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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.

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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 (\rightarrow) for positive effect and circle-head link ($\rightarrow\bigcirc$) 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 $j - i^{\text{th}}$ 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).

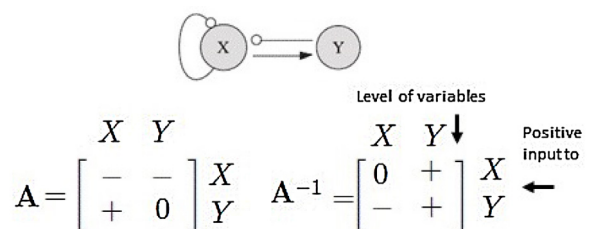


Fig. 1. Graph of a predator-prey system, its community matrix (A) and the matrix of predictions (A^{-1}). Predictions can be read as follows: for a press perturbation that increases the rate of change of X (positive input) no variation $(a_{XX})^{-1} = 0$ is expected for X itself and an increase $(a_{YX})^{-1}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

Numerical values are extracted from a uniform distribution. This procedure was executed, for each model, $N \times N \times 100$ times, where N is the dimension of the matrix A . Of these matrices, only those that satisfied the asymptotic Lyapunov criteria (Logofet, 1993) were accepted and inverted. On this set of inverse matrices the routine calculated predictions. Each prediction becomes a probability of sign determined on the base of the percentage of positive signs, negative signs and zeroes that characterize the response of a given variable over the entire set of the matrices. To compile the final table of predictions a set of rules has been defined to translate the percentage of cases obtained from simulation into signs. According to these rules a variable is expected to increase if the sign + appears in 75% or more of the matrices (this means that 25% or less of the matrices yield a negative sign). If this percentage is between 60% and 75% we considered a likely tendency to increase (it is signaled by the “?” in the table of predictions). If the percentage of + is between 40% and 60% the routine considered that variable as remaining the same (“0”), pathways carrying positive and those responsible for negative effect compensate each other). These rules hold also for the negative signs. All routines were written in R language. The code used for the simulations is in the SM (Appendix A)

By predicting directions of change for the variables in response to parameter variations entering as input in a system, qualitative models can also predict correlation patterns between variables. If two variables change in the same direction in response to a particular input, then they will show positive correlation over a range of that parameter. If they change in opposite directions they will show a negative correlation. If one or both show a null response, this input would result in no correlation between the variables. Predictions can thus be used to analyze observed correlation patterns (Puccia and Levins 1986; Bodini, 2000).

The qualitative approach that is used in this exercise (i.e. loop analysis) exploits the properties of signed digraphs. These latter have a long history in ecological applications: because of their versatility they have been used in different contexts and with different goals. In the early 1970s they supported scholars in their effort to unveil stability properties of ecosystems (Jeffries, 1974; Levins, 1974). As a convenient way to represent who eats whom in the ecosystem they have been used to understand keystone species (Liu et al., 2010) and energy delivery in ecosystems (Allesina et al., 2005; Bellingeri and Bodini, 2016). Because they pictorially describe multiple interactions between dynamic variables they have become ideal tools to represent the structural complexity of ecosystems and the possibility they offer to analyze paths and feedbacks have been exploited to understand ecosystem response to change. In this framework they have greatly contributed to the development of the ecosystem based management approach (Dambacher et al., 2007; Carey et al., 2013).

2.2. Savanna qualitative models

2.2.1. The core model

Several models for the persistence of tree-grass mixtures in savannas have been advanced thus far. These models can be divided in two groups: one set considers these systems as governed by competition based mechanisms; the other group concentrates on demographic mechanisms where disturbance factors such as fires, herbivores and rainfall play a decisive role. In this paper we do not give prominence to one view over the other; rather, we focus on how each variable interacts with the others so that a whole linkage structure is reproduced. No single model can account for the variety of phenomena at all savanna locations, and the range of behaviors exhibited at one location in different seasons or stages of succession is quite diverse (Scholes and Archer, 1997). The models we present here have been conceived to

emphasize on realism and generality (Puccia and Levins 1986; Knapp et al., 2004) and necessarily leave out details in favor of a more general representation, the typical approach that qualitative analysis privileges.

According to the bulk of the literature, core variables for savanna ecosystem models are the biomass of grass and woody vegetation (Scholes and Archer, 1997). Trees and grasses are said to compete for water in the upper soil profile, and grass is a superior competitor for this resource (Le Roux et al., 1995). Trees however have exclusive access to deeper water (Schenk and Jackson, 2002; van Langevelde et al., 2003). Percolation of water from the upper to the lower soil profile is a recognized mechanism through which deep water reserves are fed by rainfall (Le Roux et al., 1995).

Grasses and trees negatively affect each other. The negative effect of trees on grass may result from rainfall interception, litter accumulation, shading, root competition or a combination of these factors (Scholes and Archer, 1997). Direct effect of grass on woody vegetation is described as reducing emergence, growth and survival of woody seedlings, but these effects rarely cause high mortality (Scholes and Archer, 1997). So the assumption that tree-grass competition is asymmetrical seems plausible (Holdo et al., 2009; Holdo, Sinclair et al., 2009).

Four variables were then used to build up an initial core model for the system: in addition to grasses (G , in the model) and woody vegetation (W), we included water that resides in the upper soil profile (w_1) and water in the deeper layer (w_2). Grass biomass consists of both grasses and herbs; woody biomass consists of wood, twigs, small trees and shrubs. With the support of a large body of literature (see e.g. Scholes and Archer, 1997 and references there in) we delineated 8 possible alternative structures for this core model. Alternative graphs present different hypothesis about interactions. In the literature G and W have been described as interacting each other either through reciprocal inhibition, one way inhibition, in general from woody vegetation to grass, or no interaction at all. This may depend on the different magnitude of the effects. For example, Scholes and Archer (1997) posited that the competitive effect of grass on woody plants may not be as intense as to heavily affect the growth of this latter component. In this case the one way inhibition from W to G seems a reliable representation for their interaction. In some cases, trees may also benefit on grasses, because they can mitigate harsh environmental conditions, modify substrate characteristics or increase resource availability (Belsky and Canham, 1993; Callaway, 1995). Given this multiplicity of effects the way one can represent the way W affects the growth rate of G must necessarily be the net effect of the positive and the negative actions.

The two water reserves are not independent from one another. Water in fact percolates down to the subsoil. Water percolation depends on a number of factors, among which the soil type plays a key role. So it may be that this supply may become null in certain combinations of soil type and rainfall regime (Ludwig et al., 2004; van Langevelde et al., 2003). Water percolation is depicted as a positive effect from w_1 to w_2 . W and G are self-damped variables. This reflects the regulation that is set up both by internal competition and the regulative effect of other variables that are not explicitly considered in the model (Levins, 1974; Bodini, 2000), such as inorganic nutrients. Finally, the self-damping on water resources (w_1 and w_2) depends on the continuous supply of water from rainfall and underground fluxes. If these fluxes depended completely on percolation then w_2 resulted not to be self-damped. Qualitative analysis requires that a set of models are developed for any given system. This is a necessary step so that various assumptions about the structure of the interactions can be tested. As many as 8 alternative graphs for the core model were developed. They are presented in the SM (Appendix B).

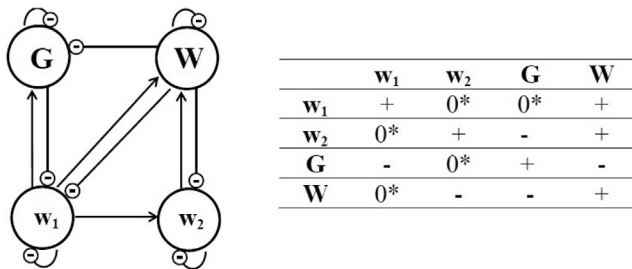


Fig. 2. Woody-grass core model for the savanna ecosystem: signed digraph and table of predictions. Keys are: W woody plants; G grasses, w₁ superficial water table; w₂ deep water table. The table shows predictions assuming positive input on the row variables. Effects of negative inputs are obtained by simply reversing the signs.

The model in Fig. 2 seems the most reliable reconstruction of relevant interactions between the variables for the core model. It corresponds to graphs “g” among the 8 alternative schemes presented in the SM (Appendix B). It was after the comparison of model predictions with evidences reported in the literature (see Results) that we selected this graphs as the most reliable description of the structure of the interactions for this system.

2.2.2. Herbivores action

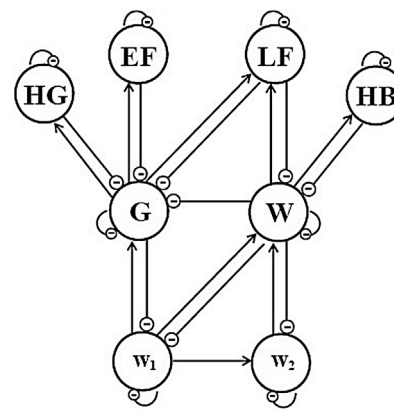
Direct and indirect effects of large herbivores are also believed to be very important regulators of variations of woody and grass biomass in space and time (van der Waal et al., 2011; Goheen et al., 2010; Roques et al., 2001; Dublin et al., 1990). Large herbivores modify plant recruitment and establishment by eating, trampling, urinating and trashing, which kill or damage plant individuals (McNaughton et al., 1988). Depending on feeding habits and physiology, it is common to distinguish between two main groups of large herbivores: those that feed mainly on woody species, or *browsers*, and those feeding on herbaceous vegetation, or *grazers*. Browsers (i.e. elephants, *Loxodonta africana* Blumenbach), heavily affect trees abundance and woody vegetation dynamics (Asner and Levick, 2012; Jeltsch et al., 2000). Their activity is expected to curb tree growth (Staver et al., 2009; Sharam et al., 2006). Experimental studies showed that tree growth, recruitment and survival increased following a reduced browsing pressure (Daskin et al., 2016; Staver et al., 2009; Asner and Levick, 2012).

Grazing is also a key regulative process because it influences grass competitive ability and fire frequency (Staver and Bond, 2014). Its role was extensively treated in the literature due to its importance for the associated socio-economic impacts (see Ellis and Swift, 1988 for a synthesis on grazing systems and development; Scholes and Archer, 1997 and references there in; Roques et al., 2001). Intensive grazing reduces the grass standing crop, which is the main fuel for fires in savannas (Trollope, 1996); as a consequence, both fire intensity and frequency are reduced. This in turn can increase the competitive advantage of the woody species (Adamoli et al., 1990; Kaufmann et al., 1994; Trollope, 1996). In some cases prolonged and intensive livestock or wildebeest grazing associated with low fire frequency or intensity results in shrub encroachment (Goetze and Hörsch, 2006; Briggs et al., 2002).

Feeding mechanisms can thus be represented as two distinct resource-herbivore interactions (Fig. 3): browsers (HB) consume woody and shrub vegetation (W); grazers (HG) feed on grass (G).

2.2.3. Fire disturbance

Fires are considered fundamental regulative elements of the savanna's vegetation structure, and a driving force that played a key role in the formation of savanna ecosystems. In Africa, for



	w ₁	w ₂	G	W	HG	HB	EF	LF
w ₁	+	+	0*	+	0*	+	0*	+
w ₂	-	+	-	+	-	+	-	?+
G	-	0*	+	-	+	-	+	+
W	-	-	-	+	-	+	-	?+
HG	+	0*	-	+	+	+	-	-
HB	+	+	+	-	+	+	+	?-
EF	+	0*	-	+	-	+	+	-
LF	+	+	-	?-	-	?-	-	+

Fig. 3. Graph representing the enlarged savanna model and its table of predictions. Grazers (HG) and browsers (HB) feed on grass (G) and woody plants (W) respectively. Early fires (not intense, EF) consume grass vegetation, whereas late fires (intense, LF) interact with both grass and woody plants.

example, fires and vegetation coexisted at least since the quaternary period (Kershaw et al., 1997). Currently, a very small proportion of fires in savanna comes from lightning, whereas the bulk of fire events have anthropogenic origin.

Many parameters can describe fire activity in a given ecosystem, like fire intensity, frequency and burning season (Gregoire, 1996; Clerici et al., 2004). Fire intensity is generally considered the most important factor affecting the dynamics of savannas (Liedloff et al., 2001). It is controlled by several parameters: amount of grass biomass (main fire fuel), grass moisture content, wind speed and air temperature (Sawadogo et al., 2005).

Fires that occur during the early dry season are generally of low intensity, due to the high moisture content of the grass vegetation; low intensity fires have little or no effects on the survival of the woody vegetation (Liedloff et al., 2001). Late-dry-season fires, on the contrary, are more intense due to the very low moisture content in the grass fuel. Intense fires thus can heavily damage woody plants and increase their mortality (Brookman-Amisshah et al., 1980; Hochberg et al., 1994). A number of studies reported that in African savanna woodlands repeated intense, late dry-season fires reduced woody biomass. Hot fires damage adult plants and kill individuals in the smaller size classes: individuals of woody species with a height less than 2 m can be killed or have a retarded growth (Trollope, 1987; Hochberg et al., 1994; van Langevelde et al., 2003).

Grasslands and savannas herbaceous plants are hardly killed by fire (van Langevelde et al., 2003). Oliveras et al. (2013) found that total aboveground biomass of herbaceous vegetation in a neotropical savanna was not affected by a variety of fire treatments of varying intensity. In South African savannas fires distributed in a gradient of intensity (from 925 to 3326 kJ/s/m) were examined for their effects on vegetation and evidences were that intensity had no significant influence in the recovery process of grass sward in

the two growing seasons after the burns (Trollope and Tainton, 1986). On the other hand, Trollope (1982) found that repeated burnings in arid savannas could negatively influence grass production when in combination with water stress. According to these evidences we decided to include two fire variables in our models (Fig. 3). They are early (EF) and late fires (LF), which can be also classified as non-intense and intense fires, respectively. We assumed that only intense fires (LF) have a direct control on woody vegetation. Grass biomass, on the other hand, is the main fuel for fires (Trollope, 1987), so it is depicted as positively affecting both intense and not intense fires.

Starting from the core model depicted in Fig. 1 we developed five graph models in which herbivores, browsers and fires variously interacted. All the graphs include interactions that could be deduced from literature, so they are plausible ecologically. Alternative structural hypothesis however have been considered due to uncertainty about certain links that emerged from the literature analysis. These five graphs and their analysis are presented in the SM (Appendix D). Here, the graph in Fig. 3 represents the most reliable representation of the system given the correspondence between predictions and evidences presented in various pieces of the literature.

3. Results: predicting observed patterns

The model in Fig. 2 has been selected among a set of 8 alternative graphs (SM, Appendix B). Its predictions design qualitative trajectories of change for the variables that may explain, better than the other models do, the patterns observed or predicted in previous studies. Walker and Noy-Meir (1982) indicated rainfall as a key driver for the transition from grassland to savanna to woodland. In their stability analysis van Langevelde et al. (2003) reiterated that increasing water availability may induce that transition. In northern hemisphere African savannas, scholars observed an increase in mean precipitation towards the Equator, with an associated increasing latitudinal gradient in tree dominance (Mayaux et al., 2004).

To simulate the effect of increased rainfall in the model of Fig. 2, we assumed positive parameter changes on both w_1 and w_2 . Precipitations in fact increment the rate at which water becomes available in the grass root zone (positive input to w_1). If rainfall increases so that the soil moisture content is exceeded, water starts to percolate in the woody plant root area and the rate of change of w_2 increases as well. The model predicts that a positive input to w_1 (first row of the table in Fig. 1) leaves G unaffected while increasing W . The positive input to w_2 (second row of the table) decreases G and increases W . Overall the model shows that an increasing rainfall regime and water availability tends to reduce G in favor of W , in agreement with the transition from grass to woody vegetation that the above cited authors observed or predicted. The intensity at which this phenomenon occurs determines the final state of the system, but the model correctly grasps the qualitative trajectory of the effect.

The model suggests that increasing percolation in the deeper layer is necessary to speed up the transition from grassland to woodland. A unique, positive input to w_1 (simply increasing the rainfall regime) in fact would leave the level of grass vegetation unchanged. This outcome would not be immediately predictable from the analysis of the pathways. Any impact affecting w_1 in fact spreads to G along three different pathways of interaction: the direct link ($w_1 \rightarrow G$), the path through W ($w_1 \rightarrow W \rightarrow oG$) and the pathway ($w_1 \rightarrow w_2 \rightarrow W \rightarrow oG$). These indirect pathways both carry a negative effect to G (the effect is product of the sign of the links that make the pathway, see SM Appendix A). The direct link has, instead, a positive effect. Thus according to the sole number of

pathways one would expect G to decrease (2 to 1 in favor of a diminishing effect).

The percentage of simulated cases (see SM, Appendix B, model g) in which the positive effect prevails is greater than that in which the negative effect predominates (56% and 44% respectively), but it remains within the range (40%–60%, see Methods and SM Appendix A) for which negative and positive effects compensate for each other and the prediction is considered null.

Two reasons can explain this outcome. First is the balance between positive and negative feedbacks. The direct pathway ($w_1 \rightarrow G$) contributes a negative feedback at level F_2 (SM Appendix C), whereas the paths ($w_1 \rightarrow W \rightarrow oG$) and ($w_1 \rightarrow w_2 \rightarrow W \rightarrow oG$) produce positive feedbacks at level three and four (SM Appendix C). It might thus happen that the whole matrix becomes unstable when these positive feedback become stronger for certain combinations of links value. In this case an excess quota of positive feedback enters the model causing the matrix to be unstable. Because only stable matrices are accepted to calculate predictions, it follows that cases in which the two pathways that carry a negative effect prevail over the direct link ($w_1 \rightarrow G$) may not take part in the calculation of the predicted change (for stability reasons). The stability analysis for this model is given in detail in the SM (Appendix C).

The other reason is that the contribution of pathways becomes of minor importance as their length increases. Link strength in fact is within the interval 0–1 and the intensity of each path is the product of the magnitude of the links that compose it. Accordingly, the longer the pathways the lower its magnitude can be.

In areas where sandy soils dominate, water infiltration rate increases, with beneficial effects on woody biomass, at the expenses of grass (van Langevelde et al., 2003). Still, this situation reflects in a positive input to w_2 , as the rate of change of this variable depends on the link ($w_1 \rightarrow w_2$) which describes water percolation rate. For positive input to w_2 we expect woody biomass W to increase whereas grass will be declining. When the amount of infiltrated water decreases, trees may find harsher environmental conditions and woodland may become savanna. This corresponds to a negative input to w_2 , which yields a diminution for W and an increase for G .

The presence of fires and herbivory shapes the model according to the graph illustrated in Fig. 3. In this model the responses of grass and woody vegetation to external impacts entering w_1 , w_2 , G and W coincide with those of the core model.

Roques et al. (2001) conducted a detailed long term (50 years, from 1947 to 1997) experimental study to investigate the dynamics of shrub encroachment in respect to fires, grazing activity and rainfall in the Lowveld savanna of Swaziland, South Africa. They found a strong negative correlation between grazing pressure and fires, which was accompanied by a positive relationship between shrub encroachment and grazing pressure. In addition, shrub encroachment showed a negative relationship with fire frequency. Finally they found that low rainfall resulted in a decline of shrub cover, whereas high rainfall favored shrub encroachment.

Over the whole period of study a general increase in shrub cover characterized the area. According to the correlation patterns above described this would be accompanied by a reduced frequency of fires and by an increased grazing pressure. These authors analyzed trends of grazing pressure, probability of fires, and shrub cover (Roques et al., 2001, Figs. 2 and 3) and concluded that high grazing pressure in the area promoted shrub encroachment indirectly through fires.

The table of predictions associated to the model in Fig. 3 shows variations expected in the level of the model's variables (number of individuals or biomass). Each variable's response to the different inputs that affect any row variables can be read along its column. According to the correlation patterns observed by Roques and

coauthors a variation in the level of grazers (HG)¹ should be accompanied by a change in woody plants (W) of the same type, whereas fires should change in the opposite direction. If we scroll down the columns of W and HG, positive covariations between these two components occur only in two cases: input to HG and input to LF (variation in the rate of change of late, intense fires). But for the model to correctly predict the correlation pattern documented by Roques et al. (2001) fires should change in opposite direction in respect to HG and W. In particular, the table of predictions in Fig. 3 shows that this pattern of correlation occurs only in the case of a positive input to grazers (a positive input to HG).

These authors did not provide any evidence for this potential positive input. Shrub cover increased sharply around 1967 (Roques et al., 2001, Fig. 3) and continued along that trend during the following years. In 1967 the area was divided into sites of different land use and this might have created the conditions for change according to the observed correlation pattern. We hypothesize that better conditions for grazers must have occurred so that a positive parameter change for HG can be assumed. Not all sites however manifested same dynamics with respect to the overall correlation pattern described above. In the first two sites, Communal land and Hlane Wildlife Sanctuary respectively (see Roques et al., 2001, Fig. 2) increased shrub cover, lower fire frequency and increased grazing pressure started more or less immediately after 1967 (Figs. 2 and 3, Roques et al., 2001).

Interestingly enough two other sites, namely Malahleni and Ranch site, did not show the same trends. Shrub cover increased, fire frequency increased as well but the grazing pressure remained unchanged. These evidences are in contrast with the mechanism proposed on the base of the observed correlation patterns according to which grazing pressure would reduce fires to the benefit of shrubs. Field data and model predictions help explain this apparent contradiction. The period 1967–1975 was one in which rainfall increased (Roques et al., 2001, Fig. 1). In our model increasing rainfall determines a positive input to w_1 , because it increases the incoming flow of water from outside the system.² If we consider this positive input (first row of the table in Fig. 3) the model predicts exactly the changes that were observed in the two sites. Grazers would not change and both intense fires (LF) and shrubs (W) would be increasing. So in Malahleni and Ranch sites improved conditions for grazers likely did not occur and the observed pattern can be attributed to the increased rainfall only. But the augmented rainfall might have affected also the other sites of the study area. We will return on this later.

Here we focus a bit on the null change in the abundance of grazers associated to the input to w_1 . It is not a real inertia of this component in respect to parameter change in the dynamics of w_1 but rather a compensation between opposite effects associates to the multiple pathways that connect w_1 to HG. The simulation (see SM Appendix D, model d) shows that the percentage of matrices in which the positive input to w_1 augments HG is 50.35% whereas a negative effect appears in the 49.65% of cases. These percentages signal that there is no prevalence of effects when link strength is assigned; accordingly we can assume that compensation between the two effects is likely to occur. However, compensation does not immediately come from counting the pathways. In fact only one path carries a positive effect: it is ($w_1 \rightarrow G \rightarrow HG$). The other pathways, ($w_1 \rightarrow w_2 \rightarrow W - oG \rightarrow HG$), ($w_1 \rightarrow w_2 \rightarrow W \rightarrow LF - oG \rightarrow HG$), and ($w_1 \rightarrow W - oG \rightarrow HG$)

carry negative effects. But these negative pathways are longer and include links that form positive feedbacks at level 3, 4 and 5 (and higher, see SM, Appendix E for a description of these positive feedbacks). So stability reasons and of pathways strength, that becomes weaker as the path elongates, as discussed for the core model above, apply here. They may explain the incongruity between the number of pathways with opposite effects and the result of the simulation.

The increased level of fires that is predicted for positive input to w_1 is associated to pathways that include same links that enter in the composition of positive feedback loops. However, positive pathways outnumber negative pathways by 3 to 1 and links that enter in the positive feedback are present in the positive pathways but also in the negative one (see SM Appendix D, model d).

As said before the rainfall regime must have affected the other two sites (Communal and Hlane) as well. Accordingly, in these areas two factors must be considered as causes of variations: the improved conditions for grazers and the increased water availability due to rainfall. By combining the predicted effects of the two sources of variation (first and fifth row of the table of predictions) one obtains the overall direction of change for the variables. Grazing pressure (level of HG) augments: the positive input on HG increases its own level and the positive input to w_1 leaves this variable unchanged. The abundance of woody plants augments because both inputs produce positive variations on this variable. Fire frequency becomes higher: again both inputs produce positive changes on this component. Likely both inputs contributed to set up conditions that determined the observed patterns of abundance (and correlation).

A prolonged drought during 1991–93 caused widespread herbivore mortality (herbivores declined by more than 50% in the study area). This increased mortality enters the model as a negative input on HG. Predicted consequences (fifth row of the table in Fig. 3, reverse the signs) are that the level of grazers and of woody vegetation would be declining; fires (both early and late) instead would be increasing. Different sites in the study area showed different patterns in respect to the effects of drought. In Hlane site less grazing pressure, more fires and less woody plants followed the drought event (Roques et al., 2001, Figs. 2 and 3).

Model predictions for the sole negative impact on HG would explain the observed pattern. However, as said earlier, if abundant rainfall increases water availability, causing a positive input to w_1 , a negative input to w_1 must be considered now to take into account the reduced water availability caused by drought. The expected effects of this negative input (first row of the table, reverse the signs) are that the abundance of grazers would not change; woody vegetation would be decreasing whereas the level of fires would be increasing. Now the effects of the increased mortality of herbivores and of the reduced water availability must be combined. Both inputs are predicted to reduce woody vegetation; the abundance of grazers would be decreasing but only because of their increased mortality (input to w_1 does not change the level of HG) whereas the two inputs have opposite actions on fires. In the absence of any quantitative assessment the net effect on the level of fires cannot be ascertained. However field observations suggest that fires increased; likely the effect on fires of the augmented mortality of herbivores dominated over that of the lower availability of water.

During the same period in the Malahleni buffer zone the frequency of fires dropped sharply and the shrub cover diminished; from the data presented in the study it is impossible to ascertain about the reduced level of grazing pressure because of the lack of annual data in 1991–1993, although it seems that such as decrease did not take place (Roques et al., 2001, Fig. 3 diagram e). If so, we could assume that only the negative input to w_1 might have affected this area. This input is predicted to lower both the

¹ Roques and coauthors used the number of individuals (i.e. population abundance) as a measure of grazing pressure.

² This inflow is included in the self-loop on variable w_1 , see Puccia and Levins, 1986.

frequency of fires (level of LF) and shrub cover (level of W) while HG remains unchanged, which correspond to the observations.

The recovery from rinderpest in the Serengeti ecosystem is perhaps the most influential case study on the role of grazing on encroachment in savannas (McNaughton, 1992; Holdo et al., 2009; Holdo, Sinclair et al., 2009). Rinderpest removed 95% of cattle, buffalo, wildebeest, gazelle, and zebra. In the 1950s a cattle vaccination campaign surrounding Serengeti resulted in the virus disappearing from the wildlife. Right after cattle were inoculated wildebeest populations began to increase in abundance. The sequence of events that followed cattle inoculation is described in the charts of Fig. 4. In these charts we show the abundance trends for the main variables. We reproduced them using the original data set (Holdo et al., 2009; Holdo, Sinclair et al., 2009, Dataset S1 Time-series data for model variables used in the analysis, <http://dx.doi.org/10.1371/journal.pbio.1000210.s001>).

The period 1960–1980 show very clear trends: concomitant with the steep increase of the grazers (i.e. wildebeest, Fig. 4A), the browsers (i.e. elephants, Fig. 4B) augmented their abundance (up to mid-seventies), fires (Fig. 4E) dropped and tree cover (Fig. 4C) remained at low levels. To assess whether inoculation could have produced the observed trends, the model in Fig. 3 can be applied by assuming a positive input that enters the system via HG (the positive effect of the inoculation on the growth rate of the grazers). The table in Fig. 3 yields the following predictions: the grazers would be increasing (HG +); so the browsers would (HB +); fires would be declining (LF –) and woody biomass would be increasing (W +). With the exception of the woody cover a qualitative correspondence between model predictions and the observed trends after inoculation emerges.

Holdo et al. (2009) and Holdo, Sinclair et al. (2009) posited that grazing and intra-annual rainfall variation contributed to the observed global patterns of fire occurrence in the Serengeti. So the variation in the rainfall regime must be considered as a further driver that, beside inoculation, was at work in that ecosystem from the beginning of the investigation period up to mid-1970s. The temporal trend for rainfall is reported in Fig. 4D (as wet:dry data, Holdo et al., 2009; Holdo, Sinclair et al., 2009). This chart indicates a tendency to decline for this feature in the considered period. Clearer is the reduction in the spatial extent of burning (Fig. 4E). Because McNaughton (1992) showed that during the period of ecosystem recovery there was a positive correlation between the spatial extent of burning in the dry season and the rainfall level during the wet season Fig. 4D and E lead to conclude that from 1960 to mid-1970s the rainfall regime declined.

As already said a lower availability of water becomes a negative input to w_1 . Consequences of this reduced availability can be obtained by reversing the signs in the first row of the table of predictions that accompanies the model in Fig. 3. A diminution is expected for woody vegetation. If combined with the expected increase due to the positive input on grazers a compensation of effects takes place. This might explain the lack of variation in the level of this component, as shown by its trend in Fig. 4C. This conjecture would however require a quantitative assessment to be confirmed.

Following the negative input to w_1 the level of grazers (HG) is expected not to change, while browsers should be declining. Fig. 4 shows that browsers markedly increased in the period 1960–1980. This requires that the effect of the reduced mortality of grazers (positive input to HG) on the abundance of the browsers must be

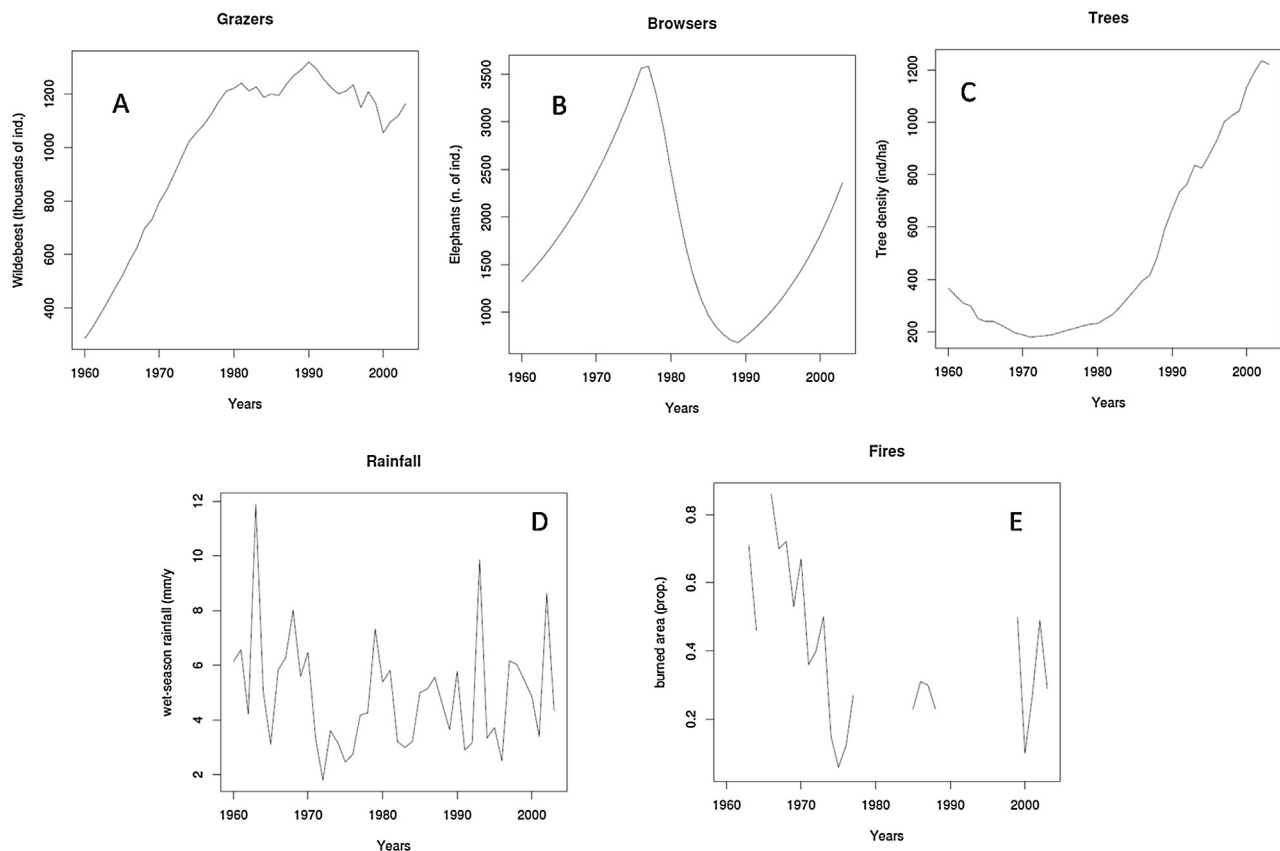


Fig. 4. Charts that show time series for 5 variables as provided by Holdo et al., 2009, Dataset S1, <http://dx.doi.org/10.1371/journal.pbio.1000210.s001>: A, Grazers (wildebeest population size, thousands of individuals); B Browsers (elephant population size, n. of individuals); C Trees (tree density, ind ha⁻¹); D rainfall (dry-season rainfall, mm y⁻¹); E, Fires (proportion of burned area).

more than enough to compensate for the decline that would be imposed by the reduced availability of water. Still, a conclusion presented with circumspection because a quantitative assessment would be necessary and we could not make it here.

The Serengeti elephant population declined because of poaching in the 1970s and 1980s, and subsequently recovered following the ivory ban in 1989 (Holdo et al., 2009; Holdo, Sinclair et al., 2009). Poaching must have affected the dynamics of the entire system. Increased mortality from poaching is a negative input on HB. Reversing the signs in the corresponding row of the table of predictions in Fig. 3 yields that browsers would be diminishing, woody biomass as well as fires would be increasing and grazers would be in decline. The trend showing the area burned in time (Fig. 4) does not allow for any comparison with model prediction due to the lack of data after 1980. The abundance of the browsers (Fig. 4B) lowered from 1980 to 1990. Woody vegetation shows a neat increase in the same period (Fig. 4C). Grazers present a steadily level around their carrying capacity (Fig. 4A). Some of the effects of the increased mortality due to poaching are captured by the model if a negative input to HB is assumed, with the exception given by the discrepancy between observed and predicted trend for grazers. Also a more complete data set about the areas burned during time would allow for a more precise assessment.

4. Discussion

The presence of multiple interacting variables increases the structural complexity of the ecosystems: more pathways are generated for indirect effects and the system feedbacks, which modulate the effects of pathways, become more intricate. This increased structural complexity affects the way variables respond to stimuli, perturbations and management interventions. One feature of this complexity is that patterns of ecosystem response become difficult to disentangle in causal terms. Roques et al. (2001) found that a significant negative correlation between grazing pressure and fires had a major impact on shrub cover. They interpreted this evidence according to the following chain of events ordered in a causative succession: sustained heavy grazing of grasses would remove combustible herbage which would reduce the probability of ignition and restrict the spread of fires, thus favoring bush encroachment. This chain of events implies high abundance of grazers (heavy grazing pressure), less grassy herbs, lower frequency of fires to end with a high shrub cover. The table of prediction in Fig. 3 reveals that such concomitant variations are possible (thus the chain of causal events is plausible), but only when a positive input on grazers (HG) occurs. It is not the sole augmented abundance of grazers that produces these effects. In fact a higher level of grazers can be obtained in several ways (i.e. negative input to w_2 ; negative input on W) but in these other cases the higher abundance of grazers is accompanied by changes in the level of the other variables that do not match with the hypothesized chain of events. For example, when a negative input affects W (its rate of change diminishes) the level of grazers increases, but so does also that of the grass vegetation G (fourth row of the table in Fig. 3, invert signs), a contrasting outcome if compared with the above described pattern.

The same approach in which correlation patterns are translated into hypothesis of dominant controlling factors is taken by Higgins et al. (2000). They hypothesized that increasing grass production³ would negatively affect tree density by increasing fire intensity. But if the increased production of grass comes about because its growth rate augments (positive input), then Higgins and colleagues' conclusion holds. The third row of the table prediction

table (Fig. 3) in fact tells us that an increase in the growth rate of G yields more grass, less woody plants and induce a higher level of fires (both early and late). But the model clearly indicates that an increased standing stock for grass is not always coupled with an increased level of fires. For input to w_2 (negative), W (negative), and HB (positive) the level of G increases but that of intense fires (LF) does not, although for all these inputs the level of woody plants is predicted to decrease.

Often the search for causative mechanisms in ecosystems is based on the correlation between abundance levels between variables; that is the search for shifts in the abundance of a population that accompanies the change in the abundance of another. In this paper we show that the reification of observed patterns of change into interactive mechanisms can be successful if we may be able to link correlation patterns, sources of change (i.e. the inputs) and community structure. Qualitative models can be useful in this respect because in mapping out interactions between relevant variables they help understanding how the links of recognized direct effects also determine indirect effects. In addition, signed digraphs may become diagnostic tools in that they allow using correlation patterns to identify source of changes, the variables through which press perturbations enter the system (Puccia and Levins, 1986; Levins and Puccia, 1988).

McNaughton (1992) indicated that the analysis of the recovery pattern (i.e. changes in the abundance of critical variables) from rinderpest in the Serengeti ecosystem allowed a plausible reconstruction of the network of interconnected chains of cause and effect induced by the rinderpest. Holdo, Sinclair et al. (2009) made McNaughton's assertion explicit by identifying a linear chain of causality that operated in that environment. They reconstructed a sort of "rinderpest trophic cascade hypothesis" that would give rise to the following events ordered in a causative succession: decreased pathogen, increased specialist consumer (wildebeest), decreased producer (grass), decreased generalist "consumer" (fire) and increased producer (trees). These authors generalized their finding by positing that dominant factors controlling tree density in the Serengeti would be essentially top down (Holdo et al., 2009; Holdo, Sinclair et al., 2009).

However, rainfall regime and poaching contributed to the long term dynamics of the Serengeti ecosystem as well, acting as inputs to variables different than grazers (water availability, large browsers). According to this the overall dynamics must have been the net outcome of the effects of different inputs produced by different sources of change (i.e. the reduced mortality for wildebeest due to cattle inoculation, the increased mortality of browsers due to poaching, and the increment of water availability due to rainfall). These effects percolated throughout the ecosystem using multiple pathways and combined with one another to yield the observed patterns. The picture that emerges from our analysis suggests that there is no unique control mechanism (i.e top down) but that the locus of control is diffuse. Controlling factors are inputs to parameters that govern the rate of change and the structure of the network of the system (Levins and Puccia, 1988; Levins and Schultz, 1996).

Discussion in ecology is often hampered by the posing of dichotomous choices: are populations regulated by density dependent or density independent factors? Do physical or biotic factors predominate? This holds also for savannas. In fact, proposed explanations for the persistence of both trees and grasses in these ecosystems fall into two categories: those that emphasize the fundamental role of competitive interactions in fostering coexistence (competition-based mechanisms), and those that focus on the limiting roles of demographic bottlenecks to tree establishment and persistence and that are influenced by external factors such as herbivory, browsing and fires (Sankaran et al., 2004). The structure of the interactions configured in the model of

³ Those authors estimated grass productions as the standing stock (Kg ha^{-1}).

Fig. 3 shows that the effect of grazing on the level of woody plants depends on pathways involving fires ($HG - oG \rightarrow LF - oW$) as well as pathways that encompass soil moisture, such as ($HG - oG - ow1 \rightarrow w2 \rightarrow W$) and ($HG - oG - ow1 \rightarrow W$). It might be that these paths have different importance in determining the effect on W in different conditions (van Wilgen, 2009) but this can be ascertained only on a quantitative basis. We think that the interesting question is not what relative weights to assign the different factors but, rather, to elucidate how they interpenetrate and how this interplay determines the overall result.

We already pointed out that the qualitative analysis is relatively uninterested in precision so that exact predictions are not its primary goal (Levins, 1974). Models for accurate quantitative predictions in savanna ecosystems must include, among others, spatial heterogeneity, temporal variability and thresholds as critical factors (van Wilgen et al., 2004; Holdo et al., 2009; Holdo, Sinclair et al., 2009; Staver and Levin, 2012). Nevertheless the qualitative approach, by predicting directions of change, can be helpful when we are interested in pushing on the system in a particular direction. In the Kruger National Park fire management approaches changed several times from 1948 to 2001. van Wilgen et al. (2004) documented the outcomes of changing fire-management policies. Because they were unable to quantitatively assess whether fire intensity was influenced by the different management approaches they suggested that managers could reduce fire intensity by preempting late dry-season fires (intense) by igniting fires early in the dry season. This was intended as a measure to curb the effect of fires on tree size. To assess the potential of this management option we must enter a positive input to variable EF as its rate of change is forced to increase by management. As a consequence (last but one row of the table in Fig. 3) late, intense fires would be reduced, and the model confirms that favoring early fires push the system in the direction of having less intense fires. But this measure should be carefully evaluated for its effects on other variables: grassy plants and grazer's population in fact are expected to diminish.

van Wilgen et al. (2004) found that the elements of the fire regime they considered, such as the extent of area burned or variability of inter-fire intervals, appear to be strongly influenced by rainfall regime. This may also be true for fire intensity. Increasing rainfall (positive input to w_1) is expected to increase the level of intense fires. On the other hand preempting intense fires, as said before, is expected to reduce the intensity of fires. However, if we look at the results of our simulations (see Supplementary material Appendix D, model d) we can observe that the positive input on w_1 generates an increment in the level of LF in 95% of the simulated matrices; the positive input to EF on the other hand yields a reduced level of LF in 77% of the matrices, whereas in some 22% of the matrices the positive input to EF tend to increase LF . This means that there is a counteracting effect that mitigates the magnitude of the negative variation predicted for LF . Our model thus confirms that high rainfall regime may obscure the effect of the management action, at least in respect to fire intensity (van Wilgen, 2009; van Wilgen et al., 2004).

Stability analysis is the framework in which most of the savanna modeling applications are discussed (van Langevelde et al., 2003; Higgins et al., 2010; De Michele et al., 2011; Holdo et al., 2012). In this paper we do not focus on stability properties of equilibria but on the evolution of equilibrium conditions that is driven by changes in the parameter values (input). The fact that our model can interpret observed patterns indicates that the moving equilibrium approach is another way to look at the effect of the variable environment. This in turn suggests that variability is matter of changing parameters (press perturbation, Bender et al., 1984) and not solely of variable fluctuations (Levins, 1974).

The qualitative analysis has certainly many limitations, among which the impossibility to make any quantitative statements is the most relevant. This precludes digging in details the dynamics of the savannas: for example several works showed that quantitative levels of rainfall define thresholds for different behaviors (i.e. bi-stability, Sankaran et al., 2005; Higgins et al., 2010). Also the need to explore quantitative details that may affect system behavior has stimulated innovative approaches to parameter quantification (Higgins et al., 2010; Holdo et al., 2012).

By recognizing these limitations of the qualitative analysis we posit that these methods are not alternatives to quantitative models; rather we see the potential for integration wherever parameter estimation is impossible or difficult to obtain. The management of savanna ecosystems will become more complex in the near future under the effects of global change. Impacts that can be hypothesized are many and will be due to altered CO_2 balances, increasing temperatures, invasion of alien plant species and the growing human population pressed by urgent needs (van Wilgen, 2009). Making predictions in that context will become more difficult because of the uncertainty associated with new, unknown events, changing dynamics and lack of quantitative data. An adaptive management approach that allows for continually assessing new evidence and changing approaches as understanding increases has been called for. There is no recipe for modelling development but great effort must be devoted to assimilation of facts, observation and hypotheses. We believe that in the new scenario that is approaching qualitative models can be helpful. They have the necessary adaptability to be used in changing contexts: when in doubt about critical linkages and dynamic features, alternative models can be developed to find out which difference matters and to reach robust conclusions. They are also flexible: they allow including and discarding variables easily and above all they permit working with variables and links that are not readily measurable, but their effects are crucial.

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AB wishes to dedicate this paper to the memory of Richard Levins, who has been a continuous source of inspiration

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecocom.2016.10.001>.

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