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Vegetation, herbivores and fires in savanna ecosystems: A network perspective

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ABSTRACT

The dynamics of savanna ecosystems depends on the interplay between multiple factors such as grazing, browsing, fires, rainfall regime and interactions between grass and woody vegetation. In most modelling applications this interplay may not be fully understood because some of these drivers enter the models as dynamically independent factors. In this paper we consider such factors as dynamic variables. To analyze their interplay we focus on the structure of the interactive network of variables and exploit the properties of signed digraphs using the algorithm of Loop Analysis. Qualitative signed digraphs for the savanna ecosystem are developed and their predictions used to interpret patterns of abundance observed in case studies selected from the literature. The outcomes of this exercise unveil that: 1) the structure of the interactions is appropriate locus for the explanation of patterns observed in savannas; 2) signed digraph can help disentangling causative mechanisms by linking correlation patterns, source of change and network structure. This study highlights that central to the understanding of savanna dynamics is our ability to diagram the important relationships and understand how they interrelate with sources of variations to cause ecosystem change.

1. Introduction

Savannas are defined as seasonal ecosystems characterized by the co-dominance of a continuous herbaceous stratum, dominated by C4 grasses, and a discontinuous layer of fire-tolerant shrubs and trees (Walker and Noy-Meir 1982; Ratnam et al., 2011). Further identification of savannas exists on the basis of their structure and on the environmental conditions (Cole, 1986). Savannas are geographically widespread and cover approximately a fifth of the world's land surface (Sankaran et al., 2004); they also represent a key carbon sink with respect to global biogeochemical cycles (Thiessen et al., 1998). Savannas are socio-economically important ecosystems because they support a large and fast growing proportion of the world's population and the bigger part of their livestock (Scholes and Archer, 1997). Also, tropical and sub-tropical savannas host a large number of species under extinction risk; because of this they are considered key ecosystems for biodiversity conservation (Gill, 2015).

The mechanisms that govern the evolution and allow the maintenance of savannas have long been the target of investigation (Dublin et al., 1990; Sankaran et al., 2004; Staver et al., 2011). It has been generally accepted that characteristic, across site (Archer, 1989; Adamoli et al., 1990; Savage and Swetnam, 1990; Kaufmann et al., 1994) patterns of co-occurrence for woody and grass vegetation depend on a complex interplay between grazing, browsing, rainfall and fire intensity (Scholes and Archer, 1997; Higgins et al., 2000; Sankaran et al., 2008). Disentangling this interplay has become a major focus of investigation (McNaughton, 1992; van Langevelde et al., 2003; Holdo et al., 2009; Holdo, Sinclair et al., 2009) and observed patterns were analyzed using both statistical (correlation, linear and multiple regression analysis, Roques et al., 2001; regression tree analysis, Sankaran et al., 2008; Bayesian state space models, Holdo et al., 2009; Holdo, Sinclair et al., 2009) and mathematical models (stability analysis of equilibria, Higgins et al., 2010; De Michele et al., 2011; Holdo et al., 2012).

Modelling applications greatly contributed to our knowledge about conditions for co-existence, bi-stability, limit cycles and feedback mechanisms in savanna ecosystems. Most of these models, however, considered only grass and trees as dynamic variables whereas other key factors such as herbivores, browsers, fires and rainfall were treated as positive or negative contributions

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to the rate of change of the variables via parameter estimation (van Langevelde et al., 2003; Higgins et al., 2010; Staver et al., 2011; Bekage et al., 2011; De Michele et al., 2011; but see Holdo et al., 2012). By these models only the dynamics of grasses and trees in respect to each other and under the effect of external drivers that were set up at different levels (i.e. levels of browsing, grazing, or fire intensity) could be investigated. This approach treats the drivers as independent factors that are not influenced by the dynamic variables, and do not affect each other.

Nevertheless browsers and grazers as well as fires may be dynamically affected by the vegetation variables and through them may also indirectly interact with each other (McNaughton, 1992; Holdo et al., 2009; Holdo, Sinclair et al., 2009). Including these factors as variables in a model can better portray the complex dynamics of savanna ecosystems and possibly enlarge our comprehension of how these ecosystems function. This paper focuses on savannas as multi component systems, in which factors that are commonly assumed as dynamically independent enter as dynamic variables.

When the number of interacting variables augments, multiple linkages are established. One obvious consequence is that complexity increases: for example system feedbacks may become intricate and their effects difficult to disentangle (Lane, 1998). The effects of such complex interactions must reflect on dynamical patterns; therefore to examine the structure of the interactions may contribute to unveil how patterns are produced. According to this, we focus here on the linkage structure that is established when woody plants, grass, browsers, grazers and fires dynamically interact. In particular we analyze how the structure of the interactions mediates the response of the variables to external press perturbations that change the parameters that govern the growth rate of the variables (Bender et al., 1984, Puccia and Levins 1986).

The objective of this exercise is twofold: a) we want to explore to what extent the structure of the interactions may explain observed patterns in savanna ecosystems; b) we examine how the analysis of the linkage structure can help interpret those patterns in terms of cause and effect. Thus, finding some new mechanism responsible for patterns in savanna ecosystems is not among the objectives of this work; rather by this study we attempt to frame known mechanisms in the perspective offered by the analysis of the network of the interactions.

To accomplish this exercise we exploited the qualitative properties of signed digraphs by means of the algorithm of Loop Analysis (Levins 1974; Puccia and Levins, 1986). This technique precludes any quantitative statement but it offers the opportunity to connect in a causal perspective the structure of the linkages between the variables and their patterns of variation (Dambacher and Ramos-Jiliberto, 2007).

Central in this effort was our ability to diagram the important causal relationship and understand how they interrelate. Signed digraphs were assembled on the base of commonly accepted interactions between the variables. Alternative models were developed and selected according to their ability to capture and describe observed patterns that were reported in selected case studies that we extracted from the literature.

2. Methods

2.1. Qualitative modelling

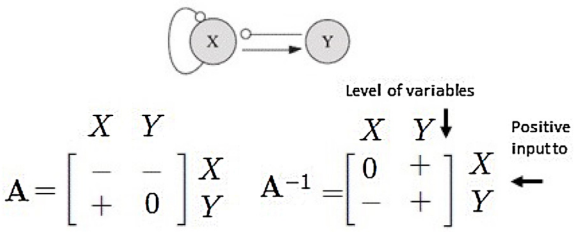
Qualitative models are used here *sensu* Puccia and Levins (1986). A qualitative model graphically represents interactions between variables in a system using only two types of connections: arrow (→) for positive effect and circle-head link (—◯) for negative effect. Effects are dynamical as they refer to the action of one variable on the growth rate of another: arrow and circle-head links originate from the signs of the coefficients of the Jacobian matrix for a system of differential equations (Puccia and Levins, 1986, see Appendix A in the Supplemental on line material, SM henceforth).

Using qualitative mathematics to analyze pathways and system feedbacks, allows the making of predictions about a variable's response to perturbations. Any perturbation emanates from the affected variable and it is transmitted along direct and indirect pathways to other variables. Such pathways determine the qualitative direction of change (i.e., whether a variable increases, decreases or remains the same) as modulated by the feedbacks formed by all the variables in the system. For relatively small systems (i.e., <5 variables), this can easily be accomplished through direct analysis of the signed digraph (Puccia and Levins, 1986, SM, Appendix A). Fig. 1 shows a simple predator-prey model as a signed digraph.

The interaction between a predator and its prey gives rise to a negative feedback. A feedback is always associated to a loop. In Fig. 1 this loop can be easily visualized by following the direction of the links: from X (Y) to Y (X) and back. This loop produces a negative feedback, according to the product of the links that make the circuit. Now suppose something happens that makes the rate of change of X increase (i.e. its fecundity augments). Some of this impact would be passed along to Y (the more prey the more predators). The final outcome will be a change in Y proportional to the magnitude of the intervention on X multiplied by the strength of the link from X to Y (effect pathway) divided by the "gain" or "feedback" of the whole system. This latter factor measures the resistance of the whole system to change. If there are no other variables in the system then our naïve expectation about this change would be easily met, depending on the relative magnitude of the links and feedbacks. A detailed explanation of how these concepts refer to a graphical algorithm to make predictions is given in the Appendix A of the SM.

In larger and more complex systems, there can be a very high number of pathways (both direct and indirect) between input and response variables; this can make graphical feedback analysis difficult. In such circumstances, one can calculate response predictions from mathematical operations on the community matrix (matrix A in Fig. 1). Hence, the net effect (the sum of the direct effects plus all the individual indirect effects) on variable i resulting from a perturbation on variable j is given by the $j-i^{th}$ element of the inverse community matrix $[A]^{-1}$. The signs of the coefficients of the inverse of the community matrix give the directions of change expected for the variables following parameter changes in the equations of the variables themselves (Montoya et al., 2009).

To obtain robust predictions we used a routine that randomly assigns numerical values to the coefficients of the community matrix (i.e. the coefficients of the links in the signed digraph).



$$\mathbf{A}=\begin{array}{cc|c} X & Y & \\ - & - & X \\ + & 0 & Y \end{array} \qquad \mathbf{A}^{-1}=\begin{array}{cc|c} X & Y\downarrow & \\ 0 & + & X \leftarrow \\ - & + & Y \end{array}$$

Fig. 1. Graph of a predator-prey system, its community matrix (A) and the matrix of predictions (A^{-1}). Predictions can be read as follows: for a press perturbation that increases the rate of change of X (positive input) no variation $(a_{XX})^{-1}=0$ is expected for X itself and an increase $(a_{YX})^{-1}=+$ is predicted for Y.