



## Research Paper

## Do spatially homogenising and heterogenising processes affect transitions between alternative stable states?

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## ABSTRACT

Large-scale sudden transitions in ecosystems are expected as result of changing global climate or land use. Current theory predicts such sudden transitions especially to occur in spatially homogeneous ecosystems, whereas transitions in spatially heterogeneous systems will be more gradual. The spatial heterogeneity of ecosystems is determined as result of opposing spatial processes that are either increasing or decreasing heterogeneity. Hence, the relative strength of these opposing processes is expected to determine how sensitive the system is to transitions, which has not been explored to date. In our study, fire, as a spatially heterogenising process, and plant dispersion, as a spatially homogenising process, in tropical savannas were modelled to analyse how these processes affect the occurrence of sudden transitions from grass dominance to tree dominance. Savannas are expected to change due to precipitation or land use changes towards either tree dominance or grass dominance. We found that high rates of grass dispersion can create homogeneous grass patches, but only when the spatial extent of fire is limited to small patches that are spread across the landscape. When fires occur in larger patches, a heterogeneous pattern is generated. In spatially heterogeneous savannas, we found a more gradual responses to increasing grazing pressure compared to the sudden transitions when savannas are spatially homogeneous. The most sudden transitions were found in near-homogeneous grass distributions where the interaction between grazing, grass dispersion and fire led to a few homogeneous patches. Within these homogeneous patches, transitions were complete and sudden. We conclude that when spatially heterogenising processes are stronger than spatially homogenising processes, heterogeneous systems are created. In these systems large-scale sudden transitions are less likely to occur, because transitions at smaller scales are averaged over space. We discuss how this has implications for responses of savannas to climatic and land use change.

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## 1. Introduction

The occurrence of large-scale sudden and significant changes in ecosystems, so called catastrophic shifts (Scheffer et al., 2001; Van Langevelde et al., 2003), is an important topic in ecology. These sudden shifts can be the result of perturbations that push a system into the basin of attraction of a different state or the result of more subtle and gradual changes in external driving forces. Theory predicting when such shifts can happen originates from modelling studies (Scheffer et al., 2009; Dakos et al., 2011) and empirical studies have tested the predictions (e.g., Dai et al., 2012; Carpenter et al., 2011). Large-scale sudden transitions in ecosystems are predicted

as result of changing global climatic conditions (Hirota et al., 2011; Staver et al., 2011) or land use (Van Langevelde et al., 2003). Initial studies were based on fairly spatially homogeneous systems such as shallow lakes (Carpenter et al., 2011). However, an important aspect of ecosystems is that they are hardly ever spatially homogeneous, most systems are spatially heterogeneous. These spatial patterns have an influence on the stability of ecosystems (Rietkerk et al., 2002; Dakos et al., 2011) and can even be used as an indicator of stability in some cases (Rietkerk et al., 2004). The existence of spatial patterns has been identified to reduce the occurrence of system-wide collapses in response to an external driving force (e.g., Peterson, 2000; Nystrom and Folke, 2001). In heterogeneous systems, only locally catastrophic shifts are predicted to occur in response to a force, that are averaged out over space, causing a more gradual response to this force at a larger scale (Van Nes and Scheffer, 2005).

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The spatial patterns in ecosystems originate from spatial processes. Some processes generate spatial patterns (Groen et al., 2008; Liu et al., 2016), so called heterogenising processes. At the same time other processes can eradicate these spatial patterns, so called homogenising processes. Van Nes and Scheffer (2005) showed that homogenising processes can nullify the impact of spatial patterns on the occurrence of catastrophic shifts in response to external driving forces. Spatially heterogeneous systems with strong presence of homogenising processes showed abrupt responses at large scales to such forces, while the same systems in absence of homogenising processes showed a more gradual response. It can be expected that homogenising and heterogenising processes interact in maintaining or eradicating patterns, depending on which process plays a more prominent role in an ecosystem. In this study we investigate how both processes interact, and whether catastrophic shifts can be expected when homogenising processes dominate and more gradual responses when heterogenising processes dominate. In this study we demonstrate how these opposing dynamics affect the occurrence of transitions between alternative stable states for tropical savannas as example ecosystem. Earlier studies showed the existence of alternative stable states in savannas (e.g., Van Langevelde et al., 2003). We focus on shifts in savanna tree cover where an open savanna can be transformed into a woodland savanna, which is also known as bush encroachment (e.g. Trollope 1974; Stafford et al., 2017), and not on shifts between savanna tree cover and forest tree cover as occurring in the forest-savanna boundary (e.g. Favier et al., 2012). Because an important spatially heterogenising process, fire, is sensitive to changes in global climatic (Andela and Van der Werf, 2014) and land use (Van Langevelde et al., 2003), we can expect that the role of spatial heterogeneity in savanna dynamics will change. We show that even though everything else is constant, differences in the strength of spatially homogenising and heterogenising processes can affect whether large-scale sudden shifts occur at all or not. This finding contributes to our understanding under what conditions sudden transitions in ecosystems will occur when conditions change.

## 2. Model ecosystem

Savannas are systems where a continuous vegetation layer of grasses and herbaceous plants (referred to as “grass” in this study for simplicity) is interspersed by the occurrence of patches of shrubby vegetation and trees (referred to as “trees”). Trees and grasses are assumed to compete for soil resources, mainly moisture (Walker and Noy-Meir, 1982). Under heavy grazing pressure, savanna systems can switch from tree and grass coexistence to a tree dominated state (Van Langevelde et al., 2003) where grasses are outcompeted. This has negative consequences for many grazing species that depend on savannas for their forage, including cattle and sheep in extensive livestock systems (Dalle et al., 2006; Angassa, 2014). One explanation for the occurrence of catastrophic shifts in savannas is related to a positive feedback mechanism between grass biomass, fire intensity and mortality of trees as a result of high fire intensities.

Fire is a prime determinant of the tree-grass balance (Scholes and Archer, 1997; Van Langevelde et al., 2003). In most savannas grass is the prime source of fuel for fire, while tree canopies form disconnected patches that cannot carry the fire. The negative effect of fires on grasses is limited because, although frequent fires reduce the build-up of total grass biomass over time, grass survival is rarely affected by fire (Van de Vijver, 1999), so grass growth is not really negatively affected by fire. The effect of fire on trees is to a large extent determined by fire intensity, which in turn is positively correlated to grass biomass (Higgins et al., 2000). Under a

given set of conditions, such as soil moisture availability and grazing pressure, the “grass biomass–fire intensity” feedback can result in a system having two ecosystem states: a situation with abundant grass biomass, high intensity fires and low tree biomass (“grass dominated”) or a situation with low grass biomass, low intensity fires and abundant tree biomass (“tree dominated”). When external driving forces (such as grazing) change across a critical level the system can shift from a grass dominated system to a tree dominated system fairly abruptly. These rapid changes in vegetation structure are observed in savannas (Roques et al., 2001).

Fire can be considered as a spatially heterogenising process in savannas. Empirical studies have shown that the impact of a fire in a savanna at a given time and space is highly variable (Govender et al., 2006). The impact of fire is determined by an array of biophysical factors, one of which is the spatial patterning of vegetation itself. For example, trees tend to cluster in frequently burned areas (Groen et al., 2008) and if tree patches are present, they can protect saplings from the negative effects of fires, enhancing clustering (Van Langevelde et al., 2014). However, the heterogenising impact of fires can be expected to depend on the size of a fire. Occasional large fires remove trees over a large extent and consequently create large homogeneous grass dominated areas while smaller fires at higher frequencies can generate a patchwork of heterogeneity. So depending on the average size of fires and the frequency of burning, fires can create spatial heterogeneity in savannas. In this study, the occurrence of fires will be considered as a spatially heterogenising process.

At the same time plants disperse, colonizing new locations. For trees this occurs mainly by dispersion of seeds. For many grass species, on top of seed dispersion, spatial spread takes place by stoloniferous growth. The dispersion of plants will be considered as a spatially homogenising effect.

## 3. Model

Our model was based on Van Langevelde et al. (2003). We used the main differential equations from their non-spatial model as the basis of our spatial model and we analysed model behaviour by means of simulations. We started by confirming that our model with fire as a homogeneous and continuous process would give similar results as the mathematical solutions presented by Van Langevelde et al. (2003). Then we included the discrete nature of fires in a stepwise approach. First, we modelled fire as a discrete process in time, and secondly, we made it spatially discrete. In every simulation we made sure that the overall fire occurrence was kept constant.

### 3.1. Modelling vegetation growth

The model distinguishes grass biomass (H) that consists mainly of herbaceous species, and woody biomass (W) that consists mainly of tree species. In the model, trees and grasses compete for water, and grasses are considered to be superior competitors for this, but only have access to the top layer. Trees are modelled to also have access to deeper layers, which makes that the system allows for coexistence of trees and grasses when sufficient water is available to percolate to the deeper layers. This implementation of water redistribution among trees and grasses is commonly known as the two-layer hypothesis (Walter, 1971; Walker and Noy-Meir, 1982). When there is a lot of soil water available, trees in the model tend to get an advantage over grasses due to their exclusive access to the lower soil layer, and they outcompete the grasses. In such wet conditions, grasses only manage to sustain themselves when they can exert a negative effect on trees through fire. Changes in grass

biomass are formulated as:

$$\begin{aligned} \frac{dH_i}{dt} = & r_H w_t H_i \frac{\theta_H}{\theta_H H_i + \theta_W W_i + w_s} - d_H H_i - c_H G H_i - k_H n H_i \\ & + D_H \left( \sum_{j=1}^8 (H_j) - 8 H_i \right) \end{aligned} \quad (1)$$

and for woody biomass as:

$$\begin{aligned} \frac{dW_i}{dt} = & r_W \left[ w_t W_i \frac{\theta_W}{\theta_H H_i + \theta_W W_i + w_s} \right. \\ & \left. + w_s \right] - d_W W_i - c_W B W_i - k_W n a H_i W_i \end{aligned} \quad (2)$$

The symbols, interpretation, units and values of all parameters and variables are listed in Table 1. Time steps in the model are in years.

The first term in Eqs. (1) and (2) describes the increase in biomass due to growth which is modelled as a function of water availability after Walker and Noy-Meir (1982). Grasses only have access to water available in the top soil layer ( $w_t$ ), and are competing with woody species for water in this stratum. Woody species also have access to the sub soil layer ( $w_s$ ). The amount of water in both sub soil ( $w_s$ ) and top soil ( $w_t$ ) is a function of the amount of infiltrated water ( $w_{in}$ ) and the water retention capacity of the top soil layer, which is expressed as:

$$\begin{aligned} w_s = & \alpha(w_{in} - \beta) \quad |w_{in} > \beta \\ w_s = & 0 \quad |w_{in} \leq \beta \end{aligned} \quad (3)$$

and

$$w_t = w_{in} - w_s \quad (4)$$

in which  $\beta$  is the soil moisture content in the top soil layer above which water starts to percolate to the sub soil layer (the water retention capacity), and  $\alpha$  is the proportion of excess water that percolates to the sub soil layer. This formulation allows that trees can always grow in locations, provided there is water in  $w_s$  because when  $W_i = 0$  the first term in Eq. (2) reduces to  $r_W w_s$ . This means that local extinction of trees is not possible in this model when  $w_s > 0$ , while for grasses it is. In the presented analyses, we look at grasses coping to survive in competition with trees ( $w_s > 0$ ) and not vice versa, and hence this formulation avoids that we have to take care of local tree extinctions.

The second term in Eqs. (1) and (2) refers to the biomass loss due to mortality and senescence ( $d$ ), and the third term in Eq. (1) refers to the loss of grass biomass due to grazing ( $G$ ) and the third term in Eq. (2) refers to the loss to woody biomass due to browsing ( $B$ ). The effects of browsing were analysed in the paper by Van Langevelde et al. (2003), and is included here for consistency, although in this study we only look at the effects of grazing. The last term in Eqs. (1) and (2) describes the loss of biomass due to fire ( $n$ ). For grass biomass this is a fraction of the grass biomass ( $k_H$ ) that is lost per fire, multiplied by the fire frequency ( $n$ ). For woody biomass, the effect of fire is stronger because it is influenced by the amount of grass biomass present as fuel load, moderated by a fire intensity coefficient ( $a$ ). This is assuming a positive relation between grass biomass availability, fire intensity and loss of woody biomass (Higgins et al., 2000). This formulation causes the positive feedback between grass biomass and fire, as shown in Van Langevelde et al. (2003).

### 3.2. Making the model spatial

We implemented the simulation by a simple Euler integration where we multiplied each time step by a factor 0.01 to ensure a smooth transition between moments. We converted this model into a spatial model, by simulating it on a lattice consisting of 100 by 100 cells with a size of 1 m<sup>2</sup>. The area is torus shaped, to avoid edge effects. The simulated area is homogeneous in incoming water and no slope is assumed. Each cell of the lattice can contain both grass and woody biomass. Dispersion of grass biomass was made spatially explicitly through the application of diffusion equations.

Fire was made discrete by treating  $n$  as a binomial variable. So fire at a given moment and location can either be on ( $n = 1$ ) or off ( $n = 0$ ). Overall fire frequency was always kept 0.5, so half of all the cells were burning ( $n = 1$ ) at a given time, as this resulted in conditions with bi-stable states (see also Model experiments). Distributing fire purely random means that every cell has an equal chance of 50% of catching fire. In this case, effectively every cell is an independent unit that randomly in time can ignite. To make truly spatial fire simulations, spatial dependence between locations is needed where the chance of catching fire is depending on conditions in neighbouring cells. This was implemented by making the chance for a cell to catch fire conditional on the amount of grass biomass present (Hennenberg et al., 2006). The chance to ignite was highest for the cell with the highest amount of grass biomass and lowest for the cell with the lowest amount of grass biomass, decreasing linearly, and with a total area of unity under this curve. Ignited locations would be the centre of a patch to catch fire and, depending on patch size, sufficient patches were ignited to make sure that each time step exactly 50% of all the modelled surface would burn. Fire was distributed in patches of various sizes to control how strongly fires created heterogeneity. A few large patches probably create more heterogeneity than many small patches, because the latter are more likely to be homogeneously distributed across space.

The last term in Eq. (1) represents the dispersion of grasses over the landscape. Dispersion was simulated as diffusion assuming that very small quantities of biomass move from one location to the next, described by:

$$\frac{\delta H_i}{\delta t} = D_H (H_j - H_i) \quad (5)$$

in which  $D_H$  is the dispersion rate (Cain, 1990; Rietkerk et al., 2002), and the subscripts stand for different locations. For each location  $i$ , dispersion of grass from or to the eight direct neighbours of  $i$  is taken into account. In an intermediate calculation all the differences between a cell and its eight neighbours ( $\sum_{j=1}^8 (H_j) - 8 * H_i$ ) is calculated and multiplied by the diffusion coefficient to calculate how much a cell will gain or lose each time step. Dispersion can be switched off in the simulations by setting  $D_H = 0$ , and on by setting  $D_H > 0$  (but  $< 1$  and normally fairly low values). We only modelled dispersion of grass biomass, because this is the vegetation component that interacts with the fire dynamics. We realize that also woody plants redistribute over space, and more complexity could be added by modelling woody biomass dispersion in a similar fashion. But as pointed out before, trees can appear anywhere given the formulation of the equations when competition with grasses or frequency of fires is sufficiently low.

### 3.3. Model experiments

For the comparison of our results with model behaviour as reported in Van Langevelde et al. (2003), we ran a number of non-spatial simulations (i.e. a single cell without any spatial interaction with neighbours occurring) with conditions for which the mathematically solved model predicted alternative stable states and system shifts (see Table 1 for used values). This means that simu-

**Table 1**  
Parameters and their values or ranges of values used in the model. Most settings are based on Van Langevelde et al. (2003) and references therein.

Symbols	Interpretation	Units	Values
$H$	Grass biomass	$\text{g m}^{-2}$	0–400
$W$	Woody biomass	$\text{g m}^{-2}$	0–1000
$r_H$	Water use efficiency by grass biomass	$\text{g mm}^{-1}$	1.0
$r_W$	Water use efficiency by woody biomass	$\text{g mm}^{-1}$	0.5
$\theta_H$	Rate of water uptake per unit grass biomass	$\text{mm yr}^{-1} \text{g}^{-1}$	0.9
$\theta_W$	Rate of water uptake per unit woody biomass	$\text{mm yr}^{-1} \text{g}^{-1}$	0.5
$d_H$	Specific loss of grass biomass due to senescence	$\text{yr}^{-1}$	0.9
$d_W$	Specific loss of woody biomass due to senescence	$\text{yr}^{-1}$	0.4
$c_H$	Consumption coefficient of grass biomass by grazers	$\text{m}^2 \text{g}^{-1} \text{yr}^{-1}$	0.02
$c_W$	Consumption coefficient of woody biomass by browsers	$\text{m}^2 \text{g}^{-1} \text{yr}^{-1}$	0.02
$k_H$	Specific loss of grass biomass due to fire	$\text{yr}^{-1}$	0.1
$k_W$	Specific loss of woody biomass due to fire expressed per unit of energy	$\text{W}^{-1}$	0.01
$n$	Frequency of fire per year	$\text{yr}^{-1}$	0 or 1
$a$	Coefficient for the increase in fire intensity with grass biomass	$\text{W m}^{-1} \text{g}^{-1}$	0.5
$\alpha$	Proportion of excess water that percolates to sub soil layer	–	0.4
$\beta$	Soil moisture content in the top soil layer above which water starts to percolate to the sub soil layer	mm	300
$w_{in}$	Annual amount of infiltrated water	$\text{mm m}^{-2} \text{yr}^{-1}$	700
$G$	Grazer density	$\text{g m}^{-2}$	0–30
$B$	Browser density	$\text{g m}^{-2}$	5
$D_H$	Dispersion coefficient for grass biomass	$\text{t}^{-1}$	0 to 0.001

lations were run at intermediate levels of precipitation (expressed by  $w_{in}$ ), which concurs with findings by Staver and Levin (2012) who concluded that fire feedback with vegetation mainly drive tree cover at intermediate rainfall levels, but not high and low rainfall levels.

We initialized these simulations either with a sufficiently high initial amount of grass biomass just above the threshold between the two alternative states for the given parameter settings ( $H=40 \text{ g m}^{-2}$ ) or too low grass biomass just below this threshold ( $H=30 \text{ g m}^{-2}$ ), to detect the alternative equilibria. We first ran a simulation where fire was included as frequency  $n=0.5$ , similarly to how it was formulated in the original model to test whether the simulation would yield similar results as the mathematically derived equilibria as reported earlier in Van Langevelde et al. (2003). Then we tested what the effect of discretizing and randomizing the fire was. For that we also ran a second simulation where fire frequency was either 0 or 1, and alternating, making that on average fire frequency would still be 0.5. Thirdly we ran a simulation where fire was also discrete but occurring randomly in time making sure that on average fire would occur with a frequency of 0.5. Lastly, a series of non-spatial simulations was made where grazer density ( $G$ ) was varied as an external driving force from  $0 \text{ g m}^{-2}$  up to  $25 \text{ g m}^{-2}$ . At high grazer density, grass biomass is suppressed, leading to a tree dominated equilibrium, whereas low grazer densities result in a grass dominated equilibrium.

Then we made simulations where fire was modelled spatially explicit and dispersion was included. To simulate the impact of homogenising (dispersion) and heterogenising (fire) processes, we varied the strengths of these processes. To change the strength of the heterogenising effect of fire, we ran simulations with different sized fire patches. In a single simulation, fire patch sizes would be of constant size and distributed such that 50% of the simulated areas is burned in each time step (thus  $n=0.5$ ). Patch sizes were varied from 2500 cells (i.e., 2 patches of 50 by 50) down to patches of 4 cells (1250 patches of 2 by 2). Many small fire patches tend to result in a more homogenous pattern than a few large fire patches. Likewise, to change the strength of homogenising effect of dispersion we varied the dispersion from no dispersion ( $D_H=0$ ), very little dispersion ( $D_H=1 \times 10^{-7}$ ) up to a fairly large amount of dispersion ( $D_H=1 \times 10^{-3}$ ).

For the most extreme cases of homogenisation (1250 burning patches and  $D_H=1 \times 10^{-3}$ ) and heterogenisation ( $D_H=0$  and 2 burning patches) we simulated how the system responded to changes in the external driver, grazer density. For these sim-

ulations, 10 repetitions were made, and each simulation was initialized with a grazer density of  $15 \text{ g m}^{-2}$  and an initial grass biomass of  $30$  or  $40 \text{ g m}^{-2}$ . When the simulation reached an equilibrium, the grazer density was changed to a values between 0 and  $25 \text{ g m}^{-2}$  and continued again until the system reached an equilibrium. Whether a simulation reached an equilibrium was determined by testing whether  $\sum_i \frac{dH_i}{dt}$  (i.e. the rate of change in grass biomass at the level of the entire area) would become 0, or started to fluctuate stably around 0.

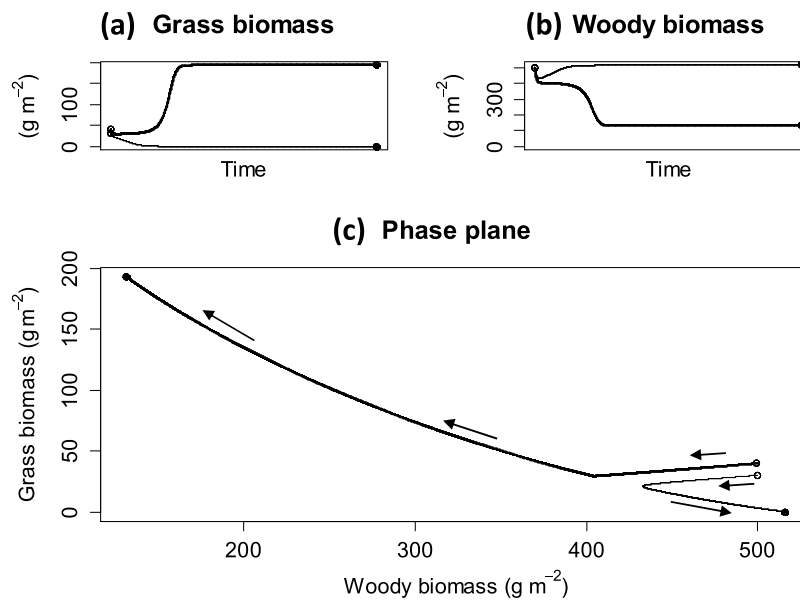
### 3.4. Quantifying the spatial patterns

To assess whether model simulations that include spatial processes actually resulted in spatial patterns, we assessed their variograms. Variograms indicate the semi-variance of an area for pairs of locations at different distances from each other (i.e. lags). Locations nearby typically resemble each other more than locations further away, and hence, variograms often show an increasing trend over increasing lags. We estimated ten different variograms per model run every 100th time step based on ten different subsets of 500 randomly selected points from the modelled surface, and extracted the maximum semi-variance from these variograms. Low maximum semi-variance will indicate that most points in a map are very similar, and hence that the map is very homogeneous. Higher maximum semi-variance indicates that locations differ from each other and hence that a certain patterning is occurring.

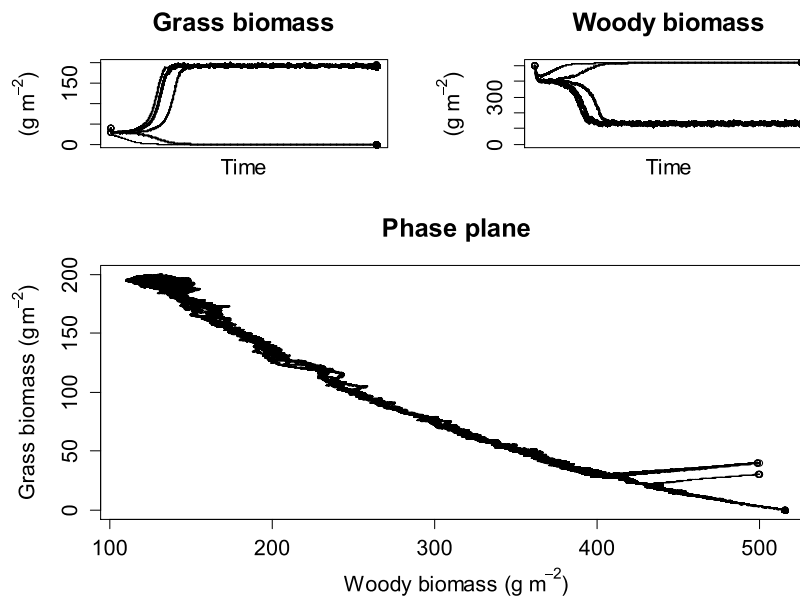
## 4. Results

The results from the first 2 simulations (Fig. 1) show the same stable equilibria in terms of grass and woody biomass under the conditions used as described by Van Langevelde et al. [2003]. If the model is initialized with sufficient grass biomass ( $H=40 \text{ g m}^{-2}$ ) for the parameter values presented in Table 1) fire can suppress woody biomass and result in an equilibrium with both grass and woody biomass (Fig. 1). With just a little bit less grass biomass ( $H=30 \text{ g m}^{-2}$ ), the system develops towards a system with only woody biomass and no grass biomass. When fire is discrete but also random (i.e. the “third” simulation) and cells are initialized with sufficient grass biomass ( $H=40 \text{ g m}^{-2}$ ) around 70% of the cells end in a grass dominated equilibrium (Fig. 2). The other 30% end up in the woody dominated equilibrium. This effect, when averaged over a modelled spatial grid, results in an overall 30% lower grass biomass in spatial simulations. When the initial amount





**Fig. 1.** Simulations showing the behaviour of the model without any spatial component, and with fire modelled as a continuous process. Given the initial amount of grass (a) and woody (b) biomass in the system, either coexistence between woody and grass biomass (thick line, initial  $H = 40 \text{ g m}^{-2}$ ) or a system dominated by woody biomass and no grass biomass (thin line, initial  $H = 30 \text{ g m}^{-2}$ ) can be found. The trajectories to either equilibria show that a very small differences in initial conditions can lead to these very different final situations (c). The result for the simulation with fire as a discrete process that occurs every 2nd time step (i.e. the second simulation) shows exactly the same result.



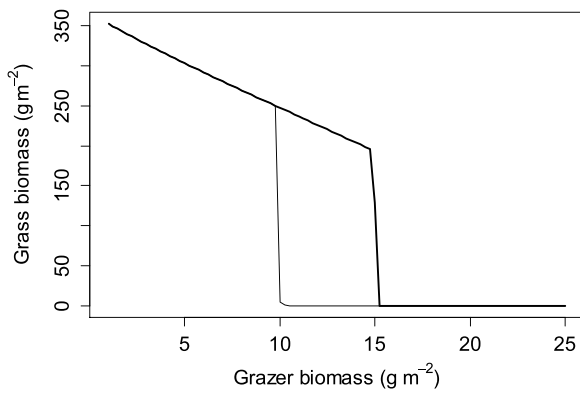
**Fig. 2.** Simulations with fire as a discrete process and where fire occurs randomly with a probability of 0.5 with a high initial grass biomass (thick line,  $H = 40 \text{ g m}^{-2}$ ) and a low initial grass biomass (thin line,  $H = 30 \text{ g m}^{-2}$ ). Around 70% of the cells that were initiated with high grass biomass developed into an equilibrium with both grass and woody biomass, while 30% developed towards the woody biomass dominated equilibrium. For cells that were initialized with low grass biomass 100% developed into the wood dominated state.

of grass biomass is below the threshold (in our simulations initial  $H = 30 \text{ g m}^{-2}$  was below the threshold), the woody biomass will immediately suppress the grass biomass. This consequently suppresses the impact of fire, regardless whether these fires occur systematically (the 1st and second simulation) or randomly (the third simulation). Therefore these simulations all develop to the wood dominated equilibrium.

Fig. 3 shows the effect of grazing on the equilibrium grass biomass when not modelled spatially. When initialized with high grass biomass, the high grass biomass equilibrium is sustained

under higher grazer densities ( $G < 15 \text{ g m}^{-2}$ ) than when initialized with low grass biomass ( $G < 10 \text{ g m}^{-2}$ ). With grazer densities between 10 and  $15 \text{ g m}^{-2}$ , alternative stable states are found.

When the model is spatially explicit, fire and dispersion settings affect the resultant spatial patterns (Fig. 4; and supplementary materials for an animation). Whether these patterns constitute different levels of spatial heterogeneity is visualized by plotting the maximum semi-variance extracted from variograms that were estimated every 100th time step (Fig. 5). When fires occur in few, but large patches and no dispersion is occurring, the highest level of



**Fig. 3.** Effect of grazing on the equilibrium biomass of grass biomass. Simulations are initialized with high grass biomass ( $H = 40 \text{ g m}^{-2}$ ; thick line) or low grass biomass ( $H = 30 \text{ g m}^{-2}$ ; thin line).

semi-variance (and thus heterogeneity) is recorded. Increasing the level of dispersion with few large fire patches decreases the level of semi-variance, but only to a limited extent. If fires occur in many smaller patches and no dispersion is occurring, semi-variance is also lower than with a few large patches and no dispersion. When dispersion increases and when many small fire patches occur, the semi-variance is the lowest. So there is a clear interaction between dispersion and size of fire patches in the model. Increasing the dispersion rate reduces spatial heterogeneity, but this effect is much more pronounced when fires create more, but smaller sized patches.

Increasing the level of grazing causes the total amount of grass biomass to decline (Fig. 6) similar to the non-spatial model. However in the spatial models grasses remain in the system at much higher grazer densities ( $G > 15 \text{ m}^{-2}$ ) albeit with lower grass biomass. When starting with a high initial amount of grass biomass, there appear no sudden transitions to the absence of grasses contrary to the non-spatial simulations. These sudden transitions do occur when simulations are initialized with low grass biomass (grey lines Fig. 6). This makes sense, because when the grass biomass is low, the system is dominated by trees. The intensity of fires is also low so no patterns are created by fires. An exception is the case where dispersion and large fires occur (lower left Fig. 6). Under these conditions, even with a low initial grass biomass, the system can become occupied with grasses, although not in every simulation (cf. dashed and solid lines). This happens when a number of large fires occur around roughly the same location in the first time steps, stimulating grass patches in these locations. Due to dispersion, these grass patches can grow, and create a growing patch of grasses, until the equilibrium is reached that sustains both grasses and woody biomass.

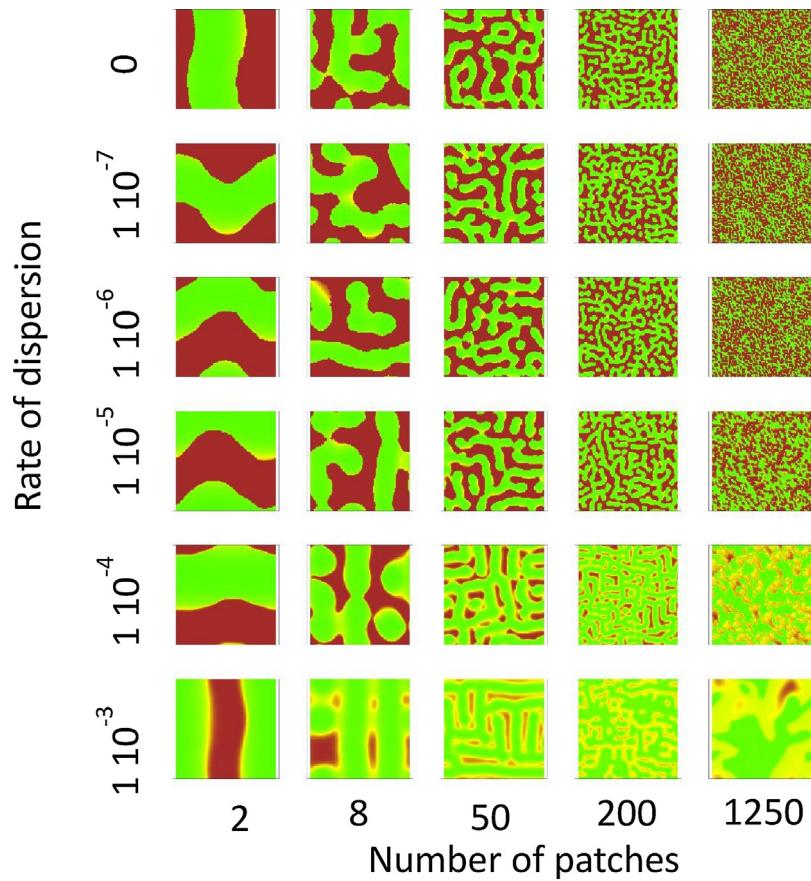
When simulations are initialized with high grass biomass, despite not showing transitions from grass dominated to tree dominated, there are non-linear responses observed. Especially for the case with dispersion and many small fires (lower right Fig. 6), where two “non-linear” drops occur. These drops occur at fairly high values of grazer densities. This is the simulation where the pattern resulting from the interaction between fire and dispersion is the most homogeneous (Fig. 5). Consequently, this is the condition where system-wide collapses are most likely to occur. Under these conditions, however, a matrix with a high grass biomass, and one large patch with lower (but stable) grass biomass develop consistently in the simulations. When grazing density increases, the first drop is when the patch with low grass biomass suddenly switches to a state without grasses. When grazer density increases even further, also the remaining matrix with grass collapses and a system-wide equilibrium without grass occurs.

## 5. Discussion

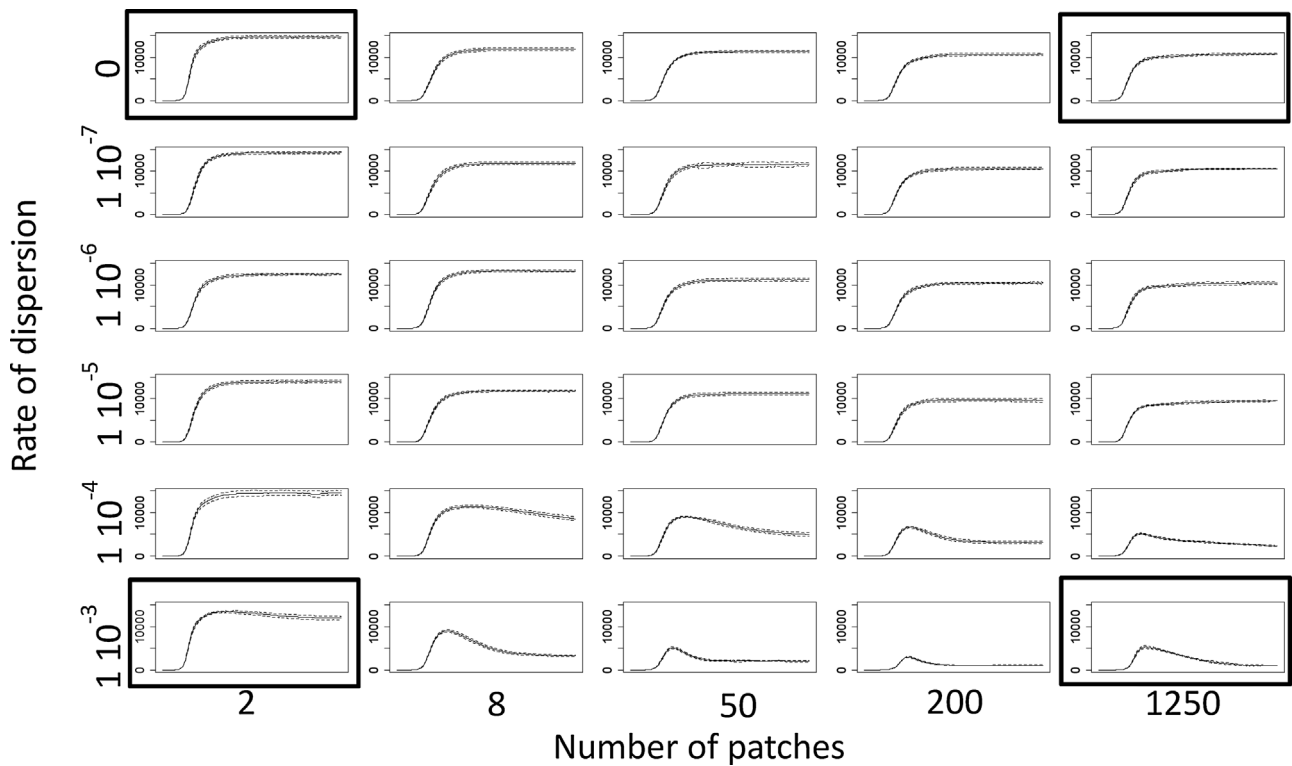
In this study, we analysed how spatially heterogenising and homogenising processes influence the occurrence of transitions between alternative stable states. We used tropical savannas as model system where fire acts as a heterogenising process and plant dispersion as a homogenising process that, depending on the spatial heterogeneity that is generated by these processes, transitions between alternative stable states disappear. The occurrence of fires is influenced by changes in climatic conditions, especially when precipitation changes, and land use, especially heavy grazing. Changes in burned area in African savannas have been correlated to changes in precipitation (Andela and Van der Werf, 2014). Dispersion is less directly influenced, but productivity of grasses is influenced by global change. Grasses are mainly  $C_4$  type plants in African savannas and benefit less from increases in  $\text{CO}_2$ -concentrations than trees which are mainly  $C_3$  type plants (Higgins and Scheiter, 2012). This could influence the capacity of grasses to colonize nearby patches via stoloniferous growth.

Our simulations show that when initial grass biomass is low, for example as a result of low rainfall, no spatial heterogeneity can be created by fires under most conditions and sudden transitions can still occur. However, when sufficient grass biomass is present under more humid conditions, spatial heterogeneity is created and the response of the system becomes more gradual, although not necessarily linear.

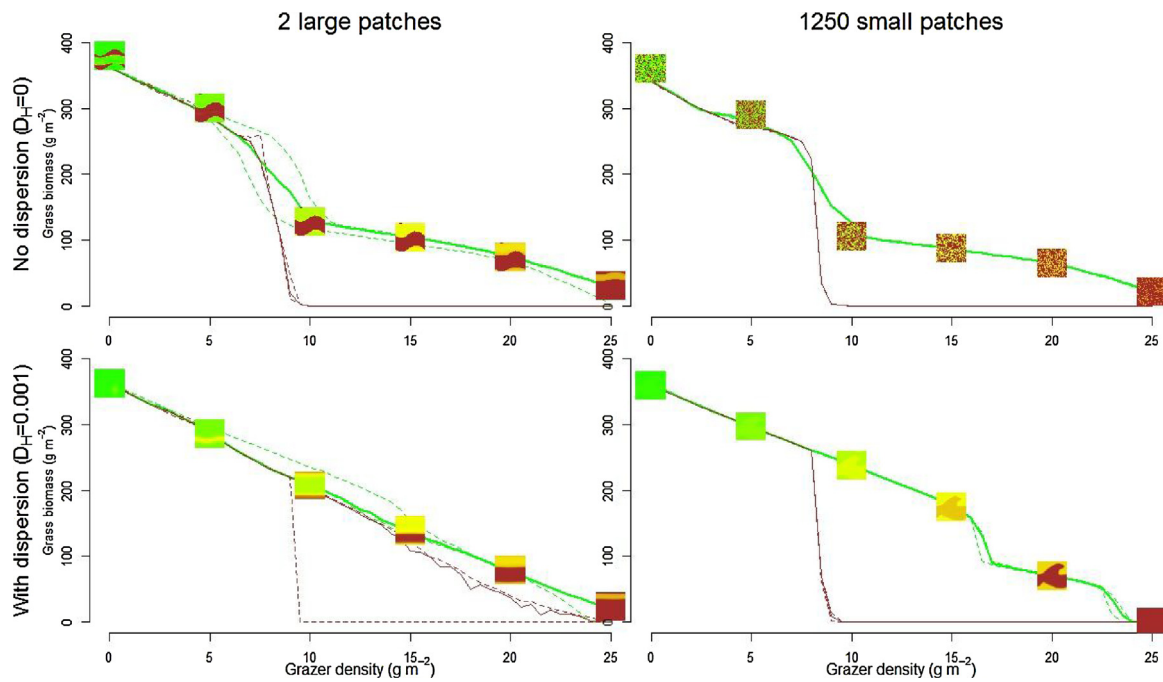
Also, the model analysis illustrates that fires can create patches in savannas when sufficient grass biomass is available, and that grass dispersion reduces this spatial heterogeneity. Previous studies that looked at the effect of spatial patterning on the occurrence of sudden system shifts have often stressed the importance of short range facilitation and long range competition (e.g., Kéfi et al., 2008). Also in our system, there seems to be a case of local facilitation. Areas with high grass biomass are more likely to ignite, and therefore locally suppress the growth of its competitor, woody biomass. This in turn is advantageous for the grass biomass, resulting in higher grass biomass. However, there seems to be no long range competition between grasses in this system. Grasses further away can still benefit from high grass biomass at a certain location when there is a continuous fuel load and fires are sufficiently large. So whether grasses further away actually benefit from an ignition at a high biomass location depends on the grass cover. Possibly, percolation theory plays a role here (MacKay and Jan, 1984; Staver and Levin, 2012). Assuming a random distribution of grasses, a grass cover higher than  $\sim 50\%$  allows fires to percolate and suppress tree growth further away from the ignition location. When grass cover is under this threshold, fires only have an effect locally. As has been shown in empirical studies, trees cluster when fire frequency increases (Groen et al., 2008) and these clusters suppress the impact of wild fires on woody species (Van Langevelde et al., 2014). So in mesic savannas, where without the effect of fires, woody biomass would be the dominant life forms, at least 40–50% grass cover is needed to sustain the grass biomass (Hennenberg et al., 2006; Archibald et al., 2009). In the study by Loehle et al. (1996) a tree cover of 20% (and hence 80% is dominated by grasses) already showed an accelerated expansion of shrubs for well-watered areas near streams in a forest-prairie ecotone in the U.S.A. This suggests that under humid conditions, perhaps even a higher grass cover is needed than predicted by percolation theory. Besides, grazing can be expected to have a moderating effect on this threshold. With heavy grazing, even in the presence of fires grasses can be excluded from the system according to our modelling results. So with increased grazing, a larger grass cover is probably needed to sustain the ‘grass-cover fire feedback’. These hypotheses are testable, where by means of remote sensing the distribution of grass cover across various mesic to arid savanna systems can



**Fig. 4.** Resulting patterns at end of simulations under different settings for fire (many small or few large patches) and dispersion (high or low rates). Green indicates high grass biomass and brown indicates low grass biomass (i.e. wood dominated). Yellow indicates areas with intermediate grass biomass. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 5.** Maximum semi-variance for variograms that were estimated for every 100th time step per simulation. Higher levels of semi-variance indicate more spatial heterogeneity in the patterns. The simulations highlighted by boxes were used for further exploration of the occurrence of transitions between states as a result of changing grazing pressures.



**Fig. 6.** Equilibrium grass biomass under different grazer densities ( $G$ ) without dispersion of grass biomass (upper row) or with dispersion of grass biomass (lower row). Models were simulated with different burn area sizes, either two large fires (left column) or many small fires (right column). The green lines indicate simulations with a high initial grass biomass ( $H_0=40$ ) and brown lines simulations with low initial grass biomass ( $H_0=30$ ). Dashed lines indicate the minimum and maximum values of 10 simulations and the solid lines median values. At intervals of  $5\ g\ m^{-2}$  of grazer densities, the resulting grass biomass pattern is depicted. Green indicates high grass biomass ( $\sim 400\ g\ m^{-2}$ ), yellow intermediate grass biomass ( $\sim 200\ g\ m^{-2}$ ) and brown no grass biomass. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

be quantified. The expectations would be that the minimum grass cover observed in mesic savannas would be higher than in arid savannas, and similarly, that this minimum cover would be higher in heavy grazed areas than in areas with a lower grazing pressure. When areas become wetter, e.g., due to climatic change, only areas with sufficient grass cover are expected to remain savanna, while regions with too little grass cover will change into a wooded state.

The exact threshold at which fires no longer can spread through a savanna landscape would depend on a number of factors, because the assumption that grass is distributed randomly in the landscape does not hold as it is found in patterns, which is demonstrated in this study. The size of fire events and the rate of grass dispersion determine what kind of patterns are created in our analyses (Fig. 4). In some instances banded patterns, rather than a random distribution of grass dominated patches appear, and these will determine how well fire can spread throughout the system. There are a number of factors, apart from the vegetation pattern itself, that influence how well fires spread through an ecosystem as well. These are mainly governed by weather conditions. For example, high wind speeds will promote fire spread. So for areas with on average high wind speeds, the critical grass cover to sustain the grass-cover-fire feedback will be much lower than in areas without wind.

More importantly, our results illustrate that a system-wide collapse can be prevented by spatial heterogeneity, as suggested by Van Nes and Scheffer (2005), and that this depends on the relative strengths of contrasting spatial processes. This complements results as presented by Villa Martín et al. (2015), who showed that the risk for system wide collapses is greatly reduced when including spatial heterogeneity or stochasticity in model simulations. Nevertheless, in their study, as in the study by Van Nes and Scheffer, spatial heterogeneity was imposed explicitly, rather than as a result of internal heterogenizing processes, as we presented here. Our results suggest that when the spatial processes tend to result in a homogeneous state (our simulations with high disper-

sion and many small fires), the response will still be fairly gradual. This is probably due to the spatial process themselves that seem to dampen the occurrence of a large-scale sudden transition.

Our parameter values for plant dispersion were more realistic than the ones used by Van Nes and Scheffer. In our analyses, a fairly small diffusion rate (maximum value for  $D_H$  was 0.001) was used in comparison to the diffusion rates used in the study by Van Nes and Scheffer (0.1 and 1), or that are suggested in other studies (e.g., Levin, 1992). The small value seems realistic, because the way dispersion was simulated by diffusion makes the implicit assumption that only a small portion of biomass is moved from one location to the next. For example, via stoloniferous growth and distribution of seeds, indeed plants can occupy new locations by placing small quantities of biomass there (Winkler and Fischer, 2002). At high values of  $D_H$ , however, this would suggest that whole plants would be moving. Even at these low diffusion rates, there was already a notable effect of grass dispersion on the impact that fire has on the occurrence of sudden system-wide shifts. It reduced the spatial heterogeneity, and at the same time, stimulated grass growth, because it allows grass patches to expand.

The suggestion that areas with high fuel load are more likely to catch fire than areas with low fuel load has been shown in analyses at continental scale (Archibald et al., 2009) and also at the level of individual patches (Hennenberg et al., 2006). At intermediate scales these studies do hardly exist to our knowledge. This is probably due to the fact that long term monitoring of wild fire ignitions and extents at such a level of precision are limited. Also, the current archives of satellite records of fires (e.g., Flannigan and Vonder Haar, 1986; Martín, 1999) are too coarse (e.g. NOAA-AVHRR) or too infrequent (e.g. LandSat) to analyse the relation between grass fuel and fire occurrence at the scale modelled in our study. The new Sentinel 2 mission might generate a more suitable data archive for this purpose (15 m resolution and  $\sim 5$  day revisit time).



An important simplification of this model was that grazing was implemented as a homogeneous external driving force, that was not influenced by the occurrence of fires or the abundance of grasses. From earlier analyses of the model presented in this study where grazing was added as a spatial process, we know grazing can generate spatial heterogeneity in the system (De Knecht et al., 2008). Whether this would result in a similar response to grazing as presented in Fig. 5 remains to be seen, because increasing grazer presence resulted in a unimodal response of patchiness. Only at intermediate grazing pressure, a mosaic is formed of smaller and larger patches. At very high or very low grazing pressure, either a homogeneous grass dominated or a homogeneous tree dominated system would develop (De Knecht et al., 2008). Nevertheless, we know that the spatial distribution of grazing is not only dependent on the amount of forage available, but also depends on the fire history. It is well known that areas that burned recently attract a lot of grazers as a result of the green flush right after the fire (McNaughton, 1985; Moe et al., 1990; Archibald et al., 2005). This effect would counter the positive impact that fire could have on competition between grass and woody biomass in our model system. How these effects would interact on each other would require further analyses with the model presented here, but probably the interaction would reduce the heterogenising effect of fires, and thus make savannas more prone to sudden system collapses.

This study showed that the heterogenising effect of fires can have a moderating effect on the occurrence of system-wide shifts in savannas given that grass biomass is high enough, such as humid savannas, and that grass cover is sufficient. Clearly, multiple spatial processes operate at the same time in savannas and we show that only when the processes that generate patchiness are dominant, a more gradual response of the system to external stressors can be expected. As savannas are a mixture of grasses and woody species (Scholes and Archer 1997), savanna systems are expected to show a more gradual response to increasing grazing pressure than earlier predicted (Roques et al., 2001; Van Langevelde et al., 2003). Nevertheless, it is interesting to further unravel these processes, because especially at the fringes of where savannas occur (and gradually change into either woodlands, or grasslands) the possible response of the system due to climate change might be either sudden or gradual. At the edge with forests (*i.e.* mesic savannas) fires are more frequent and grazing is less prevalent, leading (according to our model) to more gradual responses. This would be in contrast with, for example, Hirota et al. (2011) who actually anticipated the occurrence of switches between savannas and tropical forest when climate changes based on the distribution of tree cover derived from remote sensing. At the edge with grasslands (*i.e.*, arid savannas) fires are less frequent and grazing is more prevalent. According to our results, this is where sudden shifts can be expected, as a result of, for example, climatic change or human interference. This is in concordance with a study by Higgins and Scheiter (2012) who studied the impact of increases in atmospheric CO<sub>2</sub> with a dynamic vegetation model on the dominance of C<sub>3</sub> (mainly woody species) and C<sub>4</sub> (mainly grass species) plants in African ecosystems. They recorded mainly transitions from C<sub>3</sub> to C<sub>4</sub> states in areas that are associated with hot semi-arid climates. However, for the entire African continent they did not record system wide shifts, only localized, smaller scale shifts. This is exactly what is observed in our modelling results suggesting that switches between alternative stable states can occur, but that at larger scales these effects are averaged out, leading to more gradual transitions. We expect that arid savanna areas are more likely to show a sudden switch when becoming wetter due to climatic change, than mesic savannas that will show a much more gradual response towards a forested area.

## Supporting information captions

Animations of examples of the development of patterns when fires occur in 2 (large), 8 (medium sized) or 200 (small) patches at a grazer density of 15 g m<sup>-2</sup>. All other parameters are as in Table 1.

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