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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.

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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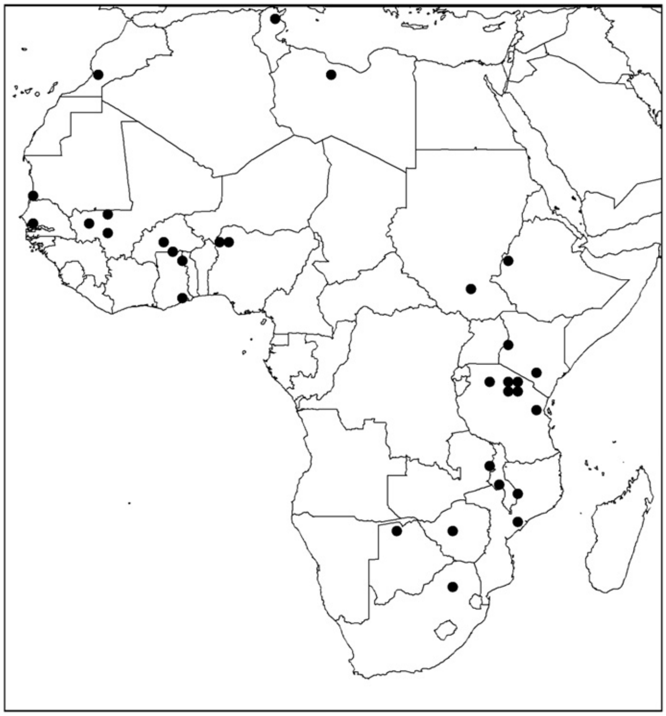

Fig. 1. Locations of the different areas with savanna vegetation for which aerial photographs were obtained on the African continent.

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.

Table 1
Overview of the different areas with savanna vegetation for which aerial photographs were analysed. Areas that are shaded were excluded after the outlier analysis.

Country	Area	Longitude	Latitude	Scale	Year	# of subsets from the area	Average area of subsets (ha)
Botswana	Okavango Delta	23° 06′ 51″ E	19° 23′ 57″ S	40,000	1973	1	1803
Burkina	Faso Ouagadougou	1° 48′ 00″ W	12° 12′ 00″ N	10,000	1988	4	149
Ethiopia	Didesa Wolega	35° 27′ 00″ E	9° 33′ 36″ N	50,000	1957	6	71
Gambia	Alicali	15° 43′ 59″ W	13° 31′ 59″ N	20,000	1956	6	443
	Jowara	16° 04′ 47″ W	13° 34′ 36″ N	20,000	1956	1	445
	Kudang	15° 43′ 59″ W	16° 40′ 59″ N	25,000	1980	3	39
Ghana	Ayensu River Basin	0° 28′ 47″ W	6° 09′ 00″ N	12,500	1975	3	97
	Gambaga	0° 15′ 36″ W	10° 19′ 12″ N	30,000	Unknown	2	212
	Tamne River Basin	0° 41′ 56″ W	10° 48′ 21″ N	30,000	1960	8	120
Kenya	Athi River	37° 51′ 00″ E	1° 51′ 00″ S	25,000	Unknown	2	340
	North of Kapenguria	35° 04′ 12″ E	1° 02′ 24″ N	20,000	1967	3	257
	Taita Hills	35° 15′ 00″ E	3° 08′ 59″ S	10,000	1993	4	127
Lybia	Wadi Meginin	16° 27′ 04″ E	30° 00′ 00″ N	24,000	1953	2	868
Malawi	Machinga	35° 31′ 00″ E	14° 58′ 00″ S	25,000	1973	2	179
	Mzimba District	33° 20′ 24″ E	11° 31′ 11″ S	25,000	Unknown	2	126
	Ntcheu Hills	34° 22′ 48″ E	14° 29′ 24″ S	25,000	1976	1	514
Mali	Balle	8° 21′ 00″ W	15° 12′ 00″ N	50,000	1975	2	264
	Fina Forest	8° 18′ 00″ W	12° 30′ 00″ N	50,000	1977	2	279
	Sandare diema doubala	10° 10′ 47″ W	14° 25′ 11″ N	50,000	1977	4	110
Morocco	Agadir	8° 33′ 00″ W	30° 23′ 59″ N	7,500	1978	2	8
Mozambique	Luabo sena Sugar Estate	36° 06′ 19″ E	18° 23′ 34″ S	20,000	1950	4	215
Nigeria	Bukkuyum	5° 28′ 00″ E	12° 07′ 59″ N	40,000	1962	1	284
	Eastern Zamtava	4° 01′ 48″ E	12° 01′ 47″ N	40,000	Unknown	2	37
	Gummi	5° 05′ 23″ E	12° 05′ 23″ N	40,000	1962	1	36
South Africa	Nylsvlei	28° 41′ 42″ E	24° 36′ 59″ S	4,000	1974	16	53
Sudan	Penko Plain	30° 59′ 52″ E	7° 12′ 03″ N	50,000	Unknown	4	292
Tanzania	Babati District	35° 27′ 00″ E	4° 07′ 47″ S	25,000	1990	3	101
	Bagamoyo	38° 23′ 59″ E	6° 15′ 35″ S	12,500	1981	6	36
	Kahama	32° 30′ 00″ E	3° 21′ 00″ S	40,000	1975	4	1112
	Lake Manyara	36° 15′ 00″ E	3° 18′ 00″ S	10,000	Unknown	1	57
	Tarangire	36° 00′ 00″ E	4° 00′ 00″ S	50,000	Unknown	11	176
Tunesia	Djebel Fkirine	9° 52′ 55″ E	35° 56′ 20″ N	25,000	1963	1	260
Zimbabwe	Piriwiri	29° 28′ 19″ E	19° 10′ 24″ S	25,000	1984	3	242

Mean nearest neighbour distances (MNN) between clusters and the C.V. of the mean of these nearest neighbour distances (CVNN) indicate how tree clusters are distributed over the area. Nearest neighbour distances are inversely related to patch density. A low value for CVNN indicates a regular distribution of tree patches, while a high value indicates a more randomly distributed distribution. Nearest neighbour distances have been used in previous studies to analyse competition. High values for MNN are suggested to indicate high levels of competition (Smith and Goodman, 1986).

Edge density (ED), mean patch shape index (MPSI) mean area shape index (MASI) and mean patch fractal dimension (MPFD) (see Table 2) give us an idea about the shape of tree patches and these indices are expected to be especially be correlated with processes that operate at the edge of tree patches. Grass fires for example will damage trees mainly at the edge of tree clusters reducing possible irregular shapes in tree clusters, and "eroding" shapes into more compact round forms (Groen et al., 2008).

2.3. Explaining factors

We used 10 explaining factors, which are listed in Table 3. The spatial resolution of most of the used sources is much coarser compared to the resolution of the aerial photographs used. Also, information about the explaining factors came from different time periods. However, the considered explaining factors are both long-term and large-scale factors that change only slowly compared to the rate at which tree patterns can change. The factors are expected to have a high spatial and temporal autocorrelation and possible correlations with landscape indices therefore still give clues about possible long-term effects of these factors.

Precipitation is a major driver in savannas, as plant growth is often water limited, especially during the dry season. It has been hypothesized that water availability is also the major driver determining the tree–grass ratio in savannas (Van Langevelde et al., 2003; Walker and Noy-Meir, 1982), where in wetter regions, trees are able to dominate, and in drier regions, grasses dominate. We included mean annual precipitation (PREC) obtained from the FAO GeoNetwork (http://www.fao.org/geonetwork/srv/en/main.home) in the analyses.

Temperature is an important factor controlling biomass production by determining potential evapo-transpiration to an extent. High temperatures favour plants that are efficient in water use, like perennial C4 grasses, which occur often in savannas (Walker et al., 1981). We used the maximum temperature over the year (TMAX; averaged over 1962–1990) obtained from FAO ClimPag (http://www.fao.org/nr/climpag/climate/index_en.asp#anchor1) as a potential explaining factor.

Soil nutrient availability has an effect on the palatability of foliage, and subsequently the herbivore pressure on the plants. Soil depth affects the tree–grass balance, as trees root deeper than grasses (Schenk and Jackson, 2002), and benefit from water at deeper layers, when these are available. In our analyses total

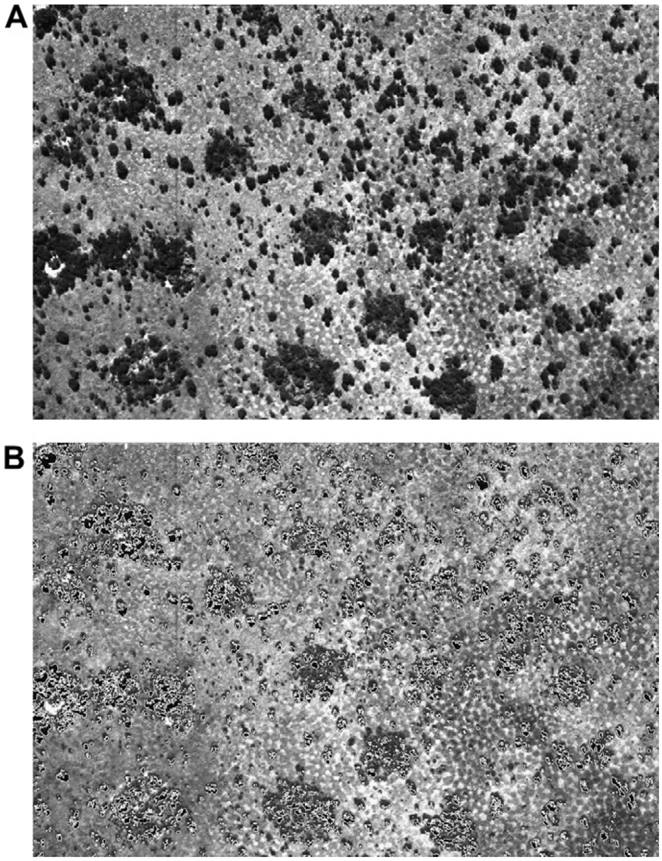

Fig. 2. Example of an aerial photograph (A) and its classifications (B) from Nylsvlei, South Africa. White delineations indicate patches of trees.

exchangeable bases (TEBT) in the top soil (first 30 cm) as well as soil depth (DEPTH) were used (Batjes, 2005).

Fire is an important determinant in the physiognomy of savannas, as it is more detrimental to the survival of small trees and saplings than to grass survival (Van De Vijver, 1999). Large trees suffer less from fires, but fires do suppress the rejuvenation of the tree community, keeping savannas open (Scholes and Archer, 1997). We included fire probability in the months June, July and August (FIREA) and the probability in the months September, October and November (FIREW) separately. Fire probability is calculated by summing the total times a $0.5^\circ \times 0.5^\circ$ cell was burned over a 17 year period, divided by the area, and number of years, as described in Carmona-Moreno et al. (2005). June, July and August (FIREA) are growing season months when grasses are growing, and thus fires in this period have a negative effect on grass growth (Trollope, 1998). September, October and November (FIREW) are the dry season in the southern hemisphere, which means that most grasses are in senescence, and therefore burn well, while they suffer little from the fire effects themselves.

Herbivory is expected to be another important determinant in savannas. Selective grazing by either grazers or browsers determines which plant type is negatively affected, and it is known that under certain conditions, herbivores are able to create spatial patterns in tree–grass systems (De Knegt et al., 2008). We therefore included sheep and goat densities (combined as shoat densities; SHOAT), and cattle densities (CATTLE) obtained from FAO GLiPHA (http://kids.fao.org/glipha/) as proxies for browsing and grazing pressure respectively. Note that this is a commonly made simplification as sheep and goats are not obligate browsers, and could be considered as intermediate feeders.

Furthermore, human presence is an important modifying factor in savannas. Although burning and grazing, two important methods of how humans affect savannas, are already included among the explanatory variables, fuel wood collection and other

Table 2
Description of the different tree pattern indices used in this study (McGarigal and Marks, 1993). E = edge length, A_i = area of individual patch i, $A_{\text{partition}}$ = total area of partition, N = number of patches in partition, n_i = nearest neighbour distance for patch i.

Symbol	Name	Units	Range	Calculation
TC	Total tree cover	Fraction	0–100	$\frac{\sum_{i=1}^{N} A_i}{A_{\text{partition}}}$
PD	Tree patch density	# km^{-2}	0–∞	$\frac{N}{A_{\text{partition}}}$
MPS	Mean tree patch size	m^2	0–∞	$\frac{\sum_{i=1}^{N} A_i}{N}$
CVPS	Coefficient of variation of the mean tree patch size	m^2	0–∞	$\frac{\sqrt{\frac{\sum_{i=1}^{N}(\text{MPS}-A_i)^2}{N}}}{\text{MPS}}$
MNN	Mean nearest neighbour distance of patches	m	0–size of partition	$\frac{\sum_{i=1}^{N} n_i}{N}$
CVNN	Coefficient of variation of the mean nearest neighbour distance of patches	m	0–size of partition	$\frac{\sqrt{\frac{\sum_{i=1}^{N}(\text{MNN}-n_i)^2}{N}}}{\text{MNN}}$
ED	Density of tree patch edge	m km^{-2}	0–∞	$\frac{\sum_{i=1}^{N} E_i}{A_{\text{partition}}}$
MPSI	Mean patch shape index	m m^{-2}	0–∞	$\frac{\sum_{i=1}^{N} \frac{0.25E_i}{\sqrt{A_i}}}{N}$
MASI	Mean area shape index	km^2 m^{-1}	0–∞	$\frac{\text{TC}}{\text{ED}}$
MPFD	Mean patch fractal dimension	–	1–2	$\frac{\sum_{i=1}^{N} \frac{2\ln(0.25E_i)}{\ln(A_i)}}{N}$

Table 3
Description of the human and environmental factors that are used in this study to explain tree patterns in savanna vegetation.

Symbol	Description	Range	Period	Spatial resolution	Units	Source
CATTLE	Cattle densities	0–951	1992–2003	5 km × 5 km	Livestock units km^{-2}	FAO GLiPHA
SHOAT	Sheep and goat density combined	0–1853	1992–2003	5 km × 5 km	Livestock units km^{-2}	FAO GLiPHA
FIREA	Fire probability in June–August	0–100	1982–1999	0.5° × 0.5°	%	Carmona-Moreno et al., 2005
FIREW	Fire probability in September–November	0–100	1982–1999	0.5° × 0.5°	%	Carmona-Moreno et al., 2005
HUMDEN	Human population density	7–235	2005	0° 0.5″× 0° 0.5″	people km^{-2}	LandScan, 2005
TMAX	Maximum mean monthly temperature	21–36	1962–1990	0.5° × 0.5°	°C	FAO ClimPag
PREC	Precipitation	254–1272	1974–2004	0.167° × 0.167°	mm	FAO GeoNetwork
TEBT	Total exchangeable bases in the top soil	1.7–32.7	n.a.	0.5° × 0.5°	cmol$_C$ kg^{-1}	Batjes, 2005
DEPTH	Soil depth	0–190	n.a.	0.5° × 0.5°	cm	Batjes, 2005
SCALE	Scale of the original aerial photograph	1:4000–1:50,000			–	–

direct and indirect effects, such as eradication of native herbivores (Scholes and Archer, 1997), may also has an effect on tree survival. Since there are no directly measurable indicators for these effects, we included human density (HUMDENS) obtained from LandScan (2005) as a potential explaining factor instead.

Finally the quality of data (the scale of the photographs; SCALE) was included in our list of potential explaining factors. We expect that small scale photos (1:50,000) do not represent tree cover and patch shape as accurately as large-scale ones (1:4000). We thus assume that large-scale photos reveal correlations between tree pattern and explaining factors better.

HUMDENS, SHOAT and CATTLE were expected to be negatively correlated with tree pattern indices that are related to abundance of trees (*i.e.*, TC, PD, MPS and CVPS), because each of them is expected to contribute to the removal of tree biomass in different degrees (Table 4). In their modelling study, De Knegt et al. (2008) showed that at intermediate levels of grazing and browsing, savannas have the highest levels of spatial heterogeneity. We therefore expect a hump shaped response to these explaining factors for indices that indicate the shape of the patches (*i.e.*, MASI, MPFD, MPSI and ED). Lastly, these explaining factors are expected to have a positive correlation with distribution indices (*i.e.*, MNN and CVNN). When tree patches are suppressed and become scarce, distances between patches should increase. For SCALE no effect was hypothesized, because it was only included to correct for the quality of the images. When scale has a significant effect on a tree pattern index, further ecological inferences for this index are assumed not to be reliable, as the quality of the data influences the result too much.

Most abiotic factors, except maximum monthly temperature and fire probability, were expected to be positively correlated with tree pattern indices because they represent availability of resources for plant growth. We expected that maximum monthly temperature correlates negatively with tree pattern indices because increased temperatures increase evapo-transpiration, which might lead to water stress. Also, fire negatively affects trees (Van Langevelde et al., 2003), and therefore, high fire probabilities could result in reduced cover of trees, and more simple and rounded off shapes. Also, higher nearest neighbour distances can then be expected and therefore fire would be positively correlated with MNN and CVNN.

2.4. Statistical analysis

Before investigating correlations between explaining factors and tree pattern indices, we started with an outlier analysis by visually inspecting histograms of the data (both in tree pattern indices and explaining variables). We excluded any observation that was two or more interval classes away from the majority of the observations. This interval class size was calculated using the Sturges equation (Sturges, 1926). Then we looked at correlations between explaining variables using principal component analysis (PCA, Van Der Brink and Ter Braak, 1998), to see if collinearity between these variables was a problem and tolerances for each explaining factor were calculated. When tolerances were larger than 0.1, no collinearity problems were expected (Quinn and Keough, 2002). Second order effects for HUMDEN, SHOAT and

Table 4
Standardized correlation coefficients and model diagnostics (R^2, R^2 adjusted, BIC and overall P-value) for each of the tree pattern indices. A priori expected directions of the correlations are indicated with shades. White indicates expected positive correlations and grey indicates expected negative correlations. Legend: na = not included in model; ns = not significant; * $0.05 \geq P > 0.01$; ** $0.01 \geq P > 0.001$; *** $P \leq 0.001$.

	HUMDEN	SHOAT	CATTLE	FIREA	FIREW	PREC	TEBT	DEPTH	SCALE	HUMDEN^2	SHOAT^2	CATTLE^2	R^2	$R_{adj}{}^2$	BIC	P
TC	**0.76****	**−0.65****	na	**0.60****	na	**−0.40 ns**	na	na	na	na	na	na	0.469	0.358	0.677	**0.0132**
PD	na	na	na	na	na	na	**0.42***	na	**−0.47****	na	na	na	0.461	0.410	−5.284	**0.0015**
MPS	na	na	na	na	na	na	na	**0.34 ns**	na	na	na	na	0.116	0.076	3.389	0.1029
CVPS[a]	**0.63***	**−0.59***	na	**0.66****	na	**−0.47***	na	na	na	na	na	na	0.460	0.346	1.106	**0.0154**
MASI[a]	**0.51***	**−3.53****	**2.78***	na	na	na	na	na	na	na	**3.37****	**−3.11****	0.478	0.333	3.483	**0.0276**
MPSI[a]	na	**−0.37 ns**	na	na	na	na	na	na	**−0.46***	na	na	na	0.303	0.237	0.862	**0.0225**
MPFD[a]	na	na	na	na	na	na	na	**0.28 ns**	na	na	na	na	0.078	0.036	4.403	0.1858
ED	na	na	na	na	na	na	na	na	**−0.49***	na	na	na	0.239	0.204	−0.186	**0.0154**
MNN	**−0.51***	na	na	**−0.43***	na	na	na	na	na	na	na	na	0.338	0.275	−0.370	**0.0131**
CVNN	**−0.45***	na	na	**−0.40***	na	na	na	na	na	na	na	na	0.271	0.202	1.939	**0.0360**

[a] Also 2nd order effects of HUMDEN, SHOAT and CATTLE were included in the analysis.

CATTLE (see below) were excluded from the collinearity analysis as they are by definition strongly related with their first order effect.

We used multiple linear regressions to analyse the relation between the explaining variables and the tree pattern indices. Only the main effects of the explaining variables on the tree pattern indices were tested, except for MASI, MPFD, MPSI and ED because for these indices a hump shaped responses with HUMDEN, SHOAT and CATTLE were expected. Then also a second order effect of these explaining factors was included. Interactions between the explaining variables were not considered because of restrictions imposed by the limited sample size. Correlations between the explaining variables and tree pattern indices were investigated by formulating for each tree pattern index a regression model for every possible combination of explaining variables as predictors. This yielded for each tree pattern index $2^9 = 512$ possible models. We estimated the parameters and statistics for all these models. The best model was then selected based on its Bayesian Information Criterion (BIC) (Quinn and Keough, 2002). BIC is a measure of the goodness of fit of a statistical model and gives a penalty for including more parameters to avoid over fitting. Lower BIC values indicate better fits. We tested the significance of the model with the lowest BIC value.

Following the regression analyses, we investigated which variables had a stronger effect on tree pattern indices. For this we calculated the independent R^2, expressed as percentage of the total R^2 of a model including all variables, for each variable on each tree pattern index using hierarchical partitioning (Chevan and Sutherland, 1991; Quinn and Keough, 2002). The basic idea behind hierarchical partitioning is to calculate the part of the explaining power of a predictor that is not "shared" by other predictors. In other words, the independent R^2 is the percentage variance explained by a predictor that cannot be explained by any other predictor in the dataset. To calculate the independent R^2 of a predictor, all possible multiple regression models with and without that predictor are calculated. Then, the differences between the R^2 of the full and reduced models for each parameter are determined. Accordingly, the average of this difference in R^2 is first calculated at each hierarchical level (so for each model with 1, 2, 3,... etc. predictors), and then over the different hierarchical levels. We used the package hier.part in R (Walsh, 2004) to calculate the independent R^2.

3. Results

In the outlier analyses, 9 observations were excluded because they were two or more interval classes away from the majority of the observations, leaving a dataset of average observations from 24 study areas. Areas that were excluded are indicated with shading in Table 1. Fig. 3 shows the PCA bi-plot for the explaining variables for the first

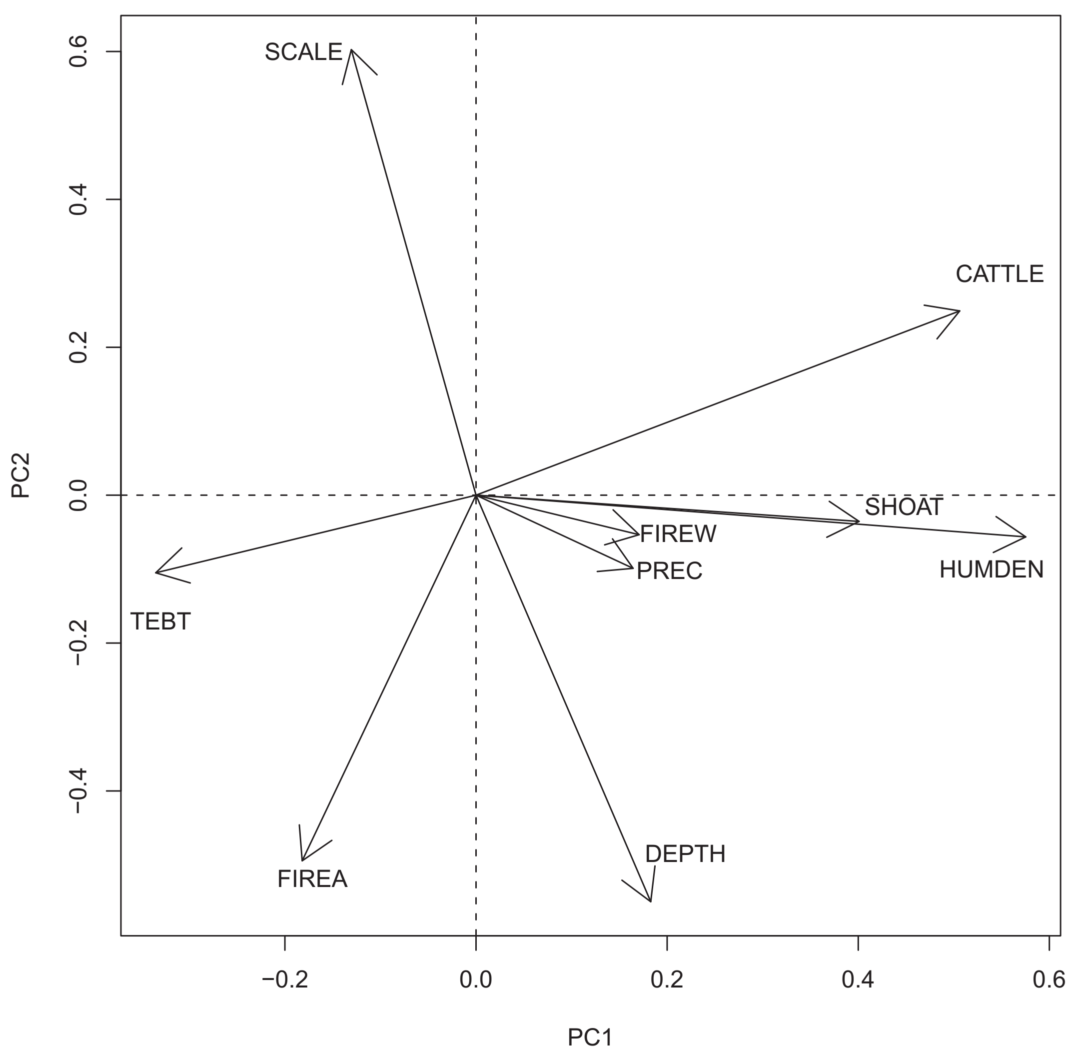

Fig. 3. The results of the principal component analysis on the explaining variables plotted along the first (x-axis) and second (y-axis) principal components. Abbreviations are explained in Table 3.

and second principal components. Arrows that point in the same direction are positively correlated; arrows in opposite directions are negatively correlated, whereas arrows that are perpendicular are not correlated. The explaining variables are well spread out over the plot suggesting that collinearity is not a problem in the dataset. TMAX was left out from the analyses, because it had a tolerance below the allowed level (<0.1). For the other explanatory variables, tolerance levels rose above 0.1 after TMAX was removed.

Table 4 shows the observed correlations for the selected models with the lowest BIC. Three models (for PD, MPSI and ED) were excluded from further investigation because they showed significant correlations with SCALE. When only looking at the significant correlations, relations with HUMDEN and FIREA were opposite to our a priori expectations. The highest R^2 was found for a model describing variation in mean area shape index (MASI; $R^2 = 0.478$), which was positively correlated with HUMDEN, SHOAT and CATTLE, as well as with the 2nd order effects of SHOAT and CATTLE. The inclusion of the later two explaining factors suggests that indeed there is a hump shaped response of MASI to both types of herbivory. In Table 5, the results of the hierarchical partitioning are presented. This gives the amount of variance explained by each explanatory variable included in the model as a percentage of the total amount of variation explained by the model. For example, fire in the period June–August (FIREA) explains 50.9% of all variation explained by the model for the coefficient of variation in patch density (CVPD). This model explains 46.0% of the total variation in patch density, so fire in the period June to August explains 46.0% $\times$ 0.509 = 23.4% of the total variation in patch density. In Fig. 4 scatter plots are given for each tree pattern index and the significant explaining variables. Fig. 5 shows the fitted functions for MASI where also 2nd order effects were found to be significant.

4. Discussion

Table 4 shows that cattle density was only included in the model for mean area patch shape (MASI) and never had the most influence on the explained variation in any of the models, according to the hierarchical partitioning. This suggests that tree patterns and cattle densities are quite independent from each other. As cows are relatively strict grazers, compared to goats and sheep, it makes sense that their presence is mainly determined by grass abundance and quality, and less by tree abundance or its spatial organisation. Sheep and goat density (SHOAT) on the other hand was several times significantly correlated with tree patterns. This explaining factor was also included in the significant model for MASI as a 2nd order effect, with a positive coefficient, suggesting a U-shaped response. Sheep and especially goats are known to browse on woody plants mainly (Breebaart et al., 2002; De Knegt et al., 2007). They had, as was a priori expected, a negative correlation with tree cover, as well as with the variation in patch sizes, suggesting that high goat and sheep densities reduce the amount of tree cover. Also, with this high herbivore pressure, small patches are likely to disappear, resulting in less variation in patch sizes. For MASI, high values indicate simple aggregated shapes, while low values correspond with highly fragmented more complex shapes. The suggested U-shaped response model found for MASI suggests that at intermediate levels of sheep and goat browsing, shape complexity is maximal, as also suggested by De Knegt et al. (2008). The data used in this study suggests a maximum complexity (*i.e.* lowest MASI value) around 500 livestock units of sheep and goats per square kilometre (Fig. 5). Summarizing, these results suggest a negative effect of small livestock species (*i.e.* shoats) on the shape of tree patterns, but suggest hardly no effect of obliged grazers (*i.e.* cattle) on the shape of tree patterns. Experiments could be set up to test this generated hypothesis.

The positive correlation found for both human density (HUMDENS) and fire probability in June, July and August (FIREA) with tree cover (TC) and the coefficient of variation of patch size (CVPS) were exactly opposite to our a priori expectations. Likewise human density and fire probability in June, July and August had unexpected positive correlations with the mean nearest neighbour distance (MNN) and its coefficient of variance (CVNN). It is difficult from our study to infer causalities, but for the case of human density, it could be that people trigger tree growth around where they live (for example by bush encroachment resulting from over exploitation of grasses; Roques et al., 2001; Van Auken, 2000), or that humans prefer to live in places where conditions are also favourable for tree growth. Furthermore, trees may be used for building materials, fuel, shade and food and are therefore an essential resource for humans, and may thus be a requirement for people to settle in particular savanna areas in the first place (Shackleton et al., 2002). The African continent is known to be the largest consumer of fuel wood in the world (FAO, 2007), supporting the idea that indeed people are attracted to areas with high tree cover. Determining which of these explanations are most likely is difficult with static information like we used in this study. Analysis of historical datasets of the development of settlements and tree cover might give further insights in this relationship and could be compared to current levels of tree cover. Using Google earth imagery, which is providing higher resolution data for African savannas every day, could in this case provide the necessary data on current tree cover values, and tree cover changes over time when compared with our historical images.

Explaining the positive relation between tree cover and fire probability in June, July and August is somewhat more complex. The expected negative relation between fire and tree cover in savannas is often indirect (Van Langevelde et al., 2003). Grass is the major fuel through which fire spreads in savannas (Bond and Van Wilgen, 1996) and the negative effect of fire on tree survival depends mostly on the intensity of the fire (Trollope, 1984). This intensity is influenced by several aspects, including amount of fuel

Table 5
The amount of variation explained per variable as percentage of the total amount of variation explained (R^2). If a model has only one explaining variable, this variable makes up 100% of the R^2. The variable explaining most per model is highlighted with a grey shade.

	HUMDEN	SHOAT	CATTLE	FIREA	FIREW	PREC	TEBT	DEPTH	SCALE	$HUMDEN^2$	$SHOAT^2$	$CATTLE^2$
TC	**28.8**	**27.8**	na	**36.9**	na	**6.5**	na	na	na	na	na	na
PD	na	na	na	na	na	na	**45.5**	na	**54.5**	na	na	na
MPS	na	na	na	na	na	na	na	**100**	na	na	na	na
CVPS	**15.6**	**22.5**	na	**50.9**	na	**11.1**	na	na	na	na	na	na
MASI	**8.0**	**36.8**	**17.4**	na	na	na	na	na	na	na	**23.0**	**14.8**
MPSI	na	**37.4**	na	na	na	na	na	na	**62.6**	na	na	na
MPFD	na	na	na	na	na	na	na	**100**	na	na	na	na
ED	na	na	na	na	na	na	na	na	**100**	na	na	na
MNN	**60.5**	na	na	**39.5**	na	na	na	na	na	na	na	na
CVNN	**56.4**	na	na	**43.6**	na	na	na	na	na	na	na	na

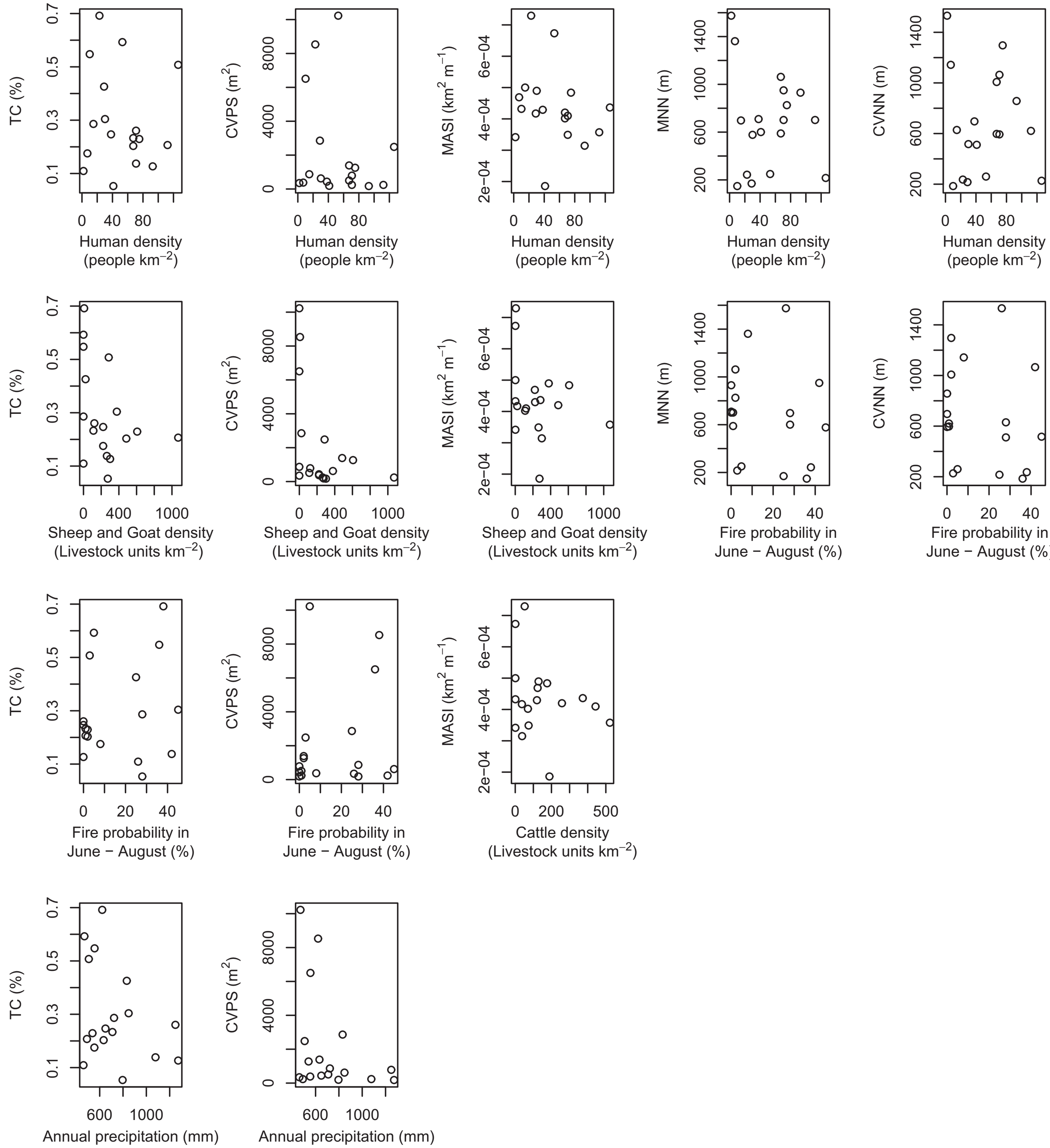

Fig. 4. Scatter plots of the different tree pattern indices plotted against the most explaining variable according to the hierarchical partitioning.

(*i.e.* grass biomass) available, the water content in the fuel, and atmospheric conditions (mainly wind speed, relative humidity and temperature; Trollope et al., 2004). On the African continent, the period June–August is normally the start of the dry season in areas south of the equator. In this period most grasses go in senescence, and loose moisture becoming more flammable. Therefore more intense fires could be expected as the dry season progresses (September–November) compared to the beginning of the dry season (June–August). Fires in the beginning of the dry season may thus result in lower tree mortality than fires later in the year and so places where fires occur early in the dry season may be better environments for trees than places where fires occur later in the dry season. On the northern hemisphere of the African continent on the other hand, the situation is different, as here the period June–August normally constitutes the wet season. Still, precipitation in most Northern African countries, especially in the Sahel, is normally very low (below 650 mm a year; in our dataset 15 out of 19 Northern African countries had precipitation below 650 mm),

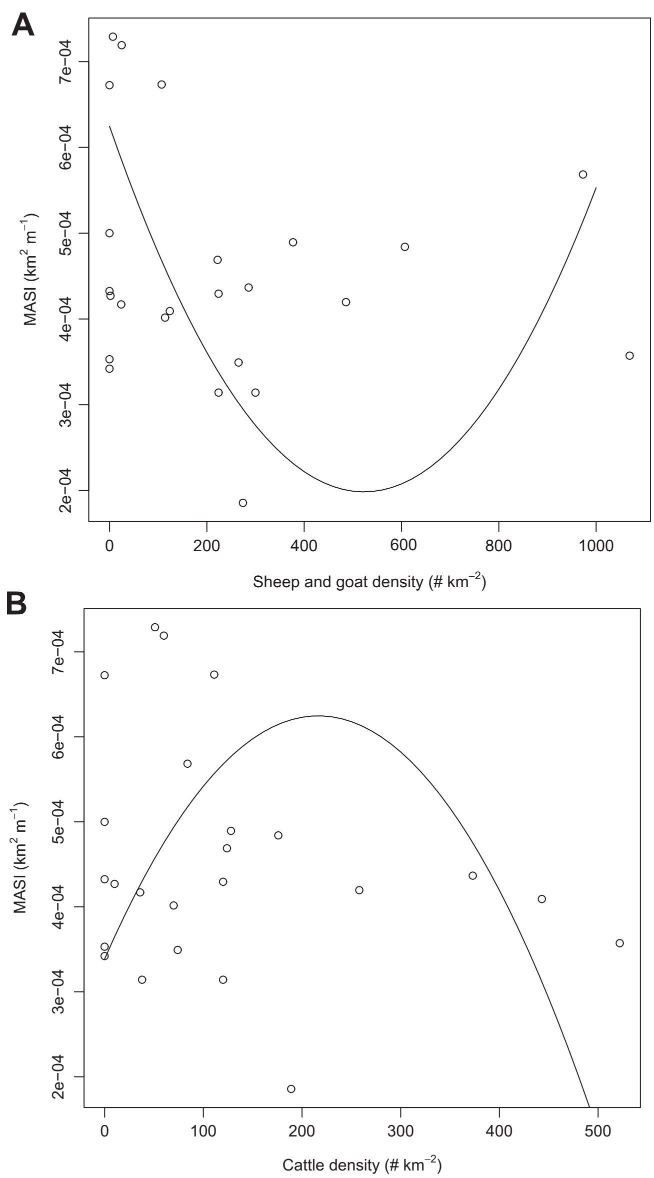

Fig. 5. U-shaped and hump shaped relations as fitted with the generated model for MASI as a function of (A) shoat and (B) cattle densities.

which puts an upper limit to the potential tree cover in itself (Sankaran et al., 2005). Fires are only likely to occur when grasses are present, and grasses will only start growing in the wet season. Places that receive sufficient rainfall to sustain grass growth will also be the places that can sustain tree growth, which may explain the positive relationship between fire probability in the wet season and tree cover.

For abiotic factors besides the occurrence of fire, only precipitation (PREC) and total exchangeable bases in the top soil (TEBT) had significant relations with some of the tree pattern indices. Strikingly, precipitation was never found to be the most important variable. Expecting that savannas would be water limited, especially in the dry seasons, this is an interesting result. In a study by Sankaran et al. (2005) the relationship between rainfall and maximum tree cover was the only significant relationship found using quantile regression. They suggested that rainfall is a limitation for tree cover in areas where rainfall is less than 650 mm per year, but that above 650 mm per year other factors are more limiting for tree cover. In our analysis, rainfall ranged from approximately 70 to 1300 mm. Although it is possible that rainfall is an important determinant in setting the upper limit as suggested by Sankaran et al., other factors (like sheep and goat presence) appear to be more limiting according to this dataset.

Overall R^2 values for our dataset were low (max R^2: 0.47) and although great care was taken to ensure the use of high quality data, the dataset still contained residual variation that was unexplained by our models. In part, this may be a result of the mismatch between the time the photographs were taken and the collection dates of the various datasets used as explaining factors. However, as mentioned before, the explaining factors were expected to have a high spatial and temporal autocorrelation, and we tried to look at long-term effects. Between savannas large variation in their physiognomy exists (Scholes and Archer, 1997), and possibly 24 sites are a limited representation of the variation for the scale we are looking at. Nevertheless, the archived historical dataset presented in our paper remains valuable because it forms an irreplaceable source of information about the state of savannas in the past, which may allow investigation of for example development trends. Comparison between historical databases such as presented in this paper and modern high resolution satellite products, like IKONOS and QuickBird that have high spatial resolutions, or Google Earth, which is freely available, can provide a valuable extension to this study, showing how savannas have been developing. These developments in tree pattern indices can then be correlated with processes like the ones analysed in this study to generate hypotheses on tree pattern formation.

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2011.03.010.

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