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# Savanna domain in the herbivores-fire parameter space exploiting a tree-grass-soil water dynamic model

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## Abstract

The tree-grass co-existence in savannas involves multiple and sometimes connected biogeophysical conditions. The savanna domain, its boundaries, and transitions (gradual or abrupt) to other vegetation types (i.e., grassland or forest) are fundamental for the management of ecosystems, and for preserving the biodiversity in present conditions and in future changing scenarios. Here we investigate the savanna domain within grazers-fire and browsers-fire parameter planes through a simple ecohydrological model of tree-grass-soil water dynamics. Stability maps allow to identify savanna domains, and to show the behavior of vegetation under increasing pressure of grazing and browsing. Stability maps shed light on the causes behind possible vegetation abrupt transitions (e.g., forest collapse and bush encroachment). An application to 15 African savannas sites is presented and discussed with the support of a local sensitivity analysis of the model's parameters.

*Key words:* herbivores, fire, savanna, state transition, gradient, model,

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sensitivity analysis

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## 1 1. Introduction

2 The dynamics of vegetated ecosystems are controlled and driven by cli-  
3 mate, substrate and disturbances such as fire, herbivory and human activ-  
4 ities. Vegetated ecosystems whose dynamics are dominated by the climate  
5 are called *climate dependent ecosystems* (Bond et al., 2003), whereas in the  
6 cases where other perturbations such as fires or herbivores are prominent,  
7 they are labeled as *fire dependent ecosystems*, or *consumer controlled ecosys-*  
8 *tems* (Bond et al., 2003, Bond and Keeley, 2005).

9 Where do savannas - that are ecosystems co-dominated by trees and grass  
10 - fit in this classification?

11 Field observations (Sankaran et al., 2005, Bucini and Hanan, 2007) reveal  
12 a complex situation: savannas can be either *climate*, or *disturbance dependent*  
13 *ecosystems*, depending on the environment they occur in.

14 Early models of savannas emphasized the role of soil water availability,  
15 and inferred savannas to be *climate dependent*. Walter (1971) describes sa-  
16 vannas as ‘broad ecotones’ between grasslands and forests depending on the  
17 mean annual rainfall; Shmida and Burgess (1988) illustrate the *subtropical*  
18 *succession* (*desert* → *grassland* → *open savanna* → *closed savanna* → *for-*  
19 *est*) as the sequence of ecosystem types observed along a rainfall gradient.  
20 In general under these conceptual models, water scarcity permits the co-  
21 existence of trees and grasses by limiting the abundance of trees allowing  
22 grass to persist: this is a mechanism of *balanced competition* (Amarasekare,  
23 2003).

24 More recent works have considered the role of fire in permitting the tree-  
25 grass co-existence in savannas (Hanan et al., 2008, D’Odorico et al., 2006,  
26 Bond et al., 2003, Baudena et al., 2010, Accatino et al., 2010), indicating  
27 savannas as possible *fire dependent ecosystems*. In ecosystems where water  
28 scarcity already limits the tree density, and allows tree-grass co-existence, fire  
29 influences only the tree-grass ratio. On the other hand, if water is sufficient  
30 to support the growth of trees, fire can be a limiting factor for tree cover,  
31 permitting again the tree-grass co-existence, through a *bottleneck* mechanism  
32 in tree demography. Under these conditions, savannas can be viewed as fire  
33 subclimaxes of forests (Scholes and Walker, 1993).

34 Yet other studies have suggested a role for herbivores in maintaining  
35 savannas (Scholes and Archer, 1997, Bond and Keeley, 2005, Baxter and  
36 Getz, 2005, Holdo, 2007). Particular attention has been paid to elephants,  
37 which are able to ‘re-engineer’ the tree layer (Dublin, 1995).

38 Accatino et al. (2010), considering the joint role of rainfall and fire, have  
39 suggested that arid savannas are *climate dependent*, while moist savannas  
40 can be *fire dependent*.

41 In the savanna literature, tree-grass co-existence is often discussed in re-  
42 lation to the existence of multiple steady states. Bifurcation analyses (van  
43 Langevelde et al., 2003, Baudena et al., 2010, Accatino et al., 2010) have  
44 pointed out the possibility that savannas may represent a bistability con-  
45 dition with forest. Beyond the mathematical formalism, the existence of  
46 multiple steady states appears evident in field observations. Among the sev-  
47 eral cases that can be mentioned, we recall the macro-mosaics observable in  
48 tropical dry forests, where fire plays a fundamental role in the abrupt tran-

49 sitions from forest to savanna (Murphy and Lugo, 1986), the savanna-forest  
50 hysteresis cycle in the Amazon basin (da Silveira Lobo Sternberg, 2001), and  
51 the changes observed in the Serengeti-Maara vegetation due to variations  
52 in fire and grazing regimes during the rinderpest pandemic period (Dublin,  
53 1995). The key pieces of evidence offered in favor of multiple steady states  
54 are abrupt state transitions over time (hysteresis cycles) and space (macro-  
55 mosaics), bimodal state variable frequency or distribution, and the dual re-  
56 sponse to driving parameters (Schröder et al., 2005). The space variability  
57 plays an important role in maintaining savannas, and many spatial models  
58 were built in order to account the dynamics in space of the vegetation (see  
59 e.g., Klausmeier, 1999, Rietkerk et al., 2002, Gilad et al., 2007, Borgogno  
60 et al., 2009). However, in this work we point the attention on a spatially  
61 implicit model.

62 In particular, we extend the spatially implicit ecohydrological model of  
63 water dynamics in a tree-grass-soil system forced by rainfall and fire proposed  
64 by Accatino et al. (2010) to explicitly consider disturbances by herbivores,  
65 distinguishing grazers from browsers. By doing so, we are able to underline  
66 the different contributions of fire and herbivore disturbances to the tree-grass  
67 co-existence in savannas.

68 Then, we use stability maps in the grazers-fire and browsers-fire param-  
69 eter planes to identify savanna domains, and to show the behavior of vege-  
70 tation under an increasing pressure of grazing or browsing. In this way, we  
71 try to answer fundamental questions about the controls on savanna struc-  
72 ture and function and explore the causes of abrupt transitions in savanna  
73 ecosystems dynamics.

74 We discuss the theoretical results using observed data collected in 15  
75 savanna sites and characterized by particularly high or low values of fire  
76 occurrences and browsers density. The data are extracted by the database  
77 reported in Sankaran et al. (2005). The comparison between model outputs  
78 and observed data is commented with the help of a local sensitivity analysis  
79 of the model's parameters.

## 80 **2. The action of fire, grazing and browsing on savannas**

81 Fires and herbivores are 'direct' disturbances to the demography of veg-  
82 etated ecosystems (Hobbs and Huenneke, 1992). The interactions among  
83 rainfall, fire and herbivores in shaping the vegetation are sketched in Fig.  
84 1(a). Fires shape savanna structure by acting as a determinant of the tree  
85 layer composition (Frost et al., 1986, Bond and van Wilgen, 1996). The  
86 quantity of tree biomass is, in general, negatively correlated with the fire  
87 frequency (Scholes and Walker, 1993). The spread and intensity of fire is  
88 supported by the abundance of dead grasses (fuel load) during the dry sea-  
89 sons (Scholes and Archer, 1997, Govender et al., 2006). Fires seldom damage  
90 adult trees, but knock back or kill tree seedlings and saplings in the flame  
91 zone, the height of which is determined by the abundance of dead grass.  
92 Thus fires act as a demographic bottleneck, restricting the recruitment of  
93 small trees to the adult class.

94 Large mammal herbivores in African savannas form a continuum from  
95 eaters of grass only (grazers) to eaters of trees only (browsers) (McNaughton  
96 and Georgiadis, 1986). It is nevertheless useful to split them into two dis-  
97 crete classes, grazers and browsers, to evidence their different feedbacks on

98 fire via the quantity of dead grass (fire's fuel load). Grazers directly reduce  
99 the quantity of dead grass which controls the spread and intensity of fires,  
100 which in turn reduces tree recruitment (negative feedback of grazers on fire),  
101 see Fig. 1(b). Browsers indirectly increase fuel load (positive feedback of  
102 browsers on fire) reducing the competitive effect of trees on grass production  
103 (Scholes and Archer, 1997, van Langevelde et al., 2003), see Fig. 1(c). The  
104 decline of woodlands in presence of browsers has been widely documented,  
105 e.g., in East Africa (Laws, 1970), in Ruaha National Park (Barnes, 1983),  
106 in Botswana (Ben-Shahar, 1993, Skarpe et al., 2004), in Serengeti-Maara  
107 (Dublin, 1995), and in Etosha National Park (de Beer et al., 2006). Among  
108 browsers, the elephants *Loxodonta africana* have the most dramatic impacts  
109 on the woody vegetation, leading to the so-called 'Elephant problem'. Ele-  
110 phants impacts are more marked when they have been confined within a  
111 remnant of a formerly wider range (Dublin, 1995).

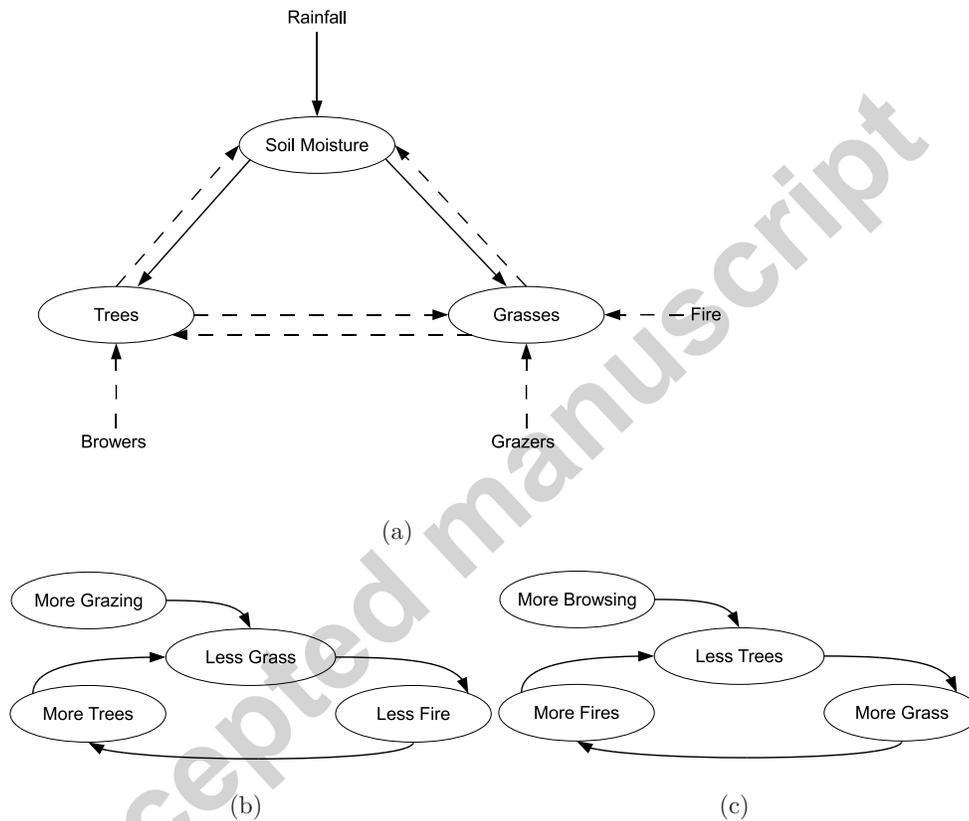


Figure 1: Panel (a) sketches interactions among rainfall, fire, herbivores, soil moisture, trees and grass. Continuous (dashed) lines indicate positive (negative) interactions. Panels (b) and (c) show respectively feedbacks of grazers-fire and browsers-fire on trees and grass.

112 **3. Ecohydrological model of tree-grass dynamics**

113 We represent the tree-grass dynamics by a minimal ecohydrological model  
 114 introduced by Accatino et al. (2010). This model implicitly considers trees  
 115 as superior competitors for space (in the sense of Tilman, 1994) since they  
 116 can overtop grass; while it explicitly models the competition between trees  
 117 and grass for soil water within the root zone, and the differential disturbance  
 118 action of fire on grass and trees. The model has been slightly modified to  
 119 explicitly consider also the role of grazers and browsers on grass and trees  
 120 respectively. The state variables are three: 1) the soil water content,  $S$ ,  
 121 within the pore volume of a column of soil unitary area with depth equal to  
 122 the root zone, 2) the fractions of area covered by trees,  $T$ , 3) the fractions  
 123 of area covered by grass,  $G$ . All the state variables are dimensionless and  
 124 range between 0 and 1 (a further condition is  $0 \leq T + G \leq 1$ ). The tree-  
 125 grass-soil water dynamics are mathematically described by the following set  
 126 of differential equations:

$$\begin{cases} \frac{dS}{dt} = \frac{p}{w_1}(1 - S) - \epsilon S(1 - T - G) - \tau_T ST - \tau_G SG \\ \frac{dT}{dt} = \gamma_T ST(1 - T) - \delta_{T0} T - bT - \delta_F fGT \\ \frac{dG}{dt} = \gamma_G SG(1 - T - G) - \gamma_T STG - \delta_{G0} G - gG - fG. \end{cases} \quad (1)$$

127 The first row of Eq.(1) represents the soil water balance in the pore volume  
 128 ( $w_1$ ) having unitary area and as depth the root zone. The term  $p/w_1$  is the  
 129 rainfall input where  $p$  [mm/yr] is the mean annual rainfall, and  $p/w_1 S$  is the  
 130 leakage, modelled as linearly dependent on  $S$  to keep the model analytically  
 131 tractable. The terms  $\epsilon S(1 - T - G)$ ,  $\tau_T ST$ ,  $\tau_G SG$  are representative respec-

132 tively of evaporation from bare soil fraction  $(1 - T - G)$ , water uptake from  
 133 tree fraction, and grass fraction. The maximum water uptake parameters  $\epsilon$ ,  
 134  $\tau_T$ , and  $\tau_G$ , all in units [1/yr], are representative of the potential evapotran-  
 135 spiration terms scaled by  $w_1$ . The second and third rows in Eq.(1) describe  
 136 the dynamics of trees and grass, respectively. Tree growth term  $\gamma_T ST(1 - T)$   
 137 is proportional to the fraction of soil not occupied by trees  $(1 - T)$ , i.e., trees  
 138 can overtop grass, and grass growth term  $\gamma_G SG(1 - T - G)$  is proportional to  
 139 the bare soil fraction  $(1 - T - G)$ . The tree fraction is reduced by senescence  
 140  $\delta_{T0}T$ , browsing activity  $bT$  and fires  $\delta_F fGT$ , where  $fG$  is representative of  
 141 the fuel load. The grass fraction is reduced by tree capability to displace  
 142 grass  $\gamma_T STG$ , senescence  $\delta_{G0}G$ , grazing activity  $gG$ , and fires  $fG$ . In partic-  
 143 ular,  $\gamma_T$  and  $\gamma_G$  represent the potential growth rate for trees and grass,  $\delta_{T0}$   
 144 and  $\delta_{G0}$  are the disappearance rates in the absence of fire and herbivores. For  
 145 the trees equation,  $b$  is an additional removal rate representing browsing, or  
 146 tree harvesting, while  $\delta_F$  represents the tree vulnerability to fires. Similarly  
 147 in the grass fraction equation, the additional removal rate is  $g$  and repre-  
 148 sents grazing, while  $f$  is the fire frequency. All parameters of the second and  
 149 third rows carry dimensions of [1/yr] except  $\delta_F$  that is dimensionless. All the  
 150 parameters of Eq.(1) are positively defined.

151 Equation (1) admits five steady state solutions (i.e.,  $dS/dt = dT/dt =$   
 152  $dG/dt = 0$ ), but only four satisfy the conditions  $0 \leq T \leq 1$ ,  $0 \leq G \leq 1$ , and  
 153  $0 \leq T + G \leq 1$ . Of these, the first solution is characterized by the absence  
 154 of vegetation, and we will refer to it as unvegetated, i.e.  $T = 0$ ,  $G = 0$ . The  
 155 second solution has grass only, i.e. (desert) grassland,  $T = 0$ ,  $0 < G \leq 1$ .  
 156 The third solution has trees only, i.e. forest,  $0 < T \leq 1$ ,  $G = 0$ . The

157 fourth solution has a co-existence of tree and grass, i.e. savanna,  $0 < T < 1$ ,  
158  $0 < G \leq 1 - T$ . The steady states are available analytically (not reported  
159 here for brevity). A linear stability analysis of the steady states has been  
160 performed evaluating the eigenvalues of the Jacobian matrix associated to  
161 the model. In particular, if the real part of all the eigenvalues is strictly  
162 negative, the steady state is stable. For further details about the model and  
163 parameters' values see Accatino et al. (2010).

164 In the following section, we will assume as reference values for the pa-  
165 rameters:  $p = 700$  [mm/yr]  $w_1 = 345$  [mm],  $\epsilon = 20$  [1/yr],  $\tau_T = 30$  [1/yr],  
166  $\tau_G = 10$  [1/yr],  $\gamma_T = 2$  [1/yr],  $\gamma_G = 200$  [1/yr],  $\delta_{T0} = 0.02$  [1/yr],  $\delta_{G0} = 2$   
167 [1/yr], and  $\delta_F = 0.35$ , while  $b$  varies between 0 and 0.1 [1/yr] and  $g$  between  
168 0 and 10 [1/yr]. Note that the total removal terms, i.e.,  $\delta_{G0} + g$  and  $\delta_{T0} + b$ ,  
169 may exceed the range indicated by Accatino et al. (2010), under conditions of  
170 a high level of disturbances - a situation of particular interest in the present  
171 work.

172 Annual rainfall, fire, and herbivores are environmental forcings treated  
173 here as constants. However, rainfall and fire are stochastic variables as prop-  
174 erly assumed by Fernandez-Illescas and Rodriguez-Iturbe (2003) for the rain-  
175 fall forcing, by D'Odorico et al. (2006), Hanan et al. (2008) for fire. Herbi-  
176 vores are more properly considered as dynamic state variables whose abun-  
177 dance depends on the resource availability as treated in May (1977), van de  
178 Koppel et al. (1997). The stochastic behavior of the environmental forcings,  
179 like rainfall and fire, could be considered through a statistical dynamical  
180 approach as outlined by De Michele et al. (2008) and Vezzoli et al. (2008).  
181 The dynamical behavior of herbivores could be treated by adding new state

182 variables to the present model. The deterministic variable-parsimonious ap-  
183 proach, we have adopted here, provides results that can be easily extended  
184 in a more realistic dynamic-stochastic framework. This extension, however,  
185 is out the scope of the present work, and it will be considered in a future  
186 study.

#### 187 4. Where are savannas in the herbivores-fire space?

188 Accatino et al. (2010) have investigated the existence and the stability of  
189 savannas with respect to rainfall and fire forcings (i.e., in the parameter plane  
190  $p-f$ ) showing that savanna is stable for low values of rainfall ( $100 \leq p \leq 600$   
191 [mm/yr]) and fire ( $0.2 \leq f \leq 0.8$  [1/yr]). In this region, savannas are the  
192 result of a limited water availability, and are *climate dependent ecosystems*.  
193 Conversely, for high values of rainfall ( $600 < p \leq 1100$  [mm/yr]) and fire  
194 ( $f > 0.8$  [1/yr]), savanna is in bistability with forest. In this case, savannas  
195 are permitted by the frequent fire disturbances making them *fire dependent*  
196 *ecosystems*.

197 In the current work, the savanna domain is explored with respect to  
198 disturbances, herbivores and fire, with the aim of clarifying the savanna  
199 steady state stability with different types and levels of disturbances. In the  
200 following two subsections, the stability maps in the planes  $g-f$  and  $b-f$  are  
201 derived and presented in panels (a) of Figs. 2 and 3, respectively. Stability  
202 maps will be used to study the changes of the vegetation composition along  
203 gradients of grazing and browsing pressure. The change in the values of tree  
204 and grass fractions at a fire frequency level of  $f = 0.5$  [1/yr] will be discussed  
205 in the light of savanna ecosystems transitions, e.g., pathways J-M and L-K

206 in panels (b) and (c) of Fig. 2 or pathways Z-X and Y-W in panels (b) and  
 207 (c) of Fig. 3.

208 In Fig. 2 the parameter  $g$  varies from 0 to 10 [1/yr] and browsing is  
 209 absent ( $b = 0$  [1/yr]). In Fig. 3 the parameter  $b$  varies from 0 to 0.1 [1/yr],  
 210 and grazing is absent ( $g = 0$  [1/yr]). The fire frequency,  $f$ , varies from 0 to  
 211 1.2 [1/yr] for both maps.

212 They show five regions, three of them are characterized by one stable  
 213 state: grassland (G), savanna (S), and forest (F), while the remaining ones  
 214 by two alternative stable states (regions of bistability): savanna/forest (S/F)  
 215 and grassland/forest (G/F). The qualitatively symmetrical behavior of the  
 216 stability maps in the parameter space  $g - f$ , Fig. 2(a), and  $b - f$ , Fig.  
 217 3(a), derives from the use of the same functional form to represent grazers  
 218 ( $-gG$ ) and browsers ( $-bT$ ) effects respectively on the state variables  $G$  and  
 219  $T$ , as underlined in Figs. 1(b) and 1(c). If grass removal rate  $g$  increases,  
 220 the possibility of trees to completely displace grass is enhanced. Conversely,  
 221 if trees removal rate  $b$  is increased, the grass competitiveness for space is  
 222 enhanced, thus savanna and grassland ecosystems appear for high values of  
 223  $b$ . A similar symmetrical behavior is expected drawing the stability maps in  
 224  $\gamma_G - f$  and  $\gamma_T - f$  parameter spaces.

#### 225 4.1. Stability map in the grazers-fire space

226 In the plane  $g-f$ , Fig. 2(a), savanna is stable in the bottom-left side of the  
 227 panel (region S) within the domain  $0 \leq f \lesssim 0.9$  [1/yr] and  $0 \leq g \lesssim 2$  [1/yr],  
 228 where the last upper limit depends on the right boundary of the region. In  
 229 this region the co-existence mechanism is the balanced competition, because  
 230 the tree growth is limited by the water scarcity and grass (provided that the

231 grazing off-take is sufficiently low) is still able to grow. Moreover, the light  
232 grazing allows the accumulation of dead grass which fosters more frequent  
233 and severe fires further limiting the tree fraction.

234 Grassland is stable in the top-left side of the panel (region G), for  $f \gtrsim 0.9$   
235 [1/yr] and  $g \lesssim 1$  [1/yr]. Here the high fire frequency and the low grazing  
236 level lead to the exacerbation of balanced competition mechanisms causing  
237 the absence of trees. Thus, at low grazing pressure, fire is fundamental in  
238 maintaining grasslands (Zimmermann et al., 2009).

239 The vegetation change from an herbaceous environment to a mixed tree-  
240 grass landscape, observed at the time of the rinderpest pandemic (late 19<sup>th</sup>  
241 century) in Masai Mara, can be discussed using the grazers-fire plane. As  
242 described in Dublin (1995), at the end of 19<sup>th</sup> century, the ecosystem was a  
243 grassland under high levels of grazing and human induced fires. When the  
244 rinderpest virus began to spread, cattle and wild herbivores died, the human  
245 population declined, having as consequence a reduction in grazing activity  
246 and human induced fires. Thus, trees appeared and spread converting the  
247 ecosystem into a savanna state - a shift from region (G) to region (S) in Fig.  
248 2(a).

249 Forest state is stable in the bottom-right side of the panel (region F).  
250 Grazing pressure is so high that, though the tree fraction may be at its  
251 bioclimatic limit as imposed by the water scarcity, grass does not have any  
252 chance to survive. Within this region the tree fraction is independent of the  
253 fire frequency ( $f$ ) and the grazing level ( $g$ ).

254 The bistability region (G/F) located in the top-right side of the panel,  
255 presents grassland and forest as potential states. Similarly region (S/F)

256 presents two alternative steady states: savanna and forest. The bistability  
257 implies that a small perturbation of the environmental forcings can provoke  
258 an abrupt transition from one state to another, resulting in changes in the  
259 landscape at the macro-scale. In both bistability regions, grass can survive  
260 because fires prevent the tree domination, causing a bottleneck in tree de-  
261 mography. Thus, these are *fire dependent ecosystems*. On the other side, the  
262 achievement of the forest state is possible thanks to the feedback illustrated  
263 in Fig. 1(b).

264 Panels (b) and (c) of Fig. 2 represent respectively the steady states of  
265 tree and grass fractions along a grazing gradient at fire frequency  $f = 0.5$   
266 [1/yr]. Starting from point A (savanna), increasing the grazing level, first the  
267 point K is reached, and thence the abrupt transition K-L occurs leading the  
268 system to the forest state (point L). Transitions like K-L (i.e., the invasion of  
269 woody species into the grass stratum) are widely encountered in the savanna  
270 literature under the name of *bush encroachment* (Skarpe, 1990, Prins and  
271 van der Jeugd, 1993, Smit, 2004, Wiegand et al., 2005, Coetzee et al., 2008,  
272 among others). Bush encroachment has been associated with periods of  
273 high rainfall (O'Connor, 1995), following after periods of drought during  
274 which there was high grazing pressure by domestic livestock (Moleele and  
275 Perkins, 1998, Roques et al., 2001). Grazers would promote the dominance  
276 of trees over grass, directly, by removing grass and, indirectly, by reducing  
277 the amount of available fuel load (dead grasses). Moleele and Perkins (1998)  
278 report that in a non-grazed zone fires are more frequent than in adjacent  
279 encroached zones, probably because of the reduced presence of dead grass in  
280 the latter.

281 Transitions like M-J can characterize also other phenomena able to in-  
282 crease the overall tree removal rate (e.g. harvesting for timber or domestic  
283 fuel) that facilitate the grass presence and the tree-grass co-existence. This  
284 condition is widespread in the most densely-settled rural savanna regions.

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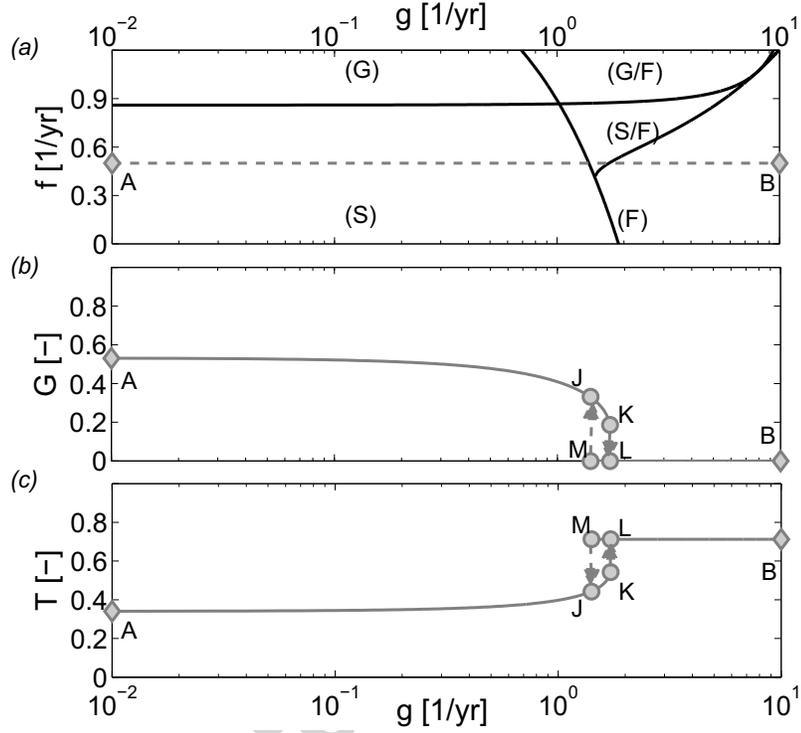


Figure 2: Type of vegetation in the grazers-fire parameter plane. Panel (a) gives the stability map in the plane  $g$ - $f$ . Panels (b) and (c) provide changes in vegetation structure over the grazing gradient A-B at fire frequency  $f = 0.5$  [1/yr]: panel (b) shows grass fraction, while panel (c) the tree fraction. Transitions K-L and M-J are described at the end of the *Stability in the grazers-fire space* paragraph. The parameters values are  $p = 700$  [mm/yr],  $w_1 = 345$  [mm],  $\epsilon = 20$  [1/yr],  $\tau_T = 30$  [1/yr],  $\tau_G = 10$  [1/yr],  $\gamma_T = 2$  [1/yr],  $\gamma_G = 200$  [1/yr],  $\delta_F = 0.35$ ,  $\delta_{T0} = 0.02$  [1/yr],  $b = 0$  [1/yr],  $\delta_{G0} = 2$  [1/yr].

285 4.2. Stability map in the browsers-fire space

286 In the plane  $b - f$  of Fig. 3(a), savanna is stable in the bottom-right side  
 287 of the panel within the domain defined by a line from  $(b = 0.001, f = 0)$   
 288 to  $(b = 0.01, f = 0.9)$  on the left, and a line from  $(b = 0.01, f = 0.9)$  to  
 289  $(b = 0.1, f = 0.6)$  on the top. In this domain the tree-grass co-existence is  
 290 due to the balanced competition: trees are limited by water scarcity, fire and  
 291 browsing pressure. Note that in this region the savanna state is stable also  
 292 in absence of fire,  $f = 0$  [1/yr]. In other words, the presence of browsers is  
 293 sufficient to prevent the formation of a woodland (Scholes and Archer, 1997).

294 In region (G) of Fig. 3(a), grassland is stable in the top-right side for  
 295  $b \gtrsim 0.01$  [1/yr] and the upper boundary of savanna region. This is due to the  
 296 high fire frequency that enhances the browsing-fire feedback shown in Fig.  
 297 1(c). In region (F), forest is stable in the bottom-left side for small values of  
 298  $f$  ( $\lesssim 0.6$  [1/yr]) and  $b$  varying between 0 and 0.004 [1/yr]. In this case the  
 299 browsing level is not enough to balance the competitive pressure of trees on  
 300 grass for space and water.

301 In region (S/F) of Fig. 3(a), characterized by  $0.6 \lesssim f \lesssim 0.9$  [1/yr] and  
 302  $b \lesssim 0.01$  [1/yr], savanna and forest are the alternative stable states. In this  
 303 region, fire is sufficient to prevent the closure of the tree canopy, whereas  
 304 browsing pressure alone is insufficient. In region (G/F), characterized by  
 305  $f \gtrsim 0.9$  [1/yr] and  $b \lesssim 0.01$  [1/yr], fire can cause the extinction of trees.  
 306 Savannas and grasslands found in these bistability regions are *fire dependent*  
 307 *ecosystems*.

308 Panels (b) and (c) of Fig. 3 represent respectively the steady states of  
 309 grass and tree fractions respectively along a browsing gradient at  $f = 0.5$

310 [1/yr]. Moving along the browsing gradient from point C (forest) to point  
311 D (savanna), the bistability region (S/F) is crossed, and the steady state  
312 is dependent on the initial condition. If the initial state is forest (point  
313 C) grasses remain absent as long as the browsing pressure is below 0.006  
314 [1/yr], (line C-X-Y in Fig. 3(b)). For further increases of  $b$ , the tree-grass  
315 co-existence is possible (line W-D in Figs. 3(b) and 3(c)) and the savanna  
316 state is reached. The transition between forest (point Y) and savanna (point  
317 W) is abrupt. Conversely, if the initial state is savanna, point D in panels  
318 (b) and (c) of Fig. 3, a browsing pressure above 0.0011 [1/yr] supports  
319 the savanna state (line D-W-Z in Fig. 3(b)), while for  $b < 0.0011$  [1/yr]  
320 grasses disappear and only trees are present at the equilibrium (line X-C).  
321 The transition between savanna (point Z) and forest (point X) is also abrupt.  
322 An example of the hysteresis cycle Y-W-Z-X may be the cyclic elephants-  
323 vegetation dynamics hypothesized by Caughley (1976). Elephants can cause  
324 a forest/woodland collapse (transition Y-W). The recovery of the woody  
325 fraction (transition Z-X) is possible only reducing the browsers pressure,  
326 e.g., when the elephants move to a different place.

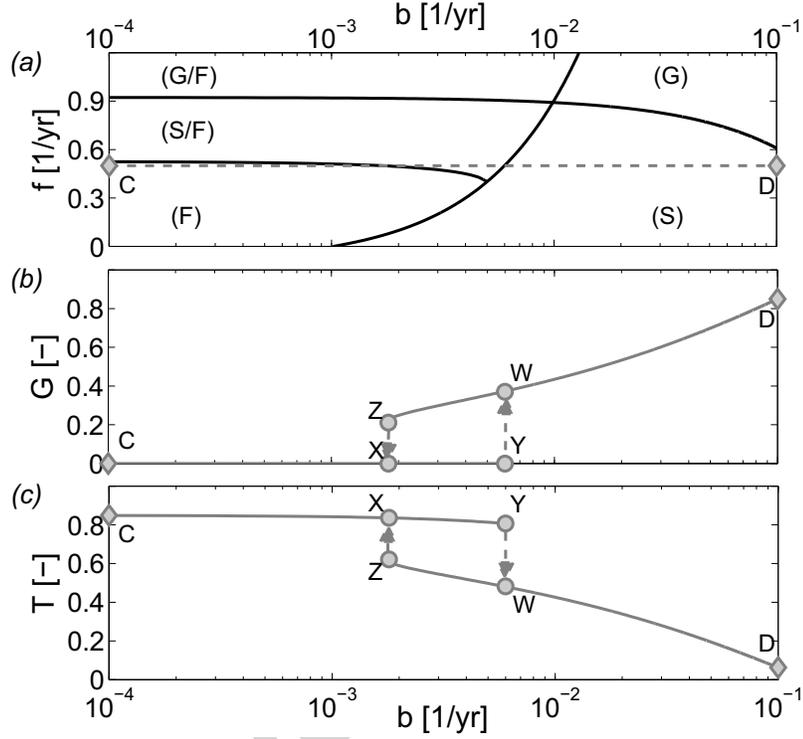


Figure 3: Vegetation type in the browsers-fire parameter plane. Panel (a) gives the stability map in the plane  $b-f$ . Panels (b) and (c) provide changes in vegetation structure over the browsing gradient C-D at fire frequency  $f = 0.5$  [1/yr]: panel (b) shows grass fraction, while panel (c) the tree fraction. Transitions X-Y and Y-W are described at the end of the *Stability in the browsers-fire space* paragraph. The other parameters values are  $p = 700$  [mm/yr],  $w_1 = 345$  [mm],  $\epsilon = 20$  [1/yr],  $\tau_T = 30$  [1/yr],  $\tau_G = 10$  [1/yr],  $\gamma_T = 2$  [1/yr],  $\gamma_G = 200$  [1/yr],  $\delta_F = 0.35$ ,  $\delta_{T0} = 0.02$  [1/yr],  $\delta_{G0} = 2$  [1/yr] and  $g = 0$  [1/yr].

327 **5. Case studies**

328 Here we examine a set of 15 sites contained in the Sankaran et al. (2005)  
329 database, which includes 854 savanna sites from all over the African conti-  
330 nent. For each of the 854 sites, measurements of mean annual rainfall, fire  
331 frequency, and woody cover are available, but information on the biomass of  
332 herbivores is available only for 129 of the sites; in particular, we are concerned  
333 with information on browsers.

334 For this reason, we selected 15 sites characterized by particularly high or  
335 low values of browsers biomass ( $\mathcal{B}$ ) and fire frequency ( $f$ ). Specifically, we  
336 mean for ‘low’ fire frequency values of  $f < 0.05$  [1/yr], and ‘low’ browsing  
337 density  $\mathcal{B} < 100$  [kg/km<sup>2</sup>]; whereas for ‘high’ fire frequency values of  $f \geq 0.5$   
338 [1/yr] and ‘high’ browsing density  $\mathcal{B} \geq 900$  [kg/km<sup>2</sup>].

339 Consequently, we examine four disturbance regimes: i) low browsing and  
340 low fire frequency (hereinafter referred to as L-L and indicated with  $\bullet$  in Figs.  
341 4-7); ii) high browsing and low fire frequency (H-L,  $\circ$ ); iii) high browsing and  
342 high fire frequency (H-H,  $\diamond$ ); iv) low browsing and high fire frequency (L-H,  
343  $\blacklozenge$ ). Figure 4 gives the geographical location of the 15 sites. Four of them are  
344 in Ivory Coast (region A), five in Kenya (region B) and six in South Africa  
345 (region C). Table 1 reports the main information about the 15 sites and  
346 indication of the disturbances regime.

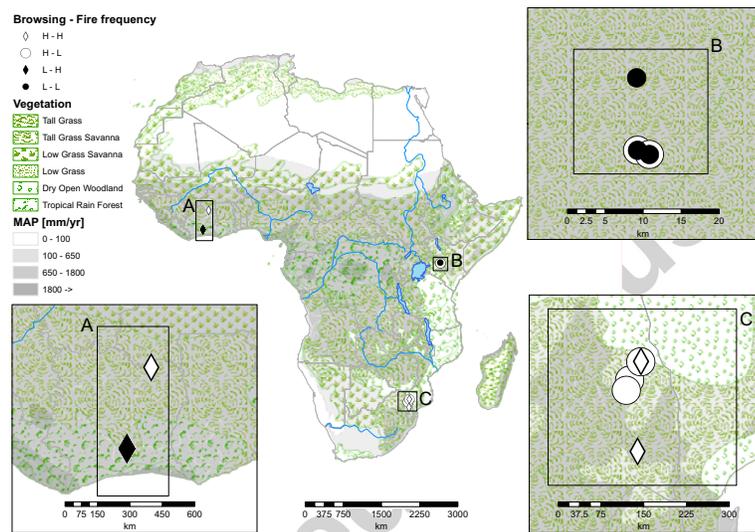


Figure 4: Location of the 15 African sites considered in Ivory Coast (A), Kenya (B), and South Africa (C). Sites symbology is representative of the disturbances regime: L-L (●), H-L (○), H-H (◇) and L-H (◊).

Table 1: Values of the main variables in the 15 African sites, after Sankaran et al. (2005). Sites labeled as A are in Ivory Coast, B in Kenya and C in South Africa. The acronymous CNP stands for Comoé National Park, MRC for Mpala Research Center, KNP for Kruger National Park.

Site	Location	MAP [mm/yr]	Woody Cover [%]	Fire return period [yr]	Browsers biomass [kg/km <sup>2</sup> ]	Disturbance regime
A1	Lamto	1163	5.5	1	88	L-H
A2	Lamto	1163	14.7	1	88	L-H
A3	Lamto	1163	40.1	1	88	L-H
A4	CNP	943	30	1	1035	H-H
B1	MRC	469	41.3	>20	0	L-L
B2	MRC	469	29.2	>20	4768	H-L
B3	MRC	530	45	>20	0	L-L
B4	MRC	530	29.8	>20	4768	H-L
B5	MRC	366	40.1	>20	0	L-L
C1	Klaserie	465	41	>10	1000	H-L
C2	Klaserie	500	35	>10	2000	H-L
C3	KNP	485	19.55	>50	907	H-L
C4	KNP	497	6.14	1	943	H-H
C5	KNP	510	1.7	1	1016	H-H
C6	KNP	435	51.9	22.25	38	L-L

347 The four sites, hereinafter referred as A1, A2, A3 and A4, in Ivory Coast  
348 (region A) are characterized by a tall grass savanna ecosystem. The sites  
349 A1, A2, and A3, located in Lamto Research Station, are characterized by a  
350 mean annual rainfall of about 1160 [mm/yr] and the vegetation is a mosaic  
351 of grass, shrub, and tree savannas on the edge of rain forests (Abbadie et al.,  
352 2006). The fourth site, A4, is located at the Comoé National Park, and is  
353 characterized by a mean annual rainfall of about 950 [mm/yr], high browsers  
354 density (about 1035 [kg/km<sup>2</sup>]), and a fire return period of 2 years, Sankaran  
355 et al. (2005). The Comoé National Park vegetation is a mosaic of dense  
356 shrubby savanna, forest islands, and gallery forests along the main rivers.  
357 The ‘climax’ vegetation of this area would be semi-deciduous forest, but its  
358 development is prevented by fires (Hovestadt et al., 1999).

359 The five sites, B1 to B5, are located at Mpala Research Centre in Kenya  
360 (region B), and are characterized by a mean annual rainfall varying from  
361 north to south between 366 [mm/yr], B5, and 530 [mm/yr], B3 and B4, and  
362 a fire return period greater than 20 years, see Table 1. A bushland community  
363 covers 99% of the landscape consisting of a discontinuous layer of perennial  
364 grasses and a shrub layer. The remaining 1% of the landscape is dominated  
365 by short-grasses (Augustine and McNaughton, 2006).

366 The South African sites (region C), C1 to C6, are located in the north-  
367 east ‘lowveld’, two of them, C1 and C2 are in the Klaserie reserve adjacent  
368 to Kruger National Park where are located sites C3, C4, C5, and C6. From  
369 north to south the mean annual rainfall varies between 435 [mm/yr] (site  
370 C6) and 510 [mm/yr] (site C5). The site C6, in the Kruger National Park,  
371 is characterized by a browsers density of 38 [kg/km<sup>2</sup>] and a fire frequency of

372 0.04 [1/yr]. The sites C1 and C2 are in the Klaserie reserve, with a browsers  
373 density of 1000 and 2000 [kg/km<sup>2</sup>] and a fire frequency of 0.1 [1/yr], and site  
374 C3 is in Kruger National Park with browsers density equal to 907 [kg/km<sup>2</sup>]  
375 and a fire return period of about 50 years (Biggs et al., 2003). The sites  
376 C4 and C5, both in Kruger National Park, are characterized by a browsers  
377 density of about 1000 [kg/km<sup>2</sup>] and a fire return period of 1 year (Sankaran  
378 et al., 2005).

379 Figure 5 shows the 15 sites in the *mean annual rainfall - woody cover*  
380 plane, where the line represents the piecewise linear regression on the 99th  
381 quantile as in Sankaran et al. (2005). The upper limit of woody cover is  
382 approximately linearly dependent on the mean annual precipitation when is  
383 below 650 [mm/yr], and independent above this value. The piecewise linear  
384 regression is representative of the maximum woody cover attainable for a  
385 given mean annual rainfall in the absence of disturbances. Ecosystems close  
386 to this limit are *climate dependent*. An ecosystem represented by a point  
387 below the piecewise linear regression is a site where disturbances allow a  
388 tree cover different from the one expected considering the climate conditions  
389 only. In this case the ecosystem is denominated *disturbance dependent* (*fire*  
390 *dependent* is one example). Conversely, if the action of fire and herbivores  
391 induces on the vegetation only small modifications with respect to the state  
392 predicted by the climate conditions, we refer to this ecosystem as *perturbed*  
393 *climate dependent*.

394 Figure 5 shows that the 15 sites are located around two values of mean  
395 annual rainfall, 400-500 [mm/yr] (L-L, H-L, and H-H sites) and 1160 [mm/yr]  
396 (L-H sites), except for Mpala research center, site B5, with a mean annual

397 rainfall of 360 [mm/yr] and Comoé National Park, site A4, that presents a  
 398 mean annual value of about 950 [mm/yr]. Using the stability maps given  
 399 in Fig. 6, we compare the observed ecosystem composition with the steady  
 400 state derived by the model. The stability maps in the  $b - f$  parameters space  
 401 are drawn at  $p = 500$  [mm/yr] in Fig. 6(a), and at  $p = 1160$  [mm/yr] in Fig.  
 402 6(b). Stability maps in Fig. 6, are obtained using the following values of the  
 403 parameters:  $w_1 = 345$  [mm],  $\epsilon = 20$  [1/yr],  $\tau_T = 30$  [1/yr],  $\tau_G = 10$  [1/yr],  
 404  $\gamma_T = 2$  [1/yr],  $\gamma_G = 200$  [1/yr],  $\delta_{T0} = 0.02$  [1/yr],  $\delta_{G0} + g = 2$  [1/yr] and  
 405  $\delta_F = 0.35$ .

406 We assume an allometric relation between the density of browsers,  $\mathcal{B}$ , in  
 407 units of [kg/km<sup>2</sup>], and the removal coefficient,  $b$ , in units of [1/yr], mathe-  
 408 matically defined by the power law function  $b = a_b \mathcal{B}^{\alpha_b}$ . This is supported by  
 409 the existing allometric law between the body mass of mammals and the cor-  
 410 responding metabolic rate characterized by an exponent approximately equal  
 411 to 0.7, (Schmidt-Nielsen, 1984, Dodds et al., 2001, White and Seymour, 2003,  
 412 Kolokotronis et al., 2010). Here the parameters of the allometric equation are  
 413 calculated as follows. The vegetation removal term  $-bT$  causes a reduction  
 414 of the tree extinction time, quantified in  $\exp(-(\delta_{T0} + b)t)$ . Thus if we assume  
 415 that in presence of a ‘low’ browsers density, say of 100 [kg/km<sup>2</sup>], the trees  
 416 extinction time is reduced of 33%, and a ‘high’ density, say of 900 [kg/km<sup>2</sup>],  
 417 the reduction is of 66% (with a reference value of  $\delta_{T0} = 0.02$  [1/yr]) then  
 418 the corresponding estimates are  $b = 0.01$  [1/yr] and  $b = 0.04$  [1/yr]. These  
 419 couples of  $b$  and  $\mathcal{B}$  allow to estimate the parameters of the allometric rela-  
 420 tionships using the Least Squares Method:  $a_b = 5.82 \cdot 10^{-4}$  [(km<sup>2</sup>/kg) <sup>$\alpha_b$</sup> /yr]  
 421 and  $\alpha_b = 0.62$  dimensionless. The estimate of the exponent  $\alpha_b$  (even though

422 an approximation) is not very different from the one used for the metabolic  
 423 rate-mass law ( $\approx 0.7$ ). Note that a similar relation could be obtained to  
 424 link the grazers density with the removal coefficient  $g$ . The allometric rela-  
 425 tionship allows to convert the browsers densities observed in the 15 sites of  
 426 interest into values of the removal coefficient  $b$ . Figure 6 gives the location  
 427 of the sites in the  $b - f$  plane.

428 The 15 sites considered have been located on the stability maps according  
 429 to the observed values of mean annual rainfall, browsers density, and fire  
 430 return period, see Table 1. Note that for sites where the fire return period  
 431 is relatively long and not given specifically (i.e., given as disequalities  $> 10$ ,  
 432  $> 20$ ,  $> 50$  years in Table 1), we have assumed  $f = 0$  [1/yr].

433 Each site falls within a stability region according to the estimated param-  
 434 eters' values. Clearly, changes in the parameters' values can cause changes  
 435 in the stability region to which a site pertains.

436 We have performed, for each site, a sensitivity analysis varying (increasing  
 437 and decreasing) one parameter at the time until the stability region changes,  
 438 obtaining a range of variability for each parameter.

439 This analysis allows to characterize, locally, which parameter is to be con-  
 440 sidered 'stiff' (i.e., a small variation in the parameter value causes a structural  
 441 change in the stable steady state) and which 'sloppy' (i.e., a small variation  
 442 of the parameter does not correspond a structural change of the steady state)  
 443 in the sense of Gutenkunst et al. (2007).

444 According to the model, Eq.(1), and in order to reduce the number of  
 445 parameters to be investigated, we have grouped together  $p$  and  $w_1$  as  $p/w_1$ ,  
 446  $\delta_{T0}$  and  $b$  as  $\delta_{T0} + b$ , and  $\delta_{C0}$  and  $g$  as  $\delta_{C0} + g$ . Note that a parameter

447 could behave asymmetrically under increasing or decreasing of its value, i.e.,  
 448 a parameter could be sloppy on the right side (increasing its value) and stiff  
 449 on the left side (decreasing its value). Here, for simplicity, we have classified  
 450 a parameter as stiff in average if its range of variability normalized by the  
 451 parameter value is below 3.5, otherwise it is considered sloppy. Here we have  
 452 considered 10 as the maximum magnification factor of a parameter.

453 Figure 7 presents the results of the sensitivity analysis for some keyed  
 454 sites: A1, B1, B2, C1, C2, C4 and C6. Site A1 is chosen as representative  
 455 of all the L-H sites. The site B1 is representative of the behavior of the  
 456 L-L sites B3 and B5, but not of the L-L site C6. The sites B2 and C4 are  
 457 representative of the behavior of the sites B4 and C5 respectively. Figure 7  
 458 will be discussed in the light of the disturbance regimes in the next section  
 459 where we examine separately the four different combinations of disturbances.

#### 460 *L-L sites*

461 In Fig. 5 L-L sites ( $\bullet$ ) are located close to the piecewise linear regression  
 462 indicating that these are *climate dependent ecosystems*. The low level of  
 463 browsing and fire disturbances makes the woody cover of these sites mainly  
 464 dependent by the mean annual rainfall. In the stability map (Fig. 6(a)),  
 465 obtained for  $p = 500$  [mm/yr], sites B1 and B3 fall in the forest region and  
 466 site C6 in the savanna region close to the boundary with the forest. The  
 467 woody cover is 41.3% and 45% respectively in sites B1 and B3, and 51.9%  
 468 in site C6, see Table 1 and Fig. 5. The fact that the sites B1 and B3,  
 469 observed as savannas, fall within the forest stability region can be explained  
 470 considering the results of the sensitivity analysis. From this, it is possible to  
 471 observe that 1) the parameters  $\delta_{T0} + b$  and  $\gamma_G$  are stiff for sites B1 and B3;

472 2) the stability region of these sites changes from forest to savanna if  $\delta_{T0} + b$   
 473 or  $\gamma_G$  slightly increase. Concerning site C6, the stiff parameters are  $\gamma_T$  and  
 474  $\delta_{G0} + g$ , Fig. 7, and the stability region of C6 changes from savanna region  
 475 to forest if small increases of  $\gamma_T$  or  $\delta_{G0} + g$  occur, from savanna to grassland  
 476 if  $\gamma_T$  decreases. These results are coherent with the position of these sites  
 477 close to the boundary between forest and savanna in the stability map, Fig.  
 478 6(a).

#### 479 *H-L sites*

480 H-L sites, namely B2, B4, C1, C2 and C3 ( $\circ$  in Fig. 5) receive approxi-  
 481 mately the same mean annual rainfall of L-L sites, but have a lower woody  
 482 cover. The high level of browsing pressure makes the ecosystems *perturbed*  
 483 *climate dependent*. All the H-L sites belong to the savanna region, as ex-  
 484 pected, Fig. 6 (a).

485 The sensitivity analysis identifies  $\epsilon$ ,  $\tau_G$  and  $\delta_{T0} + b$  as stiff parameters for  
 486 sites B2 and B4,  $\gamma_T$  and  $\delta_{G0} + g$  for sites C1 and C3, and  $\delta_{T0} + b$  for site C2.  
 487 For sites B2 and B4 a small increase of one among  $\epsilon$ ,  $\tau_G$  and  $\delta_{T0} + b$  moves the  
 488 equilibrium from savanna to grassland, while a decrease of  $\delta_{T0} + b$  transforms  
 489 the ecosystem in forest. A variation of  $\gamma_T$  induces a change in the stable  
 490 region of sites C1 and C3: from savanna to forest if  $\gamma_T$  is increased, and to  
 491 grassland if  $\gamma_T$  is decreased. An increase in  $\delta_{G0} + g$  also causes a change from  
 492 savanna to forest for sites C1 and C3. Site C2 belongs to grassland region  
 493 when  $\delta_{T0} + b$  is increased, and to forest if the parameter value is reduced.

494 *H-H sites*

495 Of the H-H sites, C4 and C5 ( $\diamond$  in Fig. 5) have approximately a mean  
 496 annual rainfall of 500 [mm/yr] with a low woody cover (1.7% and of 6.1%, re-  
 497 spectively), and are the result of the browsers-fire synergy. These ecosystems  
 498 are considered *perturbed climate dependent*. According to the parametriza-  
 499 tion, these sites do not fall into savanna (as expected) but in grassland region  
 500 (see Fig. 6(a)). This disagreement could be explained noting that the woody  
 501 cover observed in the sites is very low, thus the ecosystems are more sim-  
 502 ilar to a grassland than to a savanna. On the other hand, the sensitivity  
 503 analysis indicates  $p/w_1$ ,  $\gamma_T$  and  $\delta_{C0} + g$  as stiff parameters; thus a slight  
 504 increase of parameters values  $p/w_1$  and  $\gamma_T$  remap the sites into a savanna  
 505 region. A small increase of  $\delta_{C0} + g$  allocates the sites into the bistability  
 506 region grassland/forest, as well as, a strong reduction in the values of  $\delta_{T0} + b$   
 507 or  $\gamma_g$ .

508 *L-H sites*

509 L-H sites, namely A1, A2, and A3 ( $\blacklozenge$  in Fig. 5) are characterized by an  
 510 observed woody cover of about 5.5%, 14.7%, and 40.1%, respectively, lower  
 511 than the ones (about 80%) expected by the model for a mean annual rainfall  
 512 of about 1160 [mm/yr], see Fig. 5. The abundance of water combined with  
 513 a low browsing pressure ( $\mathcal{B} = 88$  [kg/km<sup>2</sup>]) would favour a forest state, but  
 514 the high fire frequency (in average one event/year) causes the reduction of  
 515 the woody cover. According to this combination of environmental forcings,  
 516 the model locates these savanna sites in the bistability region savanna/forest,  
 517 see Fig. 6(b). This result is supported by the geographical location of sites  
 518 A1, A2, and A3: they are close to the edge of the rainforest (Abbadie et al.,

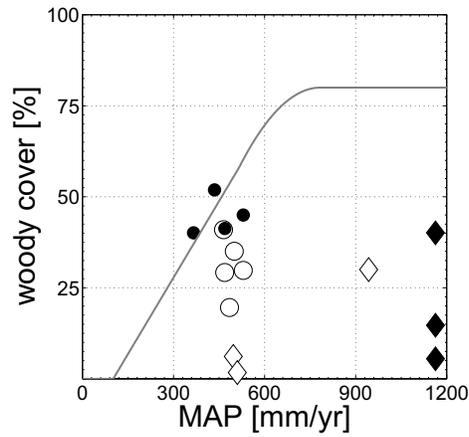


Figure 5: Representation of the 15 African sites in the *mean annual rainfall - woody cover* plane. Sites are represented according to the disturbances regime: L-L ( $\bullet$ ), H-L ( $\circ$ ), H-H ( $\diamond$ ), and L-H ( $\blacklozenge$ ).

519 2006). This is an example of bistability in space between savanna and forest  
 520 (Schröder et al., 2005).

521 For L-H sites, the sensitivity analysis shows that all the parameters, ex-  
 522 cept for  $\tau_T$ , are stiff, see Fig. 7: this is coherent with the hypothesis that  
 523 these savannas are fragile, and their vegetation structure can be completely  
 524 modified by small environmental variations.

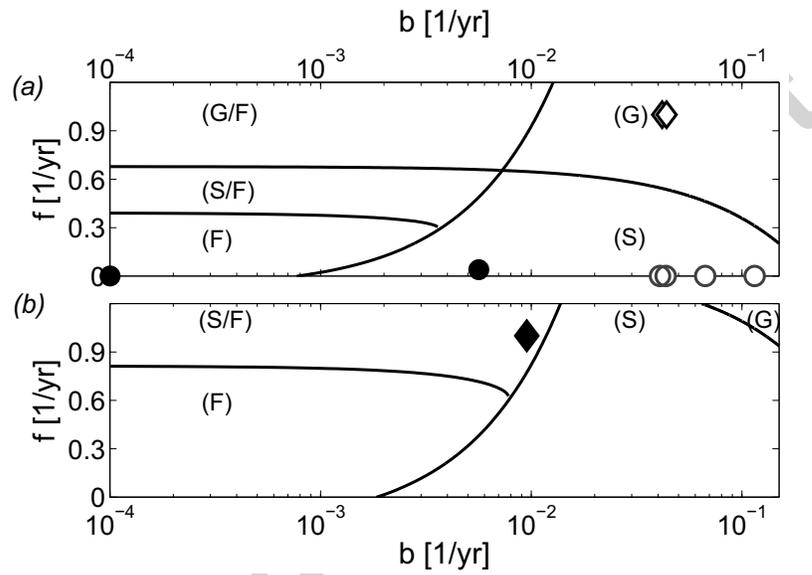


Figure 6: Representation of the 15 African sites in the *herbivores - fire* plane. Panel (a) shows the points in the stability map  $b - f$  for  $p = 500$  [mm/yr]; Panel (b) gives the points in the stability maps  $b - f$  for  $p = 1160$  [mm/yr]. The other parameters values are  $w_1 = 345$  [mm],  $\epsilon = 20$  [1/yr],  $\tau_T = 30$  [1/yr],  $\tau_G = 10$  [1/yr],  $\gamma_T = 2$  [1/yr],  $\gamma_G = 200$  [1/yr],  $\delta_{T0} = 0.02$  [1/yr],  $\delta_{G0} + g = 2$  [1/yr],  $\delta_F = 0.35$ . Sites are represented according to the disturbances regime: L-L ( $\bullet$ ), H-L ( $\circ$ ), H-H ( $\diamond$ ), and L-H ( $\blacklozenge$ ).

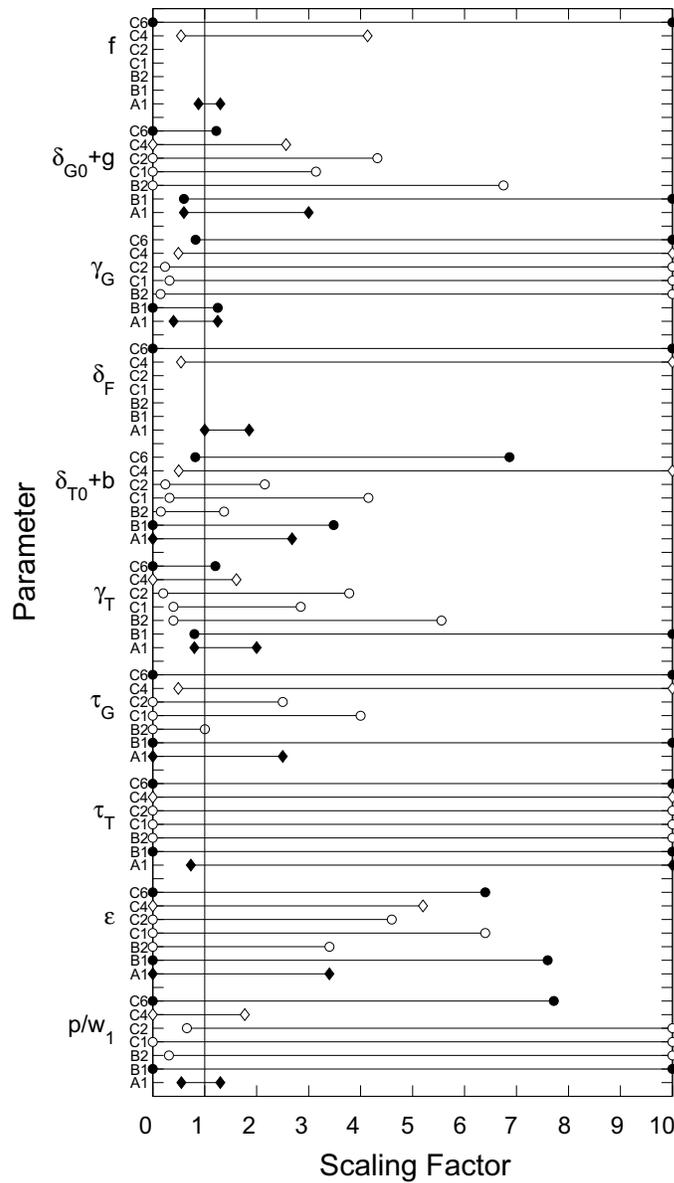


Figure 7: Scaling factor for each of the parameters in order to realize a change of the stable equilibrium, for the sites: A1, B1, B2, C1, C2, C4, C6. Values of the scaling factor  $> 1$  indicate a magnification of the parameter, while values  $< 1$  a reduction. Note that the sensitivity analysis for  $f$  (and consequently for  $\delta_F$ ) at B1, B2, C1, and C2, has not been represented because for these sites the fire occurrence is  $\approx 0$  [1/yr]. Symbols at the end points of each line stand for L-L (●), H-L (○), H-H (◇), and L-H (◆) sites.

525 **6. Conclusions**

526 We have investigated the conditions for the existence and the stability  
527 of the savanna domain in the herbivores-fire parameter space, distinguishing  
528 between browsing and grazing disturbances. This analysis is based on a  
529 minimal ecohydrological model and shows how depending on the level of  
530 disturbances savanna can be stable, or bistable with the forest.

531 In particular, when the innate tendency of trees to overtop grasses is  
532 weakened by fire and/or browsing, and grasses are favored by low grazing  
533 pressure, the existence of a savanna is mainly due to balanced competition  
534 mechanisms. This happens when water is scarce and browsing pressure or  
535 harvesting of trees is high. In this situation fire is not fundamental for the  
536 tree-grass co-existence and the savanna stability. The system is a *climate*  
537 *dependent* or a *perturbed climate dependent ecosystem*.

538 When the water availability and the grazing pressure are high and the  
539 browsing pressure is low, savannas are maintained by fire, creating a demo-  
540 graphic bottlenecks in tree population recruitment. In this case, savannas  
541 are in bistable condition with forests, and must be considered a *disturbance*  
542 *dependent ecosystem*, more precisely *fire dependent ecosystem*. Bistability  
543 implies that, under certain conditions, a small variation of a parameter (such  
544 as grazing and browsing parameters) can cause macroscopic changes in the  
545 vegetation. These transitions can be sometimes irreversible.

546 This analysis suggests that the tree-grass co-existence in savanna is pos-  
547 sible as a *climate dependent ecosystem*, or a *disturbance dependent ecosystem*  
548 (classification introduced by Bond et al., 2003), or a *perturbed climate de-*  
549 *pendent ecosystem*. However it is important to point out that a *disturbance*

550 *dependent savanna* is a more fragile ecosystem than a *climate dependent sa-*  
551 *vanna*, because the presence of bistability can induce abrupt transitions to  
552 other vegetated states.

553 The analysis of data available in 15 African sites (referring to particularly  
554 high or low values of fire occurrence and browsers density) helps to illustrate  
555 the theoretical findings. Since the comparison between model and data is  
556 conditioned by the uncertainty associated to parameters' estimates, we have  
557 discussed and commented the results of the comparison within the framework  
558 of a local sensitivity analysis of the parameters. This type of analysis is  
559 fundamental in order to 1) quantify the reliability of the model predictions,  
560 and 2) understand what happens if modifications in a parameter value occur.

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#### 565 **References**

#### 566 **References**

567 Abbadie, L., Gignoux, J., Le Roux, X., Lepage, M., 2006. Lamto, Structure,  
568 Functioning, and Dynamics of a Savanna Ecosystem. Springer & Verlag,  
569 New York.

570 Accatino, F., De Michele, C., Vezzoli, R., Donzelli, D., Scholes, R., 2010.

- 571 Tree-grass co-existence in savanna: Interactions of rain and fire. *J. Theor.*  
572 *Biol.* 267, 235 – 242.
- 573 Amarasekare, P., 2003. Competitive coexistence in spatially structured en-  
574 vironments: a synthesis. *Ecol. Lett.* 6, 1109 – 1122.
- 575 Augustine, D., McNaughton, S., 2006. Interactive effects of ungulate herbi-  
576 vores, soil fertility, and variable rainfall on ecosystem processes in a semi-  
577 arid savanna. *Ecosystems* 9, 1242 – 1256.
- 578 Barnes, R.F., 1983. The elephant problem in Ruaha National Park, Tanzania.  
579 *Biol. Cons.* 26, 127 – 148.
- 580 Baudena, M., D'Andrea, F., Provenzale, A., 2010. An idealized model for  
581 tree-grass coexistence in savannas: the role of life stage structure and fire  
582 disturbances. *J. Ecol.* 98, 74 – 80.
- 583 Baxter, P.W.J., Getz, W.M., 2005. A model-framed evaluation of elephant  
584 effects on tree and fire dynamics in African savannas. *Ecol. Appl.* 15, 1331  
585 – 1341.
- 586 de Beer, Y., Kilian, W., Versfeld, W., van Aarde, R.J., 2006. Elephants and  
587 low rainfall alter woody vegetation in Etosha National Park, Namibia. *J.*  
588 *Arid Environ.* 64, 412 – 421.
- 589 Ben-Shahar, R., 1993. Patterns of elephant damage to vegetation in northern  
590 Botswana. *Biol. Cons.* 142, 3099 – 3107.
- 591 Biggs, R., Biggs, H.C., Dunne, T.T., Govender, N., Potgieter, A.L.F., 2003.

- 592 Experimental burn plot trial in the Kruger National Park: history, exper-  
593 imental design and suggestions for data analysis. *Koedoe* 46, 1 – 15.
- 594 Bond, W.J., Keeley, J.E., 2005. Fire as a global 'herbivore': the ecology and  
595 evolution of flammable ecosystems. *Trends Ecol. Evol.* 20, 387 – 394.
- 596 Bond, W.J., Midgley, G.F., Woodward, F.I., 2003. What controls South  
597 African vegetation - climate or fire? *S. Afr. J. Bot.* 69, 79 – 91.
- 598 Bond, W.J., van Wilgen, B.W., 1996. *Fire and Plants*. Chapman & Hall,  
599 London, UK.
- 600 Borgogno, F., D'Odorico, P., Laio, F., Ridolfi, L., 2009. Mathematical mod-  
601 els of vegetation pattern formation in ecohydrology. *Rev. Geophys.* 47,  
602 RG1005.
- 603 Bucini, G., Hanan, N.P., 2007. A continental-scale analysis of tree cover in  
604 African savannas. *Glob. Ecol. Biogeogr.* 16, 593 – 605.
- 605 Caughley, G., 1976. The elephant problem - an alternative hypothesis. *East*  
606 *Afr. Wildl. J.* 14, 265 – 283.
- 607 Coetzee, B.W.T., Tincani, L., Wodu, Z., Mwasi, S.M., 2008. Overgrazing and  
608 bush encroachment by *Tarchonanthus camphoratus* in a semi-arid savanna.  
609 *Afr. J. Ecol.* 46, 449 – 451.
- 610 De Michele, C., Vezzoli, R., Pavlopoulos, H., Scholes, R.J., 2008. A minimal  
611 model of soil water-vegetation interactions forced by stochastic rainfall in  
612 water-limited ecosystems. *Ecol. Model.* 212, 397 – 407.

- 613 Dodds, P.S., Rothman, D.H., Weitz, J.S., 2001. Re-examination of the 3/4-  
614 law of metabolism. *J. Theor. Biol.* 209, 9 – 27.
- 615 D’Odorico, P., Laio, F., Ridolfi, L., 2006. A probabilistic analysis of fire-  
616 induced tree-grass coexistence in savannas. *Am. Nat.* 167, E79 – E87.
- 617 Dublin, H.T., 1995. Vegetation Dynamics in the Serengeti-Mara ecosystem:  
618 the Role of Elephants, Fire and Other Factors, in: Sinclair, A.R.E., Arcese,  
619 P. (Ed.), *Serengeti II: Dynamics, Management, and Conservation of an*  
620 *Ecosystem*. The University of Chicago Press, Chicago, pp. 71 – 90.
- 621 Fernandez-Illescas, C., Rodriguez-Iturbe, I., 2003. Hydrologically driven hi-  
622 erarchical colonization-competition models: the impact of interannual cli-  
623 mate fluctuations. *Ecol. Monographs* 73, 207 – 222.
- 624 Frost, P.G.H., Medina, E., Menaut, J.C., Solbrig, O.T., Swift, M., Walker,  
625 B.H., 1986. Responses of savanna to stress and disturbance. *Biol. Int.*  
626 *Spec. Issue* 10, 1 – 82.
- 627 Gilad, E., Shachak, M., Meron, E., 2007. Dynamics and spatial organization  
628 of plant communities in water-limited systems. *Theor. Popul. Biol.* 72, 214  
629 – 230.
- 630 Govender, N., Trollope, W.S.W., van Wilgen, B.W., 2006. The effect of fire  
631 season, fire frequency, rainfall and management on fire intensity in savanna  
632 vegetation in South Africa. *J. Appl. Ecol.* 43, 748 – 758.
- 633 Gutenkunst, R.N., Waterfall, J.J., Casey, F.P., Brown, K.S., Myers, C.R.,

- 634 Sethna, J.P., 2007. Universally sloppy parameter sensitivities in systems  
635 biology models. *PLoS Comput. Biol.* 3, e189.
- 636 Hanan, N.P., Sea, W.B., Dangelmayr, G., Govender, N., 2008. Do fires in sa-  
637 vannas consume woody biomass? A comment on approaches to modelling  
638 savanna dynamics. *Am. Nat.* 171, 851 – 856.
- 639 Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion -  
640 implications for conservations. *Cons. Biol.* 6, 324 – 337.
- 641 Holdo, R.M., 2007. Elephants, fire, and frost can determine community  
642 structure and composition in Kalahari woodlands. *Ecol. Appl.* 17, 558 –  
643 568.
- 644 Hovestadt, T., Yao, P., Linsenmair, K.E., 1999. Seed dispersal mechanisms  
645 and the vegetation of forest islands in a WestAfrican forest-savanna mosaic  
646 (Comoé National Park, Ivory Coast). *Plant Ecol.* 144, 1 – 25.
- 647 Klausmeier, C., 1999. Regular and irregular patterns in semiarid vegetation.  
648 *Science* 284, 1826 – 1828.
- 649 Kolokotronis, T., Savage, V., Deeds, E.J., Fontana, W., 2010. Curvature in  
650 metabolic scaling. *Nature* 464, 753 – 756.
- 651 van de Koppel, J., Riekerk, M., Weissing, F., 1997. Catastrophic vegetation  
652 shifts and soil degradation in terrestrial grazing systems. *Trends Ecol.*  
653 *Evol.* 12, 352 – 356.
- 654 van Langevelde, F., van de Vijver, C.A.D.M., Kumar, L., van de Koppel, J.,  
655 de Ridder, N., van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder,

- 656 L., Bond, W.J., Prins, H.H.T., Rietkerk, M., 2003. Effects of fire and  
657 herbivory on the stability of savanna ecosystems. *Ecology* 84, 337 – 350.
- 658 Laws, R.M., 1970. Elephants as agents of habitat and landscape change in  
659 East Africa. *Oikos* 21, 1 – 15.
- 660 May, R.M., 1977. Thresholds and breakpoints in ecosystems with a multiple  
661 of stable states. *Nature* 269, 471 – 477.
- 662 McNaughton, S.J., Georgiadis, N.J., 1986. Ecology of African grazing and  
663 browsing mammals. *Annu. Rev. Ecol. Syst.* 17, 39 – 65.
- 664 Moleele, N.M., Perkins, J.S., 1998. Encroaching woody plant species and  
665 boreholes: is cattle density the main driving factor in the Olifants Drift  
666 communal grazing lands, south-eastern Botswana? *J. Arid Environ.* 40,  
667 245 – 253.
- 668 Murphy, P.G., Lugo, A.E., 1986. Ecology of tropical dry forest. *Annu. Rev.*  
669 *Ecol. Syst.* 17, 67 – 88.
- 670 O'Connor, T.J., 1995. Acacia karroo invasion of grassland: environmental  
671 and biotic effects influencing seedling emergence and establishment. *Oe-*  
672 *cologia* 103, 214 – 223.
- 673 Prins, H.H.T., van der Jeugd, H.P., 1993. Herbivore population crashes and  
674 woodland structure in East-Africa. *J. Ecol.* 81, 305 – 314.
- 675 Rietkerk, M., Boerlijst, M.C., van Langevelde, F., HilleRisLambers, R.,  
676 van de Koppel, J., Kumar, L., Prins, H.H.T., de Roos, A., 2002. Self-  
677 organization of vegetation in arid ecosystems. *Am. Nat.* 160, 524 – 530.

- 678 Roques, K.G., O'Connor, T.G., Watkinson, A.R., 2001. Dynamics of shrub  
679 encroachment in an African savanna: relative influences of fire, herbivory,  
680 rainfall and density dependence. *J. Appl. Ecol.* 38, 268 – 280.
- 681 Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J.,  
682 Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo,  
683 J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B.,  
684 Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hier-  
685 naux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W.,  
686 Tews, J., Worden, J., Zambatis, N., 2005. Determinants of woody cover in  
687 African savannas. *Nature* 438, 846 – 849.
- 688 Schmidt-Nielsen, K., 1984. *Scaling. Why is animal size so important?* Cam-  
689 bridge University Press, Cambridge.
- 690 Scholes, R.J., Archer, S.R., 1997. Tree-grass interactions in savannas. *Annu.*  
691 *Rev. Ecol. Syst.* 28, 517 – 544.
- 692 Scholes, R.J., Walker, B.H., 1993. *An African Savanna: synthesis of the*  
693 *Nylsvley study. 1*, Cambridge University Press, Cambridge.
- 694 Schröder, A., Persson, L., De Roos, A.M., 2005. Direct experimental evidence  
695 for alternative stable states: a review. *Oikos* 110, 3 – 19.
- 696 Shmida, A., Burgess, L., 1988. Plant growth-form strategies and vegeta-  
697 tion types in arid environments, in: Werger, M. J. A., Aart, P. J. M. V.  
698 D., During, H. J., Verhoeven, J. T. A. (Ed.), *Plant form and vegetation*  
699 *structure*. SPB Academic Pub, The Hague, pp. 211 – 241.

- 700 da Silveira Lobo Sternberg, L., 2001. Savanna-forest hysteresis in the tropics.  
701 Glob. Ecol. Biogeogr. 10, 369 – 378.
- 702 Skarpe, C., 1990. Structure of the woody vegetation in disturbed and undis-  
703 turbed arid savanna, Botswana. Vegetatio 87, 11 – 18.
- 704 Skarpe, C., Aarrestad, P.A., Andreassen, H.P., Dhillion, S.S., Dimakatso, T.,  
705 du Toit, J., Halley, D.J., Hytteborn, H., Makhabu, S., Mari, M., Marokane,  
706 W., Masunga, G., Modise, D., Moe, S.R., Mojaphoko, R., Mosugelo, D.,  
707 Motsumi, S., Neo-Mahupeleng, G., Ramotadima, M., Rutina, L., Sechele,  
708 L., Sejoe, T.B., Stokke, S., Swenson, J.E., Taolo, C., Vandewalle, M.,  
709 Wegge, P., 2004. The return of the giants: Ecological effects of an increas-  
710 ing elephant population. Ambio 33, 276 – 282.
- 711 Smit, G.N., 2004. An approach to tree thinning to structure southern African  
712 savannas for long-term restoration from bush encroachment. J. Environ.  
713 Manage. 71, 179 – 191.
- 714 Tilman, D., 1994. Competition and biodiversity in spatially structured habi-  
715 tats. Ecology 75, 2 – 16.
- 716 Vezzoli, R., De Michele, C., Pavlopoulos, H., Scholes, R.J., 2008. Dryland  
717 ecosystems: The coupled stochastic dynamics of soil water and vegetation  
718 and the role of rainfall seasonality. Phy. Rev. E 77, 397 – 407.
- 719 Walter, H., 1971. Ecology of tropical and subtropical vegetation. Oliver and  
720 Boyd, Edinburgh, UK.

- 721 White, C.R., Seymour, R.S., 2003. Mammalian basal metabolic rate is pro-  
722 portional to body mass<sup>2/3</sup>. *Proc. Natl. Acad. Sci. U.S.A.* 100, 4046 – 4049.
- 723 Wiegand, K., Ward, D., Saltz, D., 2005. Multi-scale patterns and bush  
724 encroachment in an and savanna with a shallow soil layer. *J. Veg. Sci.* 16,  
725 311 – 320.
- 726 Zimmermann, J., Higgins, S., Grimm, V., Hoffman, J., Linstder, A., 2009.  
727 Grass mortality in semi-arid savanna: the role of fire, competition, and  
728 self-shading. *Perspect. Plant Ecol. Evol. Syst.* 12, 1 – 8.

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#### Highlights of the manuscript

- We investigate the existence and stability of savannas in the herbivores-fire space
- The analysis is based on a spatially implicit ecohydrological model
- The results show the types of savannas as function of the disturbance levels
- An application is discussed with the help of a local sensitivity analysis
- The comparison between model and data supports the theoretical findings

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