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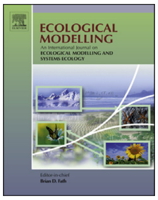

Research Paper

# 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 stated (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

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