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Hierarchy and scale: testing the long term role of water, grazing and nitrogen in the savanna landscape of Limpopo National Park (Mozambique)

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Abstract This paper compares vegetation dynamics at two sites in the savanna landscape of Limpopo National Park (PNL), Mozambique. In order to test the relationship between vegetation cover and hydrology, nutrient availability and disturbance from grazing and fire over the last 1,200 years at local (100 m²) scales, we use palaeoecological data (i.e. pollen assemblages, charcoal abundance, C/N ratio, stable isotopes and herbivore-associated spore abundance). Two pans governed by similar rainfall regimes (on average 600 mm/year) but different hydrologies are compared. Chixuludzi Pan is responsive to the Limpopo River and is more water rich than Radio Pan, which is situated in a dry landscape with little surface water. The analysis suggests that in savannas where water is scarce, the recruitment of woody taxa is constrained mainly by the availability of underground water. In the Radio Pan sequence, the present grassland savanna has been stable throughout the time studied. In contrast, the Chixuludzi Pan

savanna landscape where local hydrology, due to the proximity of Limpopo River, allows for a higher water availability the relationship between grass-herbivore pollen suggests a greater variability in vegetation cover, and other factors such as grazing, herbivory and nitrogen availability are important as controlling mechanisms for woody cover. The historical depth of the analysis enables a sub-hierarchy of local scale process to be identified, in this case local hydrology. Local water availability is shown to override the effect of regional rainfall and, in turn, to control the influence of other local scale factors such as nutrients and grazing.

Keywords Hierarchical patch dynamics · Savanna ecology · Pollen · Coprophilous spores · Nitrogen · Fire

Introduction

The mechanisms of grass–tree coexistence in the savanna system are complex and the subject of much debate (Scholes and Archer 1997; Higgins et al. 2000; Jeltsch et al. 2000; Bond et al. 2003; Scholes et al. 2003; Sankaran et al. 2004). On the landscape scale, a general correlation between rainfall and woody cover has been shown; however, this relationship is far from simple. Through a comprehensive review of a multitude of savanna localities in the

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whole of Africa, [Sankaran et al. \(2005\)](#) identified a rainfall boundary of 650 ± 134 mm rain/year. Below this boundary, maximum tree cover increases with rainfall (although actual tree cover was usually below this maximum), while in areas with rainfall above this, there was no increase of woody cover with rainfall. Many savannas have woody cover well below its climatic potential, suggesting that other factors, notably fire, herbivory and nutrients, limit tree cover. The further a site is above Sankaran et al.'s boundary line of maximum tree cover versus rainfall, the more important factors other than rainfall are likely to be. These factors are likely to be nested hierarchically according to spatial scale; rainfall exerts a higher-level control that determines the upper maximum boundary of tree cover, while local factors determine how far actual tree cover differs from the maximum boundary ([Coughenour and Ellis 1993](#); [Gillson 2004](#); [Sankaran et al. 2005](#); [Levick and Rogers 2008](#)).

Contemporary studies on vegetation patterns have gone a long way in elucidating the hierarchy of influences on vegetation, but the lack of time depth is a fundamental limitation to these studies. Landscape and local scale processes may act over the scale of centuries, the intricacies of which cannot be resolved without a long term understanding of vegetation change ([Gillson 2004](#)). Long term records of vegetation change allow us to trace the long-term processes that structure the response of short-term fluctuations and vice versa. This paper contributes with a temporal assessment of hierarchical relationships between different spatio-temporal scale ecological processes covering the last 1,200 years. This time interval encompasses periods of significant climatic changes, the warm-wet Medieval Warm Period (MWP) (900–1300 AD) and the cool-dry Little Ice Age (LIA) (ca. 1500–1800 AD), which are examples of possible long term forcing mechanisms in the landscape. Palaeoecological data, i.e. fossil pollen assemblages, charcoal abundance, C/N ratio, stable isotopes of carbon and nitrogen, and herbivore-associated spore abundance forms the basis of this analysis. These tools does not allow for a full understanding of all variables involved when it comes to vegetation dynamics. Here we will focus on the importance of hydrology, fire, herbivory, nitrogen availability and the interaction between them. Sedimentary sequences from two pans, i.e. semi-seasonal waterbodies, situated in Limpopo

National Park (PNL), Mozambique, are compared. These are both governed by a similar rainfall regime, ca. 600 mm/year ([FAO 2004](#)), but different hydrological systems, one being responsive the Limpopo river and the other situated in a dry landscape with little surface water. The long-term patterns in the relationship between hydrology, nutrient availability, fire and herbivory and the centennial timescales addressed in this analysis will allow for to the identification hierarchies of spatio-temporal scale processes that has not been addressed previously in savanna ecology.

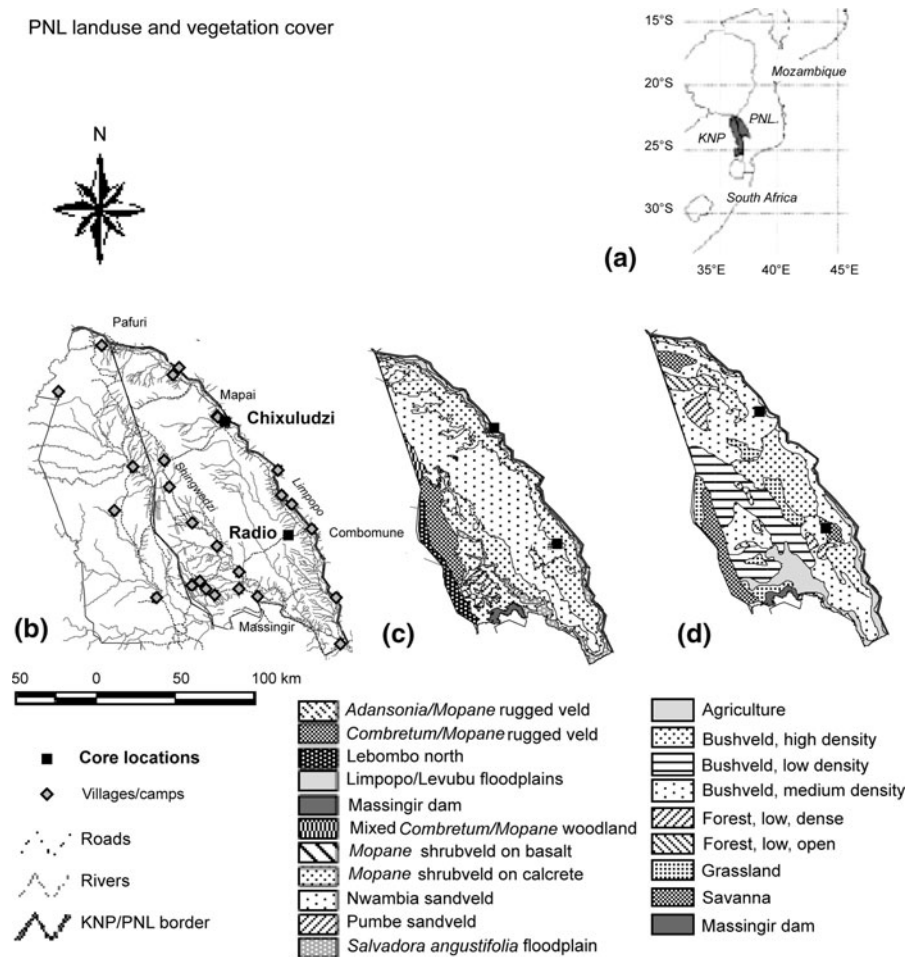
Area description

Limpopo National Park (PNL), Mozambique, was formally designated in 2001 by the Mozambique government. It borders Kruger National Park (KNP) to the west and is delimited by the Limpopo River to the north and east and the Elephant-Limpopo River confluence in the south (Fig. 1a, b).

Limpopo National Park can be divided into two main landscape types: the dry sandy plateaus of the interior and the incised river valleys. The Limpopo River borders the park and the Shingwedzi River cuts through the middle of the park, in a northwest-southeast direction. Most of the settlements in the park are concentrated in these river valley areas, where water is available all year round. This is also where most of the cattle are grazed. In between the river valleys, the landscape is dry and characterised by deep sands. Surface water availability in this area is restricted to semi-seasonal pans and there are no settlements here (Fig. 1a).

The vegetation in PNL is broadly classified as a dry deciduous tree savanna within which *Colophospermum mopane*, commonly referred to as *mopane*, is the most abundant arboreal taxon. *Colophospermum mopane* is completely dominant in the dry sandy plateau and usually occur as small trees or multistemmed shrubs interspersed with grasses, while woodlands of *Acacia*, *Commiphora* and *Terminalia* at lower elevations. Close to the Mapai village, mature *Colophospermum mopane* woodlands can be observed. More varied vegetation occurs near watercourses or in the vicinities of the pans, with riparian elements such as various species of *Acacia xanthophloea*, *A. tortilis* and *A. nilotica* and shrub thickets of *Salvadora persica* ([FAO 2004](#)) (Fig. 1c, d). *Diospyros mespiliformis*,

Fig. 1 The location of Limpopo National park (PNL) (a), hydrology, main roads and settlements/camps in PNL and KNP and the location of Chixuludzi and Radio Pan (b), vegetation of PNL (c), landuse of PNL (d). (FAO data provided by Peace parks foundation)



Ziziphus pubescens subsp. *glabra*, *Boscia mossambiquensis*, *Rhus guenzii* have also been reported near the rivers (Wild and Fernandes 1968).

Rainfall is marked by a cyclicity of near decadal dry and wet phases together with an interannual variability (Tyson and Preston Whyte 2000). The park has a north–south rainfall gradient with 375–420 mm/year in northern Pafuri and 600 mm/year in the Massingir area (FAO 2004). Rainfall is markedly seasonal with 95% of the yearly rainfall occurring between October and April. The mean daily temperatures are 30–34°C in the summers and 22–26°C in the winter (FAO 2004). The two sampling points are semi-permanent pans situated 80 km apart in the in the north–south rainfall gradient. Thus, rainfall is probably slightly higher in the northernmost Chixuludzi Pan than in Radio Pan located to the south. However, both pans are governed by the same synoptic meteorology.

The investigated pans are fed by underground aquifers. Radio Pan (given name) is located on the dry deep sands as described above (23°30′40.3″ S, 32°18′09.2″ E). Chixuludzi Pan is situated on the palaeo-floodplain of Limpopo River and recent alluvial soils (22°51′37.1″ S, 31°56′33.5″ E). The pan lies close to Mapai village that has been settled over the last century and, as our pollen record suggests, for many centuries. Local vegetation near Chixuludzi Pan has more varied arboreal taxa, with *Acacia xanthophylla*, *Xanthocercis zambesiaca*, *Diospyros mespiliformis*, *Cardiogyne africa*, *Grewia sulcata* being represented in the near vicinity and *mopane* shrubveld and riparian vegetation in the surrounding area. In Radio Pan local vegetation shows few types of trees/shrubs as *Terminalia sericeae*, *Sclerocarya* sp., *Dichrostachys cinerea*, *Combretum imerbe* and *mopane* and grasslands are dominant here.

The hydrological system of the dry sandy plateaus of PNL, where Radio Pan is located, is complex and the response of pans in this area to rainfall is unpredictable. The coarse textured sandy soils of the area (Solonetz) have a very low water retention capacity (FAO 2004). During dry years, some pans retain water, while others do not and this pattern changes from year to year (pers communication with gameguards). No measurements of recharge periods and water depth fluctuations have been carried out for these pans and the character of feeding underground aquifers is not well known. Chixuludzi Pan is situated in the incised river valley and the paleofloodplain of Limpopo River where water availability is generally high (FAO 2004). Most probably Chixuludzi pan is fed by an aquifer that is responsive to the Limpopo River. This river in turn has a very large drainage area that would effectively buffer water supplies and mitigate local water scarcity. Water availability in Chixuludzi Pan is therefore expected to have been proportionally higher than in Radio Pan throughout time.

Methodology

Sampling methodology and representativity of the cores

The pans were selected on the basis of their small surface drainage areas (ca. 50 m/diameter and 100 m/diameter in the Radio and Chixuludzi Pans, respectively). Water depth varies seasonally, and at the time of sampling during the dry season, water bodies were reduced to damp wetlands. These small pans, with no surface inlets or outlets are assumed to reflect local to semi-local (within 20–ca. 300 m) scale changes in vegetation (Jacobsen and Bradshaw 1981; Prentice 1985). Pollen grains are deposited by air or surface runoff (Jacobsen and Bradshaw 1981). In theory, pollen may also be brought to the basin through the feeding underground aquifers but this signal is assumed to be low as pollen would effectively be filtered through the soil. A sedimentary core (1 m length, 5 cm in diameter) from the deepest areas of each pan was obtained in August 2006 using a Russian corer (Aaby and Digerfeldt 1986). Cores have been stored in a cold store with a controlled temperature at the OxLEL, Oxford University.

The amount of damaged grains is relatively high as would be expected in sediments that have been exposed to temporary droughts when pollen grains are likely to become eroded due to temporary oxidation of sediment and enhanced microbial activity. Prolonged periods of drought would be reflected in peaks of eroded grains, a skewed representation of taxa and low pollen concentrations (as shown in the base of the Chixuludzi core), as the sediments would have become exposed to oxidation which would result in the degradation and loss of pollen grains in the sediments. Damaged pollen grains are more numerous in Chixuludzi (commonly ranging between 45 and 60%) than in Radio Pan (commonly ranging between 30 and 40%) and both concentration and influx of pollen grains are higher in the Radio Pan than in Chixuludzi (42,170–22,178 cm²/year, compared to 15,884–1,589 cm²/year). Despite the relatively high amount of damaged pollen grains there is no indication of an overall selective preservation of pollen taxa. Overall the presence of well preserved pollen grains, the absence of selective preservation of pollen grains and the high concentrations of pollen grains in the cores suggest that the pans have been wet during most of the time investigated.

Palaeoecological analysis

Preparation of fossil pollen, microscopic charcoal and spore preparation was carried out through a digestion of humic acids with NaOH, sieving through a 150- μ m mesh, digestion of quartz particles through HF and digestion of cellulose by Acetolysis and with the addition of exotic *Lycopodium* spores for concentration estimates (Stockmarr 1971; Faegri and Iversen 1992) following the protocol published by Bennett and Willis (2001). We compare the proportional changes (i.e. the magnitude of the internal variation of each site) rather than the absolute abundance/values, which is why pollen and spore data is presented on the basis of percentages. A minimum of 300–500 terrestrial pollen grains was counted for each level to ensure statistical significance (Maher 1981). Pure limnic and aquatic groups such as *Typha* and *Nymphaea* were excluded from the pollen sum, together with sedges (Cyperaceae), which are abundant in lake margins. Damaged/degraded grains were also excluded from the pollen

sum. The percentages of these groups are based on the representation of individual taxa/type over the pollensum. The indigenous African cereals overlap in size with other Poaceae and cannot be separated morphologically (Tomlinson 1973). Based on size classes we have separated a $>40\ \mu\text{m}$ Poaceae group as a 'possible' cereal group as these tend to co-occur with Maize. Pollen identification was carried out using Bonnefille and Riollet (1980), Scott (1982), Oxford Long-Term Ecology Laboratory reference collection and the African pollen database. We assume here that arboreal pollen (AP) percentages are representative of woody cover and Gillson and Duffin (2007) have shown in the KNP context that there is quadratic equation relating AP percentage to percentage of woody cover.

Spores were tallied alongside the pollen grains and abundance is expressed as percentages over the total pollen sum. A number of references were used for spore identification (van Geel et al. 1983, 2003; Jarzen and Elsik 1986; Graf and Chmura 2006; van Geel and Aptroot 2006). The majority of the represented spores are ascospores or basidiospores of fungi living in soil or terrestrial plant material. We will focus on the spore types that may be associated with coprophilous fungi. Sordariaceae, *Chaetomium* and *Podospora* have been reported by Ebersohn and Eicker (1992) as growing on herbivore dung from KNP and are commonly found in association with both wild and domestic herbivory (Graf and Chmura 2006; van Geel and Aptroot 2006). Sordariaceae occurs together with *Coniochaeta* cf. *lignaria*, Taxa that are commonly referred to as coprophilous (van Geel et al. 2003; Marinova and Atanassova 2006; van Geel and Aptroot 2006). *Sporormiella* which is commonly reported as coprophilous (Davis 1987; Burney et al. 2003; Robinson et al. 2005; Davis and Shafer 2006), is not represented in any of the cores. This genera is present in low numbers in only one KNP core (Ekblom and Gillson 2010b). The correlation between the abundance of spores from coprophilous fungi and herbivore abundance is assumed and well utilised in the literature (Davis 1987; Burney et al. 2003; van Geel et al. 2003; Robinson et al. 2005; Davis and Shafer 2006; Graf and Chmura 2006; Marinova and Atanassova 2006). The correlation between fungal spores and herbivore abundance has been investigated by Raper and Bush (2009) in Florida, USA.

Duffin et al. (2008) have shown a good correlation between the charcoal record and both fire area and intensity. Microscopic charcoal abundances were estimated in relation to the added *Lycopodium* spores using the point count method (Clark 1988; Finsinger and Tinner 2005). The charcoal that "touches" selected points on the eyepiece graticule was counted in a grid over the slide and related to the number of *Lycopodium* spores encountered in the same fields of view. This gives an estimation of the area of charcoal (cm^2/cm^3) in relation to sediment volume and these values have here been converted to influx (cm^2/year) on the basis of age depth as this provides a better comparison between sites/periods with different rates of sediment accumulation. The magnitude of changes in the charcoal signal between concentration and influx values is very similar. Charred grass cuticles, i.e. rectangular particles with sinuous margins with or without and papillae or traces of stomata or silica bodies, were separated from a general undiagnostic charcoal group and possible charcoal particles with a length/width ratio >3 . Macroscopic particles ($>150\ \mu\text{m}$) were extracted during pollen preparation through $150\ \mu\text{m}$ mesh sieving, and were counted using a stereomicroscope in 10–60 \times magnification.

The carbon and nitrogen elements and stable isotopes are primarily related with the origin and formation of the organic matter in the sediment but may also give information on the influx of nutrients, and vegetation composition of the surrounding landscape (Meyers and Lallier-Vergès 1999; Meyers 2003; McLauchlan et al. 2007). The carbon and nitrogen elements and stable isotopes were analysed using EA-IRMS (elemental analyser isotope ratio mass spectrometry). Samples for $\delta^{13}\text{C}$ were first acid washed using 10% (w/v) HCl. Total carbon and nitrogen were measured alongside the stable isotopes and are given as % of element and as the C/N ratio, while the δ values describe the ratio of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ in relation to a standard.

Zonation of the whole pollen assemblage was carried out in Psimpoll (Bennett 1996, 2000) using optimal splitting by information content to identify statistically significant zones. The results of the zonation were then re-interpreted on the basis of the other proxies to identify phases.

Chronology

The time scales we are addressing here are on the scale of centuries. The chronology is based on AMS ^{14}C dates of the bulk sediment, six in the case of the Chixuludzi core and two in the case of the Radio core. These were calibrated using in BCal (Buck et al. 1999) using the southern hemisphere calibration curve (McCormack et al. 2004) (Table 1). As seen in Table 1, the calibration gives a range of 100–200 years. This is a margin of error that is inherent in the ^{14}C dating method. The uppermost 40 cm of the core from Radio Pan have been dated using ^{210}Pb isotopes and calibrated using the Constant Flux:Constant Supply CF:CS model which gives a higher resolution than the ^{14}C method (Robbins and Herche 1993). The Chixuludzi ^{210}Pb series was inconclusive due to the low amount of unsupported lead, which is why it is not used here. Age-depth was modelled in Psimpoll (Bennett 2000) assuming that sedimentation of the cores has been continuous until the present day and that accumulation rates between dated levels was linear. This is an idealisation of how sedimentation in drought prone environments work, as the rate of sedimentation is likely to vary with water-depth. The effects of

bioturbation and other mixing create a “running average” of sediment deposition and pollen rain, thus effectively smoothing out variable sedimentation rates. This means that short-term events such as temporary droughts or floods may not be reflected in the record, as extreme values are smoothed out (Jacobsen and Bradshaw 1981) (Table 2).

Results

Radio Pan

A stable savanna, dominated by grasses with low tree cover, has been present in Radio Pan over the past 600 years. Arboreal taxa represent ca. 6% of the pollen sum, ranging from 3 to 11% of the pollen sum. The range of arboreal taxa represented is low with only 19 different pollen taxa represented. Typical riparian elements (e.g. *Diospyros*) are present in very low numbers, constituting <1% of the AP (Figs. 2, 3). Two distinct phases, both interpreted as constituting a savanna type vegetation, have been identified based primarily on the representation of spores, aquatics and isotopes, as the terrestrial pollen assemblage is relatively homogenous.

Table 1 ^{14}C dates and Pb^{210} series of presented cores

Dates and calibrations					
Site/depth	Lab no.	Age AD	Calibration Bcal	Est. age AD	
Chix 29-30	Ua-38832	346 ± 30	1,503–1,602 1,608–1643	1,625	
Chix 38-37	Ua-38833	381 ± 30	1,457–1,595	1,503	
Chix 40-41	Ua-38834	533 ± 31	1,406–1,450	1,432	
Chix 43-44	Ua-38835	605 ± 30	1,318–1,352 1,384–1,425	1,401	
Chix 48.5-49.5	Poz-25104	1,065 ± 30	983–1,046 1,084–1,135	1,020	
Chix 79.5-80	Poz-22197	1,270 ± 30	709–748 764–893	862	
Radio 0-0.5	OxLel	2,000	Pb 210, CF:CS model	2,000	
Radio 10-10.5	OxLel	1,980	Pb 210, CF:CS model	1,980	
Radio 20-20.5	OxLel	1,960	Pb 210, CF:CS model	1,960	
Radio 30-30.5	OxLel	1,950	Pb 210, CF:CS model	1,950	
Radio 40-45.5	OxLel	1,925	Pb 210, CF:CS model	Not used	
Radio 35-35.5	OxA-16674	109.8 ± 0.4 ^a	709–748, 764–893	1,905 ^b	
Radio 79-80	Poz-25106	690 ± 40	1,287–1,394	1,394	

^a Modern

^b Oxcal calibration

Table 2 Represented pollen types and ecological groupings

Identified pollentypes and ecological groupings				
AP (included in the pollensum)				
Rip.	<i>Celtis</i>	<i>Eugenia</i>	Moraceae	<i>Syzygium</i>
	cf. <i>Dialium</i>	<i>Macaranga</i>	Myrtaceae	<i>Trema</i>
	<i>Diospyros</i>	Meliaceae	<i>Olea</i>	
Gen.	<i>Acacia</i>	Combretaceae	<i>Fagara</i>	Rhamnaceae
	<i>Brachyleana</i>	<i>Corchurus</i>	<i>Faurea</i>	<i>Rhus</i>
	Celastraceae	<i>Euclea</i>	<i>Grewia</i>	<i>Vitex</i>
Sav.	<i>Brachystegia</i>	<i>Mopane</i>	<i>Sclerocarya</i>	<i>Spirostachys</i>
	<i>Dichrostachys</i>	<i>Pseudolachnostylis</i>		
Ungr.	<i>Juniperus</i>	Hyphaene	<i>Pinus</i>	Palmae
	<i>Podocarpus</i>			
Herbs (included in the pollensum)				
	Acanthaceae	ChenAm	Lamiaceae	<i>Ocimum</i>
	Asteraceae	<i>Commelina</i>	Liliacea	Polygalaceae
	<i>Canthium</i>	<i>Croton</i>	Malvaceae	<i>Tribulus</i>
Grasses (included in the pollensum)				
Aquatics and eroded/damaged grains (excluded from the pollensum)				
	Cyperaceae	Hydrochariaceae	Nyctaginaceae	<i>Potamogeton</i>
	<i>Typha</i>	<i>Laurembergia</i>	Ranunculaceae	<i>Urticularia</i>
	<i>Nymphaea</i>			Eroded pollengrains

Radio phase 1, 1400–1600 AD (78–64 cm depth)

Grasses dominate the pollen assemblage with few representatives of riparian and generalist tree/shrubs (Combretaceae, *Rhus* and *Acacia*). Asteraceae dominates the herb group. Cyperaceae, belonging to the limnic-aquatic group, displays low to moderate values, while the aquatic *Nymphaea* is well represented throughout the phase. The silty lithology in this part of the core, together with the relatively high abundance of damaged pollen grains (ca. 60%), indicates that the pan was frequently dry. This, as deposited pollen grains are likely to have become degraded/corroded when sediments were exposed to oxidation. The presence of charcoal is low (0.03 cm²/year). The high $\delta^{13}\text{C}$ values (15‰) and the high C/N ratio (>40) shows that organic matter is constituted mostly by C₄ grasses in the (Fig. 6). This gives support to the dominance of grasses in the landscape, as suggested by the pollen assemblage. There is a very high abundance of spores in general (7 × the pollensum) and coprophilous fungi (Sordariaceae and *Coniochaeta* sp.) is well represented (11%). Values of $\delta^{15}\text{N}$ are high, ranging from 7 to 9‰ (Fig. 5).

Radio-Phase 2, 1400 AD to present (60–0 cm depth)

This phase represents a period of continued dominance of grasses. The decreased C/N ratio (from >40 to ca. 10) suggests a higher influence of algal organic matter (Fig. 6). This may be indicative of either a slightly higher water table than before and/or an increase in algal growth. Despite this possible small rise in water table, the variable Cyperaceae curve implies a continued fluctuating water table (cf Gillson and Ekblom 2009a) with frequent droughts as shown by the variable representation of damaged pollen grains (from 17 to 60%). The progressive decrease of $\delta^{13}\text{C}$ values, which indicates higher inputs from C₃ and aquatic plants, may be linked with an increase of woody taxa in the landscape. There is a concurrent increase in AP (seen in the representation of Combretaceae, *mopane* and *Spirostachys*) though this is of a very small magnitude. Asteraceae continues to be common and Chenopodiaceae/Amaranthaceae (Chen/Am) occurs from ca. 1800 AD. *Nymphaea* shows stable values until approximately 1800 AD (44 cm depth) after which values fluctuate. The abundance of spores from coprophilous fungi is low throughout most of this phase. Charcoal abundance remains low during

Fig. 2 Percentage pollen and spore diagram of Radio Pan, showing terrestrial (AP, Herbs and Poaceae), aquatic/limnic (aqua.) pollen groups and coprophilous spores. Vertical axis shows the depth (cm), estimated ages and lithology. Horizontal axes show the pollen types and their percentage distribution (black graphs). Note that less common taxa have been exaggerated by 10 (hashed curves) for visibility

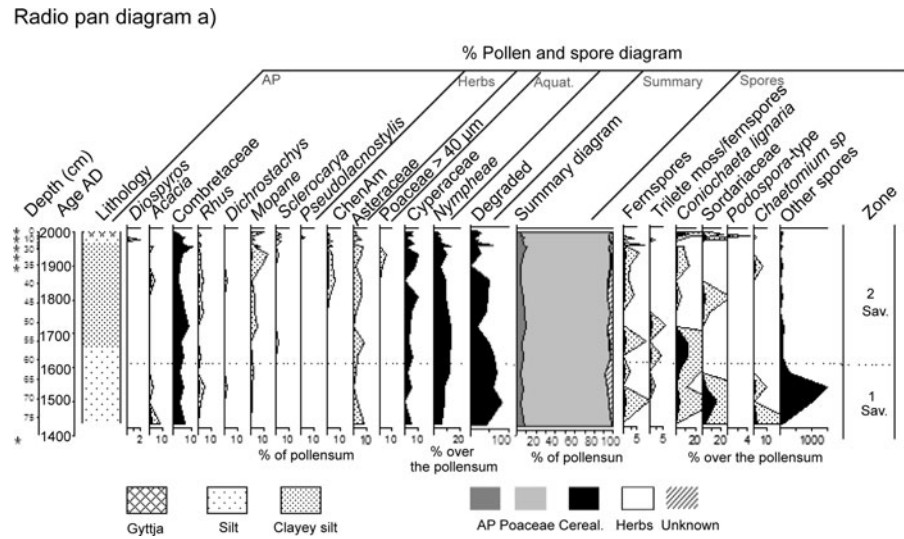
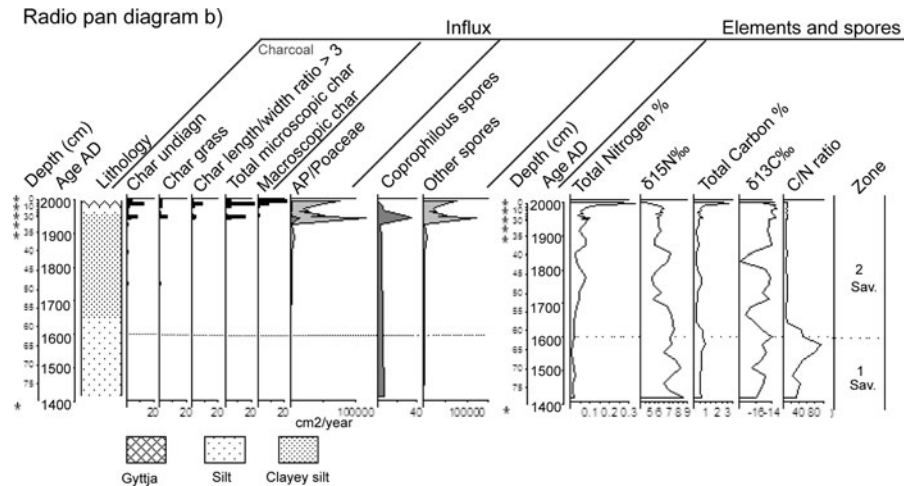


Fig. 3 Influx charcoal diagram (cm^2/year) of Radio Pan with AP/Poaceae and coprophilous spore/other spore influx values (cm^2/year). The results of isotopic and elemental analysis are shown to the right



the major part of the phase, on average $0.2 \text{ cm}^2/\text{year}$. However, during the twentieth century (top 30 cm) charcoal abundance shows a significant increase to as high as $22 \text{ cm}^2/\text{year}$. Both pollen influx and concentration (not shown) are very high in this section of the core. In the same time period there is an increase of coprophilous spore types (*Coniochaeta cf lignaria* and *Sordariaceae*). The $\delta^{15}\text{N}$ drops to below 7‰ in the early part of the zone (from ca. 1700 AD).

Chixuludzi Pan

Chixuludzi Pan has a higher abundance and a higher variability of AP taxa than Radio Pan. The AP sum

makes up for 11% of the pollen sum, ranging between 5 and 34%. 27 different arboreal taxa are represented of which 9% constitutes typical riparian elements such as *Diospyros* and *Moraceae* (Figs. 4, 5). Four zones were identified (78–44, 44–26, 26–24, 24–0 cm depth) in the pollen assemblage based on the behaviour of *Combretaceae*, *Sclerocarya*, *Chenopodiaceae/Amaranthaceae*, *Poaceae*, *Cyperaceae*, *Typha*, *Nymphaea* and unknowns. We have identified three phases based, two savanna phases (80–40 cm depth) on the basis of the pollen and spore assemblage and the isotope record, and another savanna-riparian phase (40–0 cm depth) based on the behaviour of the pollen assemblage.

Fig. 4 Percentage pollen diagram of Chixuludzi Pan, terrestrial (AP, Herbs and Poaceae) and aquatic/limnic (aqua.) pollen groups. Vertical axis shows the depth (cm), estimated ages and lithology. Horizontal axes show the pollen types and their percentage distribution (black graphs). Note that less common taxa have been exaggerated by 10 (hashed curves) for visibility

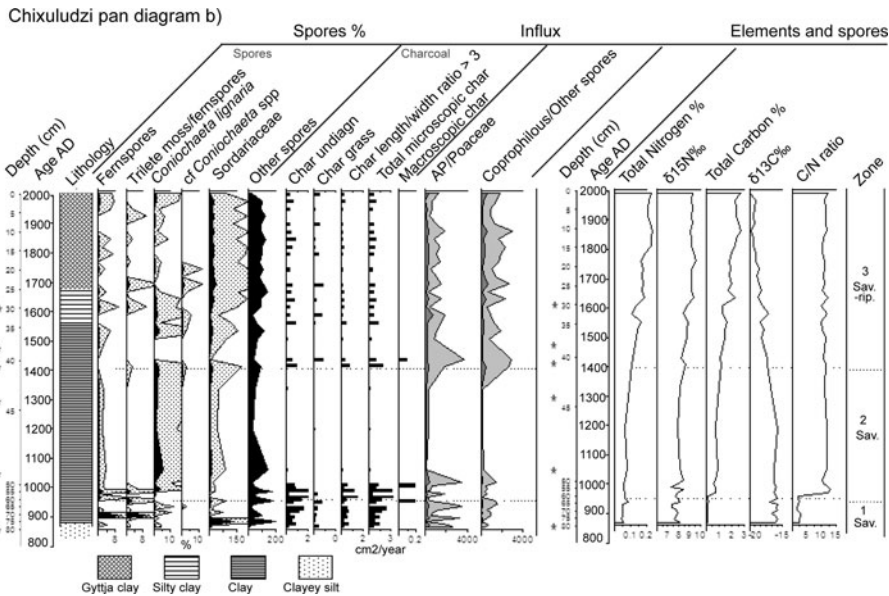
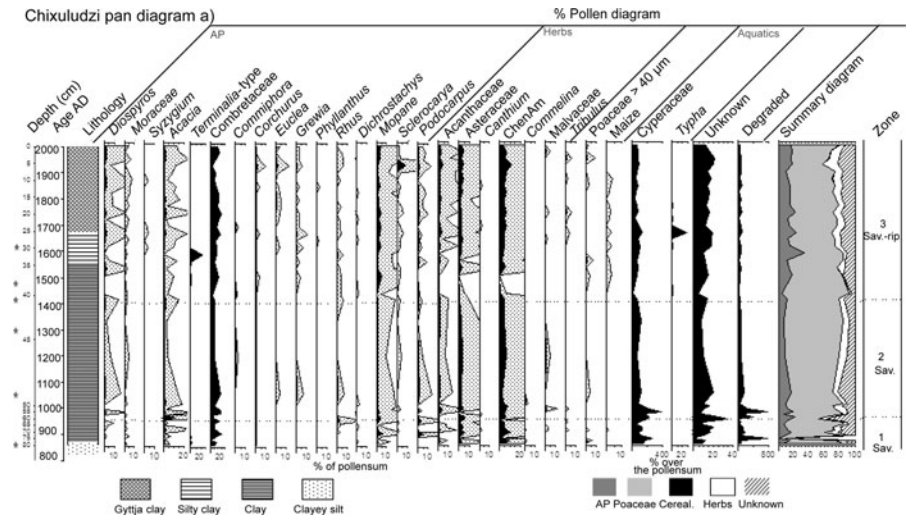


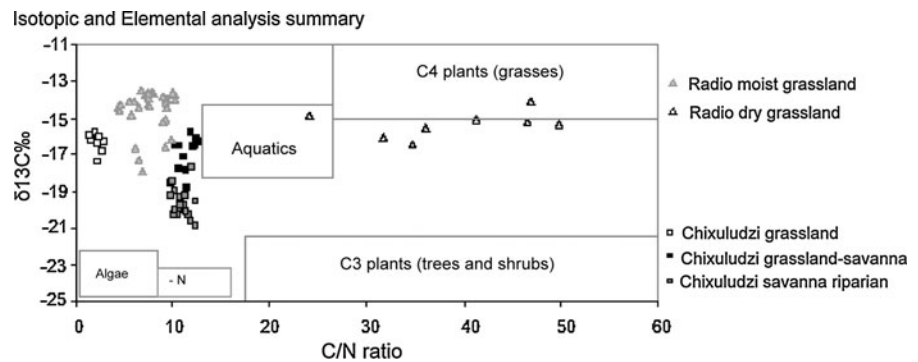
Fig. 5 Percentage diagram of spores from Chixuludzi Pan together with charcoal influx and AP/Poaceae influx values. Isotopic and elemental analysis are shown to the right

Chixuludzi phase 1, 800–ca. 950 AD (80–60 cm depth)

This savanna phase is dominated by grasses, with high values of Cyperaceae and aquatics, which suggests a fluctuating water table. The C/N ratio is extremely low (around 2), and could be explained by diagenetic processes (Meyers and Lallier-Vergès 1999), although the low C/N ratio may also imply that the organic matter in the sequence was

dominated by the autochthonous algal production (Fig. 6). A low input of terrestrial organic matter is supported by the low presence of fungal spores in this part of the core. All these factors together indicate that the water table at Chixuludzi Pan in this part of the sequence was high overall, although the presence of hiatuses, seen in the very high amount of damaged pollen grains (as much as 7 × the pollen sum at ca. 880 AD) implies repeated dry periods within this phase. AP is well represented but variable (7–22%)

Fig. 6 Values of $\delta^{13}\text{C}$ and C/N of the vegetation phases of Radio Pan (*triangles*) and Chixuludzi Pan (*squares*) together with the generalised $\delta^{13}\text{C}$ and C/N values of major sources of plant organic matter (from Talbot and Lærdal 2000; Meyers 2003; Brenner et al. 2006, -N *right pointed triangle* denotes values of nitrogen starved Algae)



and dominated by generalist taxa as Combretaceae and *Acacia* and savanna type taxa as *mopane*. Herbaceous taxa are mainly represented by Asteraceae and Chenopodiaceae/Amaranthaceae. Microfossil charcoal abundance is high, ($1.5 \text{ cm}^2/\text{year}$) over the whole phase, with very high values ($3.4 \text{ cm}^2/\text{year}$) in the end of the phase (ca. 950 AD) that is reflected also in the macrofossil charcoal curve. Changes in the abundance of charred grass cuticles and possible grass charcoal (i.e. particles with a length/width ratio >3) types are synchronous with the representation of undiagnostic charcoal though of much lower abundance (values being on average <0.04 and ca. $0.5 \text{ cm}^2/\text{year}$, respectively). Fern and moss spores are very well represented in this phase. Coprophilous spore types occur in moderate numbers (16% over the pollen sum) and there are few Poaceae $>40 \mu\text{m}$ (possible Cerealea). Values of $\delta^{15}\text{N}$ values are high (ca. 8‰) suggesting a high nutrient availability.

Chixuludzi phase 2, 950–1400 AD (60–40 cm depth)

The subsequent savanna phase is marked by an increase in the C/N ratio to 12, suggesting a higher influence of terrestrial plant material in the organic matter (Talbot and Lærdal 2000; Meyers 2003) (Fig. 6). The very high values of damaged grains in the beginning of the phase indicate that the pan was dry at times between 950 and 1000 AD. The $\delta^{13}\text{C}$ values indicate an increased influence of C_3 trees and shrub in the transition between phases 1 and 2 that is not seen clearly in the pollen diagram were the amount of woody taxa stabilises to around 10%. Riparian taxa as *Diospyros* and Moraceae are better

represented than before and a wider range of species, mainly generalist taxa, is represented. Chenopodiaceae/Amaranthaceae decrease briefly between 1000 and 1100 AD, while Asteraceae shows similar values as before. Other herbs (Acanthaceae, Malvaceae) are now represented continuously. Microfossil charcoal abundance continues to be high in the beginning of the phase ($1.4 \text{ cm}^2/\text{year}$) but decrease to low ($0.6 \text{ cm}^2/\text{year}$) values after this. There is a very low representation of grass and possible grass type charcoal. Spores from coprophilous fungi are represented with low numbers (7%). *Coniochaeta lignaria* is well represented throughout the phase while Sordariaceae shows an increase in the end of the phase at ca. 1400 AD. The $\delta^{15}\text{N}$ values show a progressive increase from 8.2 to 9.2.

Chixuludzi phase 3, 1400 AD–present (40–0 cm depth)

This phase will be referred to as ‘savanna-riparian’ and shows an increase in the representation of woody taxa to ca. 16%, ranging between 10 and 34%. An increase can be seen particularly of riparian types as *Diospyros*, Moraceae, *Syzygium* and *Terminalia*-type (the latter which should possibly be included in the riparian group) together with generalist taxa such as *Corchurus*, *Euclea*, *Grewia* and *Rhus*. *Mopane* shows an increase in the phase that should be seen as significant (2.4% compared to 1.7% in previous phases), considering that *mopane* pollen generally is usually underrepresented. The increase of woody taxa reaches its highest values (34%) just before ca. 1600 AD, linked with a peak in *Terminalia*-type. The general expansion of woody cover indicated by the

pollen assemblage is supported by the progressive decrease of $\delta^{13}\text{C}$ values that reflect an increased influence of C_3 trees and shrubs in the sediment organic matter. A brief expansion of grasses is shown in the very beginning of this phase (1400 AD) and all herbs display a contemporary decline. Chenopodiaceae/Amaranthaceae show very high values (as much as 11%) from ca. 1900 AD as well as the herbaceous taxa previously represented. *Tribulus* now occurs occasionally throughout the phase. Maize pollen appears from 1500 AD together with high values of $<40\ \mu\text{m}$ grass (i.e. possible cerealea). Pollen influx and concentration (not shown) increases in this phase compared to the earlier phase. Microfossil charcoal values are fluctuating with three peaks around ca. 1550, 1650 and 1850 AD (1.2, 0.9 and $1\ \text{cm}^2/\text{year}$, respectively) that are not reflected in the macrofossil charcoal curve. Changes in grass and possible grass type charcoal are synchronous with the representation of undiagnostic charcoal though, of much smaller magnitude. Coprophilous spore types, particularly Sordariaceae and *Coniochaeta lignaria*, show an increase in abundance to ca. 20% (over the pollen sum) from 1500 AD, after which their abundance remains continuously high. The $\delta^{15}\text{N}$ shows a continued progressive increase to 9.5%.

Discussion

Differences in vegetation history

The two sites show markedly different vegetation histories, both in terms of stability and species composition. The pollen assemblage of Radio Pan suggests relatively stable savanna grassland throughout its 600-year history. The changes taking place at 1600 AD are most likely related with hydrological changes however these did not affect vegetation patterns significantly. Vegetation cover in Chixuludzi change from a moist savanna phase dominated by grasses, sedges and herbs, dated 800–950 AD and second savanna phase, dominated by grasses, post-dating 950 AD. After 1400 AD there is a change to a savanna-riparian phase with marked expansion of AP generally and riparian types in particular. This suggests an expansion of riparian type vegetation around Chixuludzi from 1400 AD.

The Radio Pan sequence has very low values of woody taxa (6%), few taxa represented and a low variability in AP abundance (3–11%). Meanwhile vegetation surrounding Chixuludzi Pan is more variable, with an overall high (11%) representation of arboreal taxa and a more variable abundance of AP (5–34%). Chixuludzi Pan also has a wider range of taxa represented with riparian (*Diospyros* Moraceae and possibly *Terminalia*-type), generalist (Combretaceae, *Euclea*, *Grewia*, *Rhus*), and savanna (*mopane*) elements.

Both pans show signs of shorter dry events but the high representation of riparian taxa at Chixuludzi Pan (9% of the AP sum) compared to that of Radio Pan ($<1\%$ of the AP sum) suggest that water availability was higher at Chixuludzi Pan throughout time.

Possible effects of regional climate change

Based on climate data from the Transvaal region supported by other proxies from the whole of the summer rainfall region, we can assume that the 1,200 years covered in this study encompass the MWP (900–1300 AD), when conditions were generally warmer (on the basis of speleothem records an estimated 3°) and wetter than today with shorter cool-dry spells. During the LIA (ca. 1500–1800 AD) conditions were generally cooler and drier with shorter warm/wet spells. The most extreme cold-dry period occurred around 1750 AD when on the basis of speleothem records, temperatures is estimated to have been 1° colder than today (Holmgren et al. 1999, 2001, 2003; Tyson et al. 2000, 2001; Lee-Thorp et al. 2001).

In terms of regional drivers, long term climatic trends, such as the MWP (900–1300 AD), seem to have been influential to the hydrologies of both pans as the 1400 AD shift to a savanna-riparian phase at Chixuludzi Pan is likely to have been linked with an increased water availability. This change is contemporary with the beginning of organic sediment accumulation in the Radio Pan record which similarly may be linked with higher water tables. The synchronicity of these records is supported by other cores from KNP/PNL (not discussed here) and indicates a regional increase of groundwater, probably as a regional response in hydrological systems linked with the MWP. However the LIA (ca. 1500–1800) appears not to have influenced vegetation patterns significantly. This is somewhat surprising given the magnitude of

the dry event around 1750 AD. There is nothing to suggest hiatuses in this period (e.g. like a slower sediment accumulation or a high amount of degraded pollen grains). Possibly the drier climate during the LIA had a low impact on vegetation as the periods of extreme drought events were short in duration and countered by a lower evaporation due to cooler temperature, in combination with the fact that vegetation in these semi-arid savannas are resilient to droughts.

Effect of local hydrology

Regional climate is the higher order organising principle in this landscape as shown by the changes taking place around 1400 AD, however, on a local scale hydrology can modify the effect of larger-scale climate patterns. Radio Pan and Chixuludzi Pan are located at a 80 km distance from each other, but the contrasting vegetation histories of the two sites cannot be sufficiently explained by the relatively small, north–south rainfall gradient that occurs between these latitudes. The lack of synchronicity in vegetation response between the two localities after 1400 AD indicates that the effect of climate variability on water availability in the two pans, particularly that of rainfall, is modified by the differential local hydrological systems. The hydrological system of Radio Pan and that of the dry interior of PNL is not well known, however the capacity of the soils in this area to store water is low. Chixuludzi Pan is responsive to the Limpopo River and local water supplies (as governed by local hydrology) in dry years would have been buffered the river itself that is controlled not only by local drainage but also by the regional drainage of both upper and middle Limpopo. The soils near Chixuludzi Pan would also be able to store rainfall for longer periods. The Radio Pan landscape is mainly controlled by the limited ability of the aquifer to store rainfall, resulting in a limited local availability of water and, by extension, restrictions on tree recruitment. On a general level, this explains the stability of the savanna vegetation in Radio Pan, as indicated by the pollen assemblage. Even with smaller variations in water table and possible increases in rainfall, local water availability was too low to facilitate local woody recruitment at a significant level.

In contrast, as the Chixuludzi landscape is not limited by water to the same degree, tree recruitment is possible which is reflected in the highly variable representation of AP. However variations in local water availability cannot by itself explain the causal mechanism between the variations in tree/grass cover shown in the pollen assemblage. As Chixuludzi pan is relatively unconstrained by water availability other variables are therefore important as drivers of woody vegetation abundance. This parallels the findings of Sankaran et al. (2005), and here we have examples of two savannas that are both climatically unstable but were differences in local hydrology create different patterns of behaviour. We hypothesize, that in Chixuludzi pan, as water availability does not constrain tree recruitment on a local scale to the same degree as Radio Pan, tree recruitment is highly responsive to changes in fire, nutrients and herbivory which—together with the changes in water availability itself—explains the variability in grass–tree pollen percentages here.

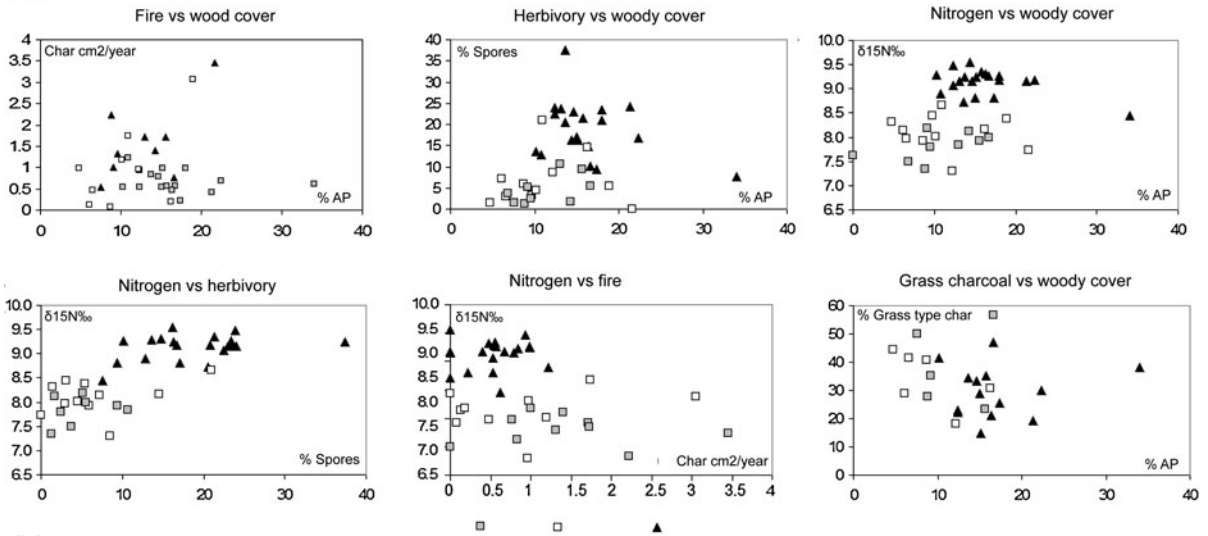
Impact of hydrology in mediating the effects of nitrogen, fire and herbivory

In order to test our hypothesis, we look at the internal relationships between AP and nitrogen availability (as reflected in the $\delta^{15}\text{N}$ values), fire (as reflected in the charcoal influx) and herbivory (as reflected by spores from coprophilous fungi) for both Radio Pan and Chixuludzi Pan (Fig. 7).

In the case of Radio Pan, the comparison shows no relationship between AP percentages and $\delta^{15}\text{N}$, charcoal influx nor abundance of spores from coprophilous fungi. This supports our hypothesis that a limited water availability, as determined by local hydrology, constrains tree abundance and acts as a limiting factor, which forestalls the effects of fire, nitrogen or herbivory on tree recruitment.

In contrast to Radio Pan, the Chixuludzi Pan record shows that AP is positively related to both $\delta^{15}\text{N}$ and spores from coprophilous taxa (Fig. 7). This shows that where water availability is not limiting nitrogen availability and herbivory abundance (as suggested by the abundance of coprophilous spore taxa) is linked with tree recruitment, though it does not determine whether they act as controlling mechanisms or merely responders to the changes in vegetation itself. The most plausible explanation for

(a) Chixuludzi pan



(b) Radio pan

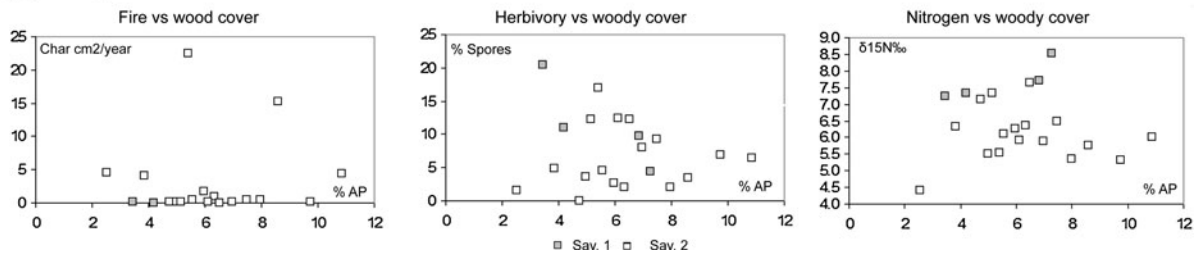


Fig. 7 Correlation between woody cover (i.e. AP) and charcoal abundance, abundance of coprophilous spores and $\delta^{15}N$ as representative of nitrogen availability

the positive relationship between the abundance of AP and spores from coprophilous taxa (i.e. herbivore abundance) at Chixuludzi is that the higher the herbivore abundance, assuming that these numbers are mainly represented by grazers, the more the reduction in competition from herbaceous plants and the greater the benefit to woody species, a finding consistent with present day observations of scrub encroachment (van Langevelde et al. 2003; Archibald et al. 2005; Mills and Fey 2005). Minor peaks in coprophilous abundance preceded increases in AP as would be expected if herbivore abundance was a driver of tree recruitment. Furthermore, the positive relationship between tree abundance and spores from coprophilous taxa is stronger in the savanna phase than in the later savanna-riparian phase. From this, we infer that herbivores are more likely to drive vegetation structure when water availability is constrained, possibly due to the aggregation of animals around the available water.

$\delta^{15}N$ appears to increase with AP abundance in Chixuludzi pan. Using palaeoecological data, Gillson and Ekblom (2009b) were able to show a threshold response between woody vegetation cover and $\delta^{15}N$, where abundance of AP does not vary with $\delta^{15}N$ until a critical threshold of 1.8‰, above which it increases with $\delta^{15}N$. As all $\delta^{15}N$ values, for both Chixuludzi and Radio Pan, are greater than 1.8‰ we do not think that tree-recruitment in any of these localities was restrained by low availability of nitrogen. The increasing $\delta^{15}N$ could be both a driver of and a responder to increased tree recruitment. In this case, as there is a very strong positive correlation between high herbivore abundance and $\delta^{15}N$ values, herbivory is likely to be a main driver in facilitating tree recruitment, through reduction of competition from grasses and increase of nitrogen abundance. However, trees are also known to increase nutrient abundance because of their effect on micro-scale temperature and water availability, as well as by

nitrogen fixation in the case of some Acacias and other Fabaceae (Belsky 1995; Fulco et al. 2001). Increased woody cover, driven by herbivory and nitrogen availability, would in itself serve to further enhance nitrogen availability. This relationship appears to be curvilinear: above ca. 18% AP percentage there is no strong relationship between AP abundance and either herbivory or $\delta^{15}\text{N}$.

There is no strong correspondence between AP abundance and charcoal for the whole time series from Chixuludzi Pan. There is similarly no correlation between $\delta^{15}\text{N}$ and the charcoal record. We interpret this lack of correlation to suggest that fire here was not a main driver of tree recruitment or responsible for the maintenance of the grass layer. As has been shown in modern situations fires can either facilitate tree recruitment, by removing competition from grasses, or fires can contribute to maintaining an extensive grass layer by preventing trees from recruiting to larger size classes (Bond et al. 2003). However, in savannas that are more wooded, fire may come to play a secondary role in regulating tree abundance, as other factors, in this case herbivory, become more important (Higgins et al. 2000; van Langevelde et al. 2003; Gillson and Ekblom 2009b; Ekblom and Gillson 2010a). In this case, fire frequency is probably strongly related with farming and clearing of vegetation. Smaller fire peaks are more common after 1600 AD when maize pollen and possible cereal grass (Poaceae >40 μm) are well represented. The influence of farming communities on the landscape has to be inferred as there have been no archaeological surveys carried out in the immediate vicinity. The combination of maize and/or possible cereal grass, peaks in herbivory and charcoal is a strong indication. This may help to explain the apparent lack of correspondence between charcoal and AP abundance since fire is being manipulated by people rather than responding to vegetation composition and rainfall, which occurs in the absence of human intervention (van Wilgen et al. 2004).

The later part of the Chixuludzi sequence, dated from 1600 AD, represents a landscape modified by humans, however this did not lead to a decrease in arboreal cover as would perhaps be expected. The high herbivory densities, assumed to be linked primarily with domestic cattle in this period as it occurs together with cultigens and charcoal, seem to have favoured recruitment of trees/shrubs. Whether

the early 900 AD peak in coprophilous spore abundance at Chixuludzi is linked with wild or domestic herbivory remain to be discussed further as it is not possible to make this distinction on the basis of the spores. Certainly by 900 AD agro-pastoral communities were settled in the larger region (Mitchell 2003; Huffman 2008).

Hierarchy and scale: the role of fire, grazing and nitrogen in landscapes with differential hydrologies

Hierarchical patch dynamics theory has been successfully applied to explain heterogeneity of the savanna system (Coughenour and Ellis 1993; Gillson 2004). However, because environmental characteristics vary locally and these effects determine the resilience and response of biological variables, scale alone cannot always be used to predict the dominant driver (Levick and Rogers 2008). Here we have focused on the importance of hydrology, fire, herbivory and nitrogen availability and the interaction between them as the palaeoecological data are not able to address all variables involved when it comes to vegetation dynamics. We have also not been able to test the reproducibility of our results in other similar sites. Despite this limitation to our study, partly inherent in the palaeoecological method, we find that we are able to resolve the long term spatio-temporal relationships of tested variables on the basis of these two sites and, by extension, to the landscapes where they are situated.

In this study, regional rainfall is a higher order constraint in the spatial and temporal hierarchy, determining overall maximum tree abundance of both sites. At the local scale, however, we find a dichotomy that is not directly climatically dictated, as both of our study sites experience the same rainfall and temperature regime. Instead, local context, here in terms of hydrology, determines the ecosystem response to other local variables such as fire, nutrient availability and grazing/herbivore pressure which is a similar pattern to that which has been observed for mesic savannas (Sankaran et al. 2005).

Our results support the idea that the savanna ecosystem is hierarchically organised, but critically, they point to the presence of two hierarchies, one dependent on interacting temporal and spatial scale,

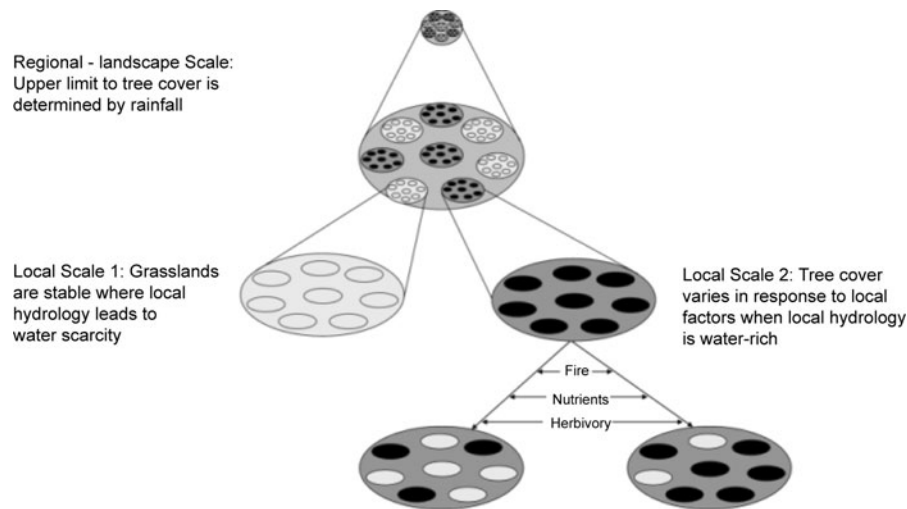


Fig. 8 A hierarchy of processes determines tree density in savannas. Higher-level systems, specifically rainfall, constrain maximum tree cover, but actual tree cover varies depending on local factors, that are lower in the hierarchy. Local hydrology can limit tree density in water-scarce environments, but where

water is plentiful, tree density is determined by the interaction between fire, herbivory and nutrient availability (after Urban et al. 1987; Pickett et al. 1989; Coughenour and Ellis 1993; Wu 1999; Gillson 2004)

and, nested within this, a hierarchy that resides within each spatio-temporal tier that relates to the presence of local environmental and ecological factors (Fig. 8). Regional rainfall imposes the highest level control of both the Radio Pan and Chixuludzi Pan landscapes. Both localities are situated in an area that receives rainfall within the 650 ± 134 mm rain/year boundary of stable/unstable savannas identified by Sankaran et al. (2005). The comparison of the two sites where regional rainfall changes over time are assumed to have been of the same magnitude allows us to investigate the effects of local factors.

In the dry landscape of Radio Pan, where hydrology does not allow for high water availability, a stable savanna has been present over the last 600 years. The stable pollen assemblage of Radio Pan supports our hypothesis that the effect of rainfall variability is checked by the long term abilities of the feeding aquifers to store water. At Radio Pan, local hydrology constrains tree recruitment regardless of variations in rainfall. There is very little variation in woody cover and in the herb population, indicating a relatively stable grass dominated system. Possible changes in the water table at ca. 1600 AD did not lead to any observable changes in the representation of grasses or woody cover. In Radio Pan, there is no relationship between woody vegetation cover and fire (as indicated by charcoal) or nutrients (as indicated by $\delta^{15}\text{N}$).

In contrast, at Chixuludzi Pan, water availability is less restricted as the pan is coupled with the Limpopo River, which has a large catchment area. Here, local hydrology does not constrict tree recruitment, which allows for a higher variability in response to other factors such as fire and herbivory. This can be seen in the variable representation of different woody taxa as well as the grass–tree pollen relationship through time. At the wetter Chixuludzi Pan, vegetation changes from a grassland phase dominated by grasses, sedges and herbs, dated 800–950 AD to a mix of grassland and savanna vegetation phase, postdating 950 AD. The third phase postdates 1400 AD and is marked by an expansion of AP in general, and riparian types in particular.

In Chixuludzi Pan, variations in woody vegetation cover show a significant relationship between woody vegetation abundance on the one hand and herbivory and $\delta^{15}\text{N}$ on the other. Here, herbivory apparently reduce competition between trees and grasses, by facilitating tree recruitment and by enhancing nitrogen availability.

Conclusion

Ecological processes controlling vegetation cover in savannas have been suggested to be hierarchically

organised, where rainfall imposes a higher-level constraint on vegetation cover than other local factors like disturbance (Coughenour and Ellis 1993; Gillson 2004; Sankaran et al. 2005; Levick and Rogers 2008). In this study, we explored the possible presence of a sub-set of local scale hierarchical relationships in the savanna by comparing two sites, with similar rainfall regimes and representing similar spatial scales but with different hydrological conditions. Results show that local divergences in hydrology control the effect of other ecological drivers.

This suggests a hierarchical organisation of ecological variables driving tree abundance in savannas. Regional rainfall imposes the highest level control, however local hydrological conditions may, as here, override the effect of annual rainfall. In a water scarce environment, such as Radio Pan, local hydrology limits woody cover and there is no correlation between woody cover and other potential drivers such as fire, grazing and nitrogen availability. This results in a remarkably stable grassland-savanna system, with little variation in woody cover over the last ca. 600 years. In a landscape where local hydrology allows for higher water availability, such as the Chikuludzi Pan, the maximum extent of woody cover is not limited by water availability. Here, other factors such as herbivory and nitrogen availability are important as controlling mechanisms (Fig. 8). Our work is consistent with the suggestion that savanna ecosystems are hierarchically organised. The results tie in with the comprehensive analysis of African savanna localities presented by Sankaran et al. (2005), but the temporal depth provided by this analysis suggests a subset of local scale hierarchies that determines the relationship between grass and woody cover.

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