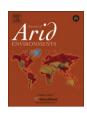
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A continental analysis of correlations between tree patterns in African savannas and human and environmental variables

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ABSTRACT

This study analyses possible relationships between natural processes taking place in savannas and the tree patterns found in savannas. This can lead to new hypotheses about which processes are driving savanna physiognomy. To do so tree patterns were quantified for African savannas from historical aerial photographs applying frequently used landscape metrics. Also, additional data for these areas were collected to quantify the processes taking place at these locations. Correlations between tree pattern indices and explaining factors were analysed. We found a negative trend between tree cover and density of sheep and goats, but no relationship between tree cover and density of cattle, suggesting that small livestock have an effect on tree cover, but that larger livestock (or obligate grazers) do not. Also, a positive correlation between human population density and tree cover was found. Possible explanations for the found relations are discussed. Subsequent ways to analyse the latter correlation are discussed, and the potential of the presented historical database of aerial photographs is highlighted.

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1. Introduction

Savannas are ecosystems with an inherently heterogeneous physiognomy. They are characterized by a continuous herb layer and a discontinuous layer of taller woody plants (Scholes and Archer, 1997). This makes savannas different from both grasslands and forests, as neither of the two life forms dominates. Often these tall woody plants are trees, although intermediate shrubby forms can occur as well. The herbs occurring in a savanna can be of any type of grasses as well as herbs and forbs, although grasses normally dominate. Savannas cover approximately 12% of the global terrestrial surface, and about half of the African continent (Scholes and Archer, 1997), and are socioeconomically important in many regions of the world. The spatial variation in tree and grass abundance influences the physiognomy of savannas. This variation is mainly determined by spatial differences in growing conditions (rainfall and soil properties) and disturbances (herbivory and fire, Higgins et al., 2000; Jeltsch et al., 1998; Scholes and Archer, 1997;

Van Langevelde et al., 2003), which vary spatially due to their inherent stochastic nature (e.g. ignition of sites, Archibald et al., 2009) or because of interplay with the existing vegetation pattern (e.g. spatially explicit herbivory, De Knegt et al., 2007, 2008). Savannas have a rich diversity of both plant and animal species (Belsky, 1993; Sinclair, 1995). A recent study by Debuse et al. (2009) also showed that patch characteristics are related to survival of certain tree species, as well as plant biodiversity within the patch. Also anthropogenic utilization of savannas depends on its heterogeneous nature, including extensive cattle ranging, tourism income and fuel wood collection (Mistry, 2000). Understanding the major factors influencing the spatial heterogeneity of savannas is therefore important to set management priorities. For example, some processes (e.g. prescribed burning or herbivory by livestock) are easier to control by managers than others (e.g. long spells of drought or wildfires).

Taller woody plants can be relatively easily recognized on aerial photographs because they contrast with grass dominated areas by both texture and colour. In this paper we will consider only trees, but we are aware of the variability in growth forms of woody plants in savannas. Quantifying tree patterns is in essence therefore equal to quantifying grass patterns, as they are negatives of each other,

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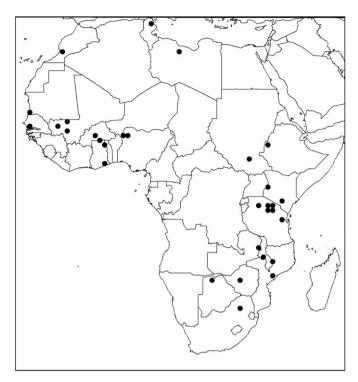


Fig. 1. Locations of the different areas with savanna vegetation for which aerial photographs were obtained on the African continent.

provided that other landscape elements, like build up area, rocky outcrops etc are outside the area of interest. Making use of a large archive of historical savanna aerial photographs available at the Faculty for Geo-Information Science and Earth Observation of the University of Twente we constructed a database of tree patterns in savannas. We combined this with globally available data on the internet on possible explaining factors such as fire probability, herbivory and climate.

With this analysis, this study addresses the question which processes (both controllable and non-controllable) could be in control by investigating their correlations with tree patterns in savannas, and their relative importance in explaining variation in these patterns. Although, finding a correlation between a process and a pattern does not necessarily imply that the process is causing the pattern, searching for existing relations between patterns and dominant spatial processes can reveal insights and help with the formulation of testable hypotheses.

2. Materials and methods

2.1. Aerial photographs

To analyse tree patterns we collected a total of 128 aerial photographs covering 33 different areas in 17 countries throughout the African continent (Fig. 1, Table 1, online additional content S1). The scale of the photographs varied from 1:4000 to 1:50,000 and were taken in the period from 1950 to 1988, as indicated in Table 1. Photos were taken during various campaigns, and for each area, photos were used from only one campaign. All photographs were scanned with a resolution of 800 DPI. This assured that the resulting pixel sizes were small enough to depict the grain size of the scanned photographs. Due to different scales of the photographs, this resulted in pixels corresponding to 0.17 m up to 2.12 m in reality. To standardize the data, all photographs were rescaled to a pixel size of 0.15 m with nearest neighbour reclassification to retain the original pixel values. We standardized to a smaller pixel

size since this allowed us to combine information from sources with different spatial resolutions without discarding information as would have happened when rescaling to a larger pixel size with which original pixel values would have been averaged over the newer larger pixels. From each photograph, we selected areas covered by a tree—grass mixture while excluding areas that contained rocky outcrops or steep slopes. Each selected aerial photograph was classified through visual interpretation into 'trees' and 'grasses'. The aerial photographs were monochromatic and the two classes were assigned by thresholding at a certain grey value. The threshold of the grey value was visually determined for each photograph separately. Fig. 2 shows an example of an original image and an image where the distinguished trees are delineated.

Representative subsets of each photograph were used for the analysis. The spatial extent of these subsets over which we quantified tree patterns varied (see Table 1), and to standardize the extent, each subset was subdivided in equally sized square partitions of 50 ha in which the tree patterning was measured using tree pattern indices (see below). These indices were averaged over the different partitions and, if available, over the different subsets in an area, yielding 33 observations of average tree pattern indices that were tested for a correlation with several potentially explaining factors.

2.2. Quantifying tree patterns

Spatial tree patterns were quantified using landscape indices (Table 2, McGarigal and Marks, 1993) that can be grouped in two different types: indices that relate to tree abundance and indices that relate to the shape of tree patches. For these last types, higher values refer to irregular or complex shapes, while low values indicate rounder and compacter shapes (McGarigal and Marks, 1993). First, tree cover (TC) is a quantitative measure of the abundance of trees, which was included in many previous studies on trees in savannas and found to be related to several factors including grazing pressure and rainfall (e.g. Archer, 1989, 1990; Brown and Carter, 1998; Bucini and Hanan, 2007; Sankaran et al., 2005, 2008).

To quantify savanna tree patterns, we distinguished patches of trees as clumps of contiguous tree cover. The number of distinct tree patches per unit area is an indicator of the spatial arrangement of trees in the landscape, high numbers indicate tree scattering while low numbers indicate tree grouping. Tree grouping or scattering is influenced by factors like interspecific competition (e.g., the interference of root systems for the uptake of water or nutrients) (Lejeune et al., 1999), facilitation (e.g., protection of each other from fire) (Groen et al., 2008; Jeltsch et al., 1996) and dispersion (Caylor et al., 2003; Smith and Goodman, 1986). In case of competition, trees are better off far away from one each other, and an over dispersed pattern (i.e. long distances between trees) is expected resulting in many small patches, while in case of facilitation trees are better off close to each other, and a clustered pattern is expected, resulting in few large patches. If neither competition nor facilitation is important or equally strong, trees would be expected to occur in a randomly scattered arrangement.

Mean tree patch size (MPS) and its coefficient of variation (CVPS) give an indication of the spatial arrangement of trees. Large tree patches (and thus a high value for MPS) can only grow when processes like facilitation or limited dispersion outweigh competition. Otherwise smaller tree patches are more likely to occur. Low values for CVPS (either only large or only small tree patches) can be the result of disturbances. For example, high fire frequencies result in survival of solely large tree patches (as is the case in arid savannas; Di Bella et al., 2006; Govender et al., 2006), and thus should result in a low CVPS, while at low fire frequencies both large and small tree patches can be present and thus a high CVPS is expected.

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