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Disturbances in savanna ecosystems: modelling the impact of a key determinant

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Abstract

Savannas are not only subject to intense, recurrent human-generated disturbances of major extent. Also natural disturbances are common: savannas typically occur in regions where the climate is characterized by spatial and temporal variability, with precipitation varying drastically in space and time. In addition to the resulting climatic extremes, recurrent grass fires and large herbivores often cause major disturbances. Some large scale disturbances, such as drought, grass fires and grazing are considered to be driving forces in savanna ecosystems. These factors are also hypothesized to allow for a long-term coexistence of trees and grasses which is one of the distinguishing features of savanna ecosystems. We use a grid-based spatially explicit simulation model to analyse the impact of various types of disturbances on questions of long-term tree-grass coexistence. The model is based on information of the southern Kalahari and simulates the dynamics of the dominating life forms in semi-arid savannas, i.e., trees, shrubs, perennial grasses and herbs, and annuals.

We investigate the impact of various scenarios of rainfall, grass fires and grazing as well as the role of small-scale disturbances of different type and spatio-temporal correlation. The model results indicate that the impact on the savanna ecosystem significantly depends on the interaction of different processes as well as on the disturbance type, rate and correlation. We show that the interaction and relative intensity of the two large scale disturbances fire and grazing may lead to both woodland and long-term coexistence of trees and grasses. However, small-scale heterogeneities and disturbances such as colonies of seed caching rodents may increase this range of long-term coexistence. Especially in the case of highly correlated small-scale disturbances more than half of the explored rain scenarios led to a persisting coexistence of the two dominant savanna life forms.

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1. Introduction

Savannas occupy about 20% of the land surface of the world, and about 40% of Africa. In Africa, savannas are home to most of the population and are the areas in which population growth is most rapid. In South Africa savannas make up 35% of the land area, and are the basis of two major industries: cattle ranching and wildlife-related tourism.[12] What is unique about savannas is the persisting long-term coexistence of trees and grasses. Any attempt to understand or even conserve or manage savanna ecosystems has to face the question for the factors and processes that allow these two life forms to coexist despite the immense ressource overlap. The identification of the responsible 'key' factors and processes of savanna dynamics is a central question in savanna ecology and its answer will help us to face the problems of the increasing human impact on this biome. Previous attempts to explain the long-term coexistence were based on Walter's[17] hypothesis that trees and grasses have different access to the limiting factor 'water' because of the different root layers of the two life forms.[1,15,16] However, recent studies [2,12] suggest that the root overlap in savannas is much higher than anticipated by Walter. An alternative explanation assumes that trees and grasses in savannas represent an inherently unstable mixture which persists only owing to disturbances such as fire, herbivory and fluctuating rainfall.[12] Without these disturbances it is assumed that savannas would either develop towards a pure grassland or a woodland. However, most of the discussion concerning the impact of disturbances on long-term tree-grass coexistence is restricted to large-scale effects.[12] Small-scale disturbances and heterogeneities have often been neglected in the discussion of coexistence of savanna trees and grasses as well as spatial influences in general, which receive more and more attention in ecology.[5,6,7,8,10] A possible reason for this neglect is the difficulty to consider spatial influences on larger scales in empirical studies. However, the significance of spatial aspects in savanna ecology is underlined by the importance of the spatial vegetation pattern for biodiversity in savannas.[11] We hypothesize that spatial aspects and small-scale disturbances are crucial for the dynamics and the long-term persistence of semi-arid savannas.

This paper presents results of a spatially-explicit, grid-based simulation model, that investigates the formation of spatial vegetation patterns in semi-arid savannas and facilitates the exploration of potential reasons of a long-term tree-grass coexistence. The model includes spatial aspects of disturbances on different scales. In this paper we focus only on model results which concern the long-term coexistence of trees and grasses. Results which concern the formation of spatial vegetation patterns have been presented elsewhere.[6,8] Although the model is based on informations about the southern Kalahari, it is also designed to allow for an insight in semi-arid savannas in general.

2. The model

Results from an earlier version of this spatially explicit, grid-based simulation model have been presented elsewhere.[6] The model has since been modified to allow for a systematic exploration of the impact of disturbances on different spatial scales, a short description of which will be given below. Our savanna model subdivides an area of 50 ha into 20,000 grid cells of a size of 5m x 5m. On the basis of these spatial subunits the model describes in annual timesteps the following processes (1) rainfall and moisture availability, (2) vegetation dynamics of the relevant life-forms, (3) large-scale disturbances (grass fires and grazing), and (4) small-scale disturbances. On the level of the individual grid cells the model distinguishes whether trees, shrubs, perennial grasses and herbs, or annuals dominate the local patch, or whether a mixture of some of these life forms is present. In addition, the model distinguishes between the age of different trees and between three different levels of potential productivity of patches of the other perennial vegetation, classified as high, moderate or low.

2.1 Rainfall and moisture availability

In the model, differing rainfall scenarios are simulated in the form of different moisture combinations in top and sub soil layer. For both top and sub soil layer we distinguish four classes of water availability. Thus, the current moisture status of a grid cell can be characterized by one of sixteen possible combinations of the topsoil (M_t) and subsoil (M_s) water availability classes, i.e., (M_t, M_s). The rainfall of a given year is described in the model by the initial moisture class in the top and in the sub soil layer for that timestep. Initially, all grid cells have the same moisture distribution, i.e., rainfall is homogeneous in the modelled area. Within each timestep the plant available moisture is further modified in each grid cell by other processes, e.g. moisture reduction by plants. We systematically explored sixteen different rain scenarios which differ in relation to the average moisture availability in the top and sub soil layer. The rain scenarios range from low mean annual precipitation to high mean annual precipitation distributed between the two soil layers.[6] For each model run, one of the combinations of water availability classes (M_t, M_s) was the most likely to occur and had a 60% probability of occuring during each timestep of a model run. However, there was also a 40% probability that one of the 15 other combinations would be chosen for a particular timestep. We systematically explored the sixteen possible rainfall scenarios by using peak probabilities for each of the sixteen possible moisture class combinations (M_t, M_s) in different runs, keeping all other parameters and factors equal.[6]

2.2 Vegetation dynamics

For shrubs and perennial grasses and herbs we distinguish three different levels of potential productivity to characterize the condition of a vegetation patch dominated by these life forms. The transitions between these levels depend on the plant available moisture in the two soil layers of the grid cell. If the moisture combination is insufficient, the potential productivity deteriorates, whereas it is preserved or improves if sufficient moisture is available.[6, 8] The model considers that the herbaceous vegetation is more dependent on top soil moisture than on sub soil moisture whereas shrubs show the opposite dependance, reflecting differences in rooting depth of these growth forms.[2, 12] Annuals are either present or absent in a grid cell. Colonization of empty space (i.e., grid cells) and extinction (i.e., grid cells becoming devoid of a certain life form) also depend on the plant available moisture in the two soil layers.[6] Shrubs only colonize empty space via short range processes, whereas the herbaceous vegetation has a spatially homogenous establishment probability. Competition for moisture occurs in grid cells with more than one life form or if a shrub or tree dominated patch is in the immediate neighbourhood (lateral root extension).[2, 6, 12] The reduction of the soil moisture in the two layers influences the level of potential productivity and such processes as extinction and colonization.

In contrast to the other life forms, trees are modelled in an individual-based approach because this life form is of focal interest and individuals are easy to identify. Tree seeds are distributed exponentially around mature seed producing trees. Seed clumpings will be discussed below. The establishment and mortality of tree seedlings in a grid cell again depend on the moisture availability in this cell. If at least one tree seedling or sapling in a grid cell survives the first 10 years, one sub-mature tree is modelled to dominate the grid cell (implicit self-thinning). After a short period of maturation the tree starts to produce seeds until death. The tree parameters are based on life-history attributes of *Acacia erioloba*, a dominant tree species in the southern Kalahari.

2.3 Large-scale disturbances: grass fires and grazing

The occurence of a grass fire is modelled probabilistically with fire probability increasing with the number of grass dominated grid cells.[4] Trees and shrub dominated grid cells are only ignited and killed with a certain probability if they are adjacent to grass dominated cells, whereas all grass cells are modelled to burn in case of fire. [4, 6, 14] Fire induced tree mortality T was varied systematically (see below). Grazing is defined here as the detrimental effects of consumption of herbaceous biomass combined with trampling. Grazing is assumed to decrease the level of potential productivity of the herbaceous vegetation in a grazed grid cell within the current timestep. In addition, grazing and trampling reduce the establishment probabilities for all life forms. The grazing intensity G describes the probability for a transition to the next lower level of potential productivity in a grazed grid cell. The influence of this parameter on long-term tree-grass coexistence is investigated below. Spatial heterogeneities in grazing are simulated by calculating the transition for each cell seperately.

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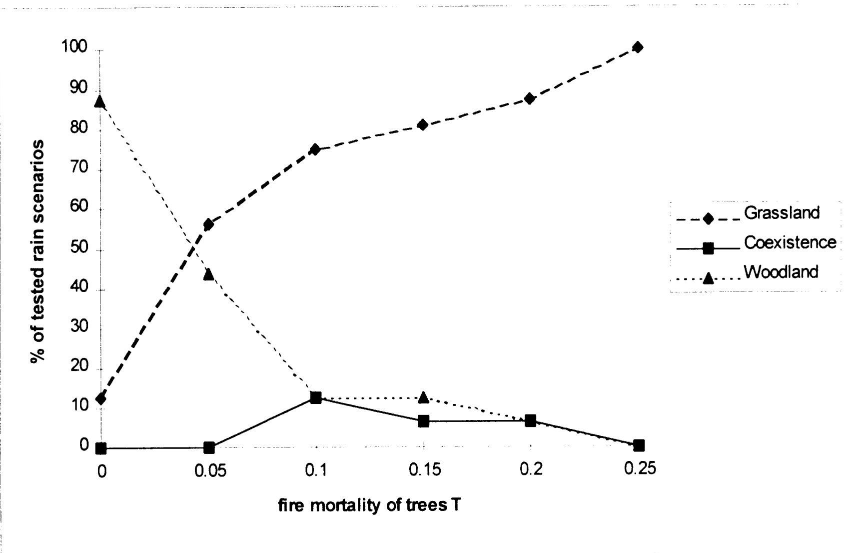

Figure 1: The impact of the tree sensitivity *T* towards fire (fire mortality) on the long-term equilibrium state of the modelled savanna system without grazing. The y-axis shows the percentage of rain scenarios that led either to grassland, coexistence or woodland in 20,000 simulated years.

2.4 Small-scale disturbances

In each timestep patches of different disturbance types are distributed in the modelled landscape in variable numbers. The modelled disturbance patch size is 4 x 4 grid cells (20m x 20m). The disturbed patches are distributed randomly either in the total area or each disturbance patch is relocated randomly within a corresponding disturbance region of a size of 20 x 20 grid cells (100m x 100m). We distinguish three different disturbance types in the model:

(C) - vegetation clearing (e.g., trampling, herbivory, rodent activities): in the selected patch all vegetation is removed except from mature trees.

(CS) - vegetation clearing in combination with local accumulations of tree seeds (e.g., trampling in combination with seed clumpings in herbivory dung): in the selected patch the number of tree seeds is additionally increased in dependance on the actual number of seed producing trees in the modelled area of 50 ha.

(CSM) - vegetation clearing in combination with tree seed clumping and locally improved moisture conditions (e.g., concentrations of herbivore dung containing tree seeds at water holes or salt licks, seed caches in rodent colonies[3]): in addition to the vegetation clearing and seed clumping, the available top and sub soil moisture in the selected patches is increased.

The disturbance rate (proportion of disturbed area per timestep) was varied

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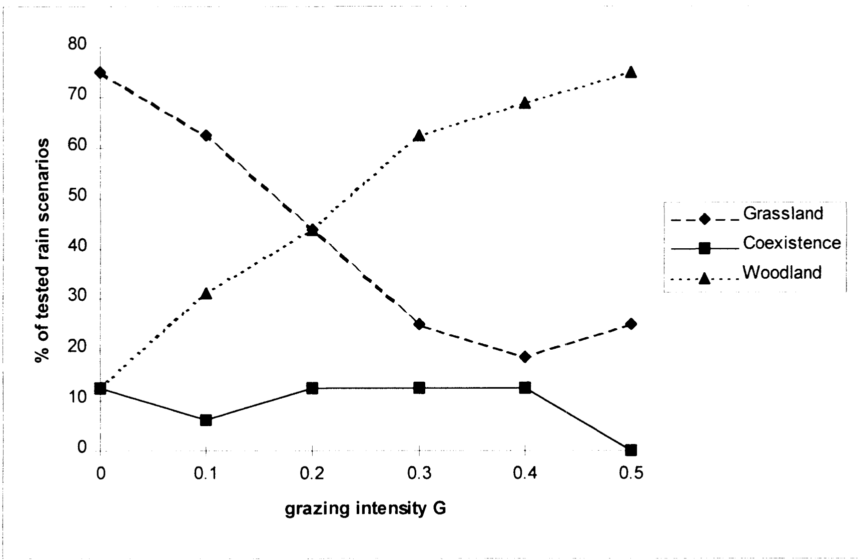

Figure 2: The impact of the grazing intensity G on the long-term equilibrium state of the modelled savanna. $T=0.1$.

systematically in the range of ecological relevance, i.e. from low (1 disturbance patch per timestep) to high (approximately 10% of the total area per timestep). We analyse here both the impact of uncorrelated disturbances, i.e., the disturbed patches are randomly rearranged in the total area in each timestep, and highly correlated disturbances, i.e., each disturbed patch is repositioned in a corresponding disturbance region. The disturbance regions are randomly located at the beginning of each simulation run and remain fixed throughout the run. Thus, any grid cell within a disturbance region has a high probability of repeated disturbances.

3. Results

3.1. Large-scale disturbances

In order to test the long term effect of the different disturbances on the question of tree-grass coexistence, we analyzed the state of the modelled savanna after 20,000 simulated years for all rainfall scenarios. Within this timespan the modelled system had reached an equilibrium state which was either a pure grassland, a woodland or a stable tree-grass mix.[6] Figure 1 indicates that without any disturbance none of the tested rainfall scenarios facilitated a long-term coexistence of trees and grasses (The results for $T=0$ correspond to the simulation results without the occurence of grass fires). An increase of the fire

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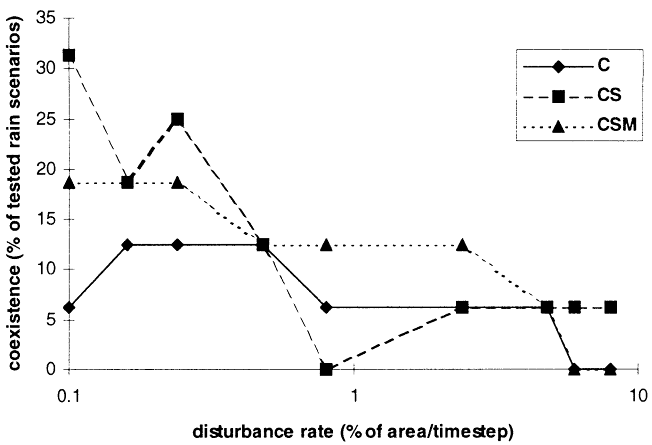

Figure 3: The impact of three types of uncorrelated small-scale disturbances on the percentage of rain scenarios that lead to long-term tree-grass coexistence. T=0.1; G=0.1. C: local vegetation clearing; S: tree seed clumping; M: locally improved moisture conditions

impact on trees (i.e., the fire induced tree mortality T) caused a shift from savanna woodland to savanna grassland in the long term. However, a moderate fire sensitivity of the trees resulted in long-term coexistence of trees and grasses in a small part of the tested rain scenarios (figure 1). The additional inclusion of grazing in the modelled savanna reversed this trend, and a transition towards a tree dominated savanna occured over a wide range of tested rainfall scenarios under an increasing grazing intensity (Figure 2). Again, long-term coexistence occured in maximally twelve percent of the rainfall scenarios that we tested.

3.2. Small-scale disturbances

For a fixed scenario of large-scale disturbances (T=0.1; G=0.1), the formation of small-scale disturbance patches was included in the model as an additional process. The simulation results indicate that the inclusion of uncorrelated small-scale disturbances that only remove the local vegetation have little effect on the long-term coexistence of trees and grasses for a wide range of disturbance rates (figure 3). If the disturbed patch additionally is subject to tree seed clumpings, eventually in combination with improved moisture conditions, the range of long-term coexistence increases up to approximately one third of the tested rain scenarios for low disturbance rates.

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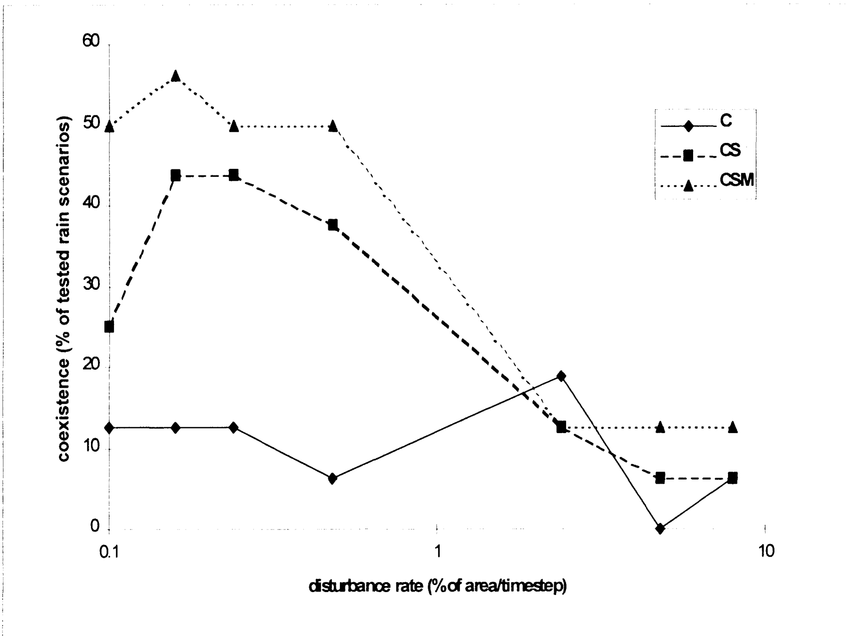

Figure 4: The impact of correlated small-scale disturbances on the long-term coexistence in the modelled savanna system. For further details see figure 3.

However, the number of scenarios that lead to long-term coexistence decreases with increasing disturbance rates. This trend is caused by an increasing transition towards savanna woodland (F. Jeltsch, unpublished analysis).
A further increase of the range of coexistence is caused by a high degree of spatio-temporal autocorrelation of the disturbance patches (figure 4).
Figure 4 shows that again vegetation clearing alone has little impact on the long-term coexistence of trees and grasses, whereas a combination with seed clumpings and improved moisture conditions in the correlated, disturbed patches may lead to coexistence in more than half of the tested rainfall scenarios and for a wide range of realistic disturbance rates.

4. Discussion

An inherent difficulty in understanding natural dynamics and determining the impact of human and other disturbances in arid and semi-arid ecosystems is the intrinsic spatial and temporal variability of these systems. Thus, for example, it is extremely difficult to establish whether an area is suffering a progressive, long-term decline in biodiversity and productivity, and hence degradation or desertification or whether it is merely suffering a short-term drought from which the land may recover if the human impact is reduced or removed. Modelling approaches, as well as long-term ecological monitoring are needed to gain a better understanding of long-term dynamics in arid and semi-arid systems. This knowledge is an indispensable basis for the identification of key factors and processes that shape both the potential for degradation and the potential for recovery therefrom. Large-scale disturbances, such as fire and herbivory, are assumed to be such key factors in savanna ecosystems. The historical view that savannas are stable in the sense of a persisting tree-grass coexistence has been replaced by a view in which long-term coexistence is achieved through these factors.[12, 13] However, it is most likely that the frequency and intensity of large-scale disturbances has to be within certain limits to allow for a long-term coexistence of the two functional types. This hypothesis is emphasized by the model results discussed in this paper. For example, grazing at too high an intensity leads to an increase of the woody component by two mechanisms: firstly, grazing favours woody seedlings by reducing grass competition and secondly, grazing lowers the fire frequency by reducing the available grass fuel. In the long term this may lead to a transition towards a savanna woodland or shrubland. Thus, considering the fact that about 20% of the land surface of the world and 40% of Africa is covered by savannas the question arises how it is possible that under so many different climatical and geological conditions the amount of disturbances is in the right limits to allow for a persisting tree-grass mix? The model results indicate that, indeed, the large-scale disturbances fire and herbivory only allow for a small climatical range of persisting savannas. This range is increased drastically if small-scale heterogeneities are included that locally favour tree seedling establishment in an otherwise grass dominated landscape. Particularly processes that lead to accumulations of tree seeds in certain patches, such as seed dispersal in herbivory dung or colonies of seed caching rodents, are probably crucial in this context.[3, 9]

We conclude that disturbances on different spatial and temporal scales, i.e. from local to regional facilitate savanna existence under a wide range of environmental conditions. Factors and processes which cause small-scale heterogeneities and disturbances in the savanna biomes, favouring tree establishment, are key determinants of savanna dynamics that so far have been neglected in the savanna discussion.

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