting the juveniles against fires. Considering this effect, we take the facilitation component to its infinitesimally short spatial limit, and study its effect in the emergence of spatially periodic structures of trees. To our knowledge, this explanation, and the interrelation between long-range competition and local facilitation, has not been explored for a vegetation system. One of our main results is that when considering the limit of local facilitation and nonlocal competition, clustering of trees appears.

Here we develop a minimalistic model of savannas that considers two of the factors, as already mentioned, thought to be crucial to structure mesic savannas: tree-tree competition and fire, with a primary focus on spatially nonlocal competition. Employing standard tools used in the study of pattern formation phenomena in physics (stability analysis and the structure function) (Cross and Hohenberg, 1993), we explore the conditions under which the model can produce non-homogeneous spatial distributions. A key strength of our approach is that we are able to provide a complete and rigorous analysis of the patterns the model is capable of producing, and we identify which among these correspond to situations that are relevant for mesic savannas. We further examine the role of demographic stochasticity in modifying both spatial patterns and the conditions under which trees persist in the system in the presence of fire, and discuss the implications of these results for the debate on whether the balance of processes affecting savanna trees is positive, negative, or is variable among systems. This is the framework of our study: the role of long-range competition, facilitation and demographic fluctuations (in the second part of the paper) in the spatial structures of mesic savannas. To complete our work we include Appendix D, where we study the effect of external fluctuations (mimicking for example rainfall) on savanna dynamics.

Our model is inspired by the one presented by Calabrese et al. (2010). It complements theirs by providing further analytical results that clearly demonstrate that this simple system, where we focus on the local limit of facilitation, can produce the full spectrum of spatial patterns reported from models employing both short-range facilitation and long-range inhibition (competition).

2. The deterministic model

In this section we derive the deterministic equation for the local density of trees, such that dynamics is of the logistic type and we only consider tree-tree competition and fire. We study the formation of patterns via stability analysis and provide numerical simulations of our model, showing the emergence of spatial structures.

2.1. The nonlocal savanna model

Calabrese et al. (2010) introduced a simple discrete-particle lattice savanna model that considers the birth-death dynamics of trees, and where tree-tree competition and fire are the principal ingredients. These mechanisms act on the probability of establishment of a tree once a seed lands at a particular point on the lattice. In the discrete model, seeds land in the neighborhood of a parent tree with a rate b, and establish as adult trees if they are able to survive both competition by neighboring trees and fire. As these two phenomena are independent, the probability of establishment is $P_E = P_C P_F$, where P_C is the probability of surviving the competition, and P_F is the probability of surviving a fire event, both dependent on the tree density. From this dynamics, we write a deterministic differential equation describing the time evolution of the global density of trees (mean field), $\rho(t)$, where the population has logistic growth at rate b, and an exponential death term at rate α. It reads

$$\frac{d\rho}{dt} = bP_E(\rho)\rho(t)(1-\rho(t)) - \alpha\rho(t). \tag{1}$$

Generalizing Eq. (1), we propose an evolution equation for the space-dependent (local) density of trees, $\rho(\mathbf{x}, t)$:

$$\frac{\partial\rho(\mathbf{x}, t)}{\partial t} = bP_E\rho(\mathbf{x}, t)(1-\rho(\mathbf{x}, t)) - \alpha\rho(\mathbf{x}, t). \tag{2}$$

We allow the probability of overcoming competition to depend on tree crowding in a local neighborhood, decaying exponentially with the density of surrounding trees as

$$P_C = \exp\left(-\delta \int G(\mathbf{x}-\mathbf{r})\rho(\mathbf{r}, t)\, d\mathbf{r}\right), \tag{3}$$

where δ is a parameter that modulates the strength of the competition, and $G(\mathbf{x})$ is a positive kernel function that introduces a finite range of influence. This model is related to earlier models of pattern formation in arid systems (Lefever and Lejeune, 1997), and subsequent works (Lefever et al., 2009; Lefever and Turner, 2012; Borgogno et al., 2009), but it differs from standard kernel-based models in that the kernel function defines an interaction neighborhood, and it has not information about the type of interaction depending on the distance. Note also that the nonlocal term enters nonlinearly in the equation.