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Vegetation and fire history of Bwabwata National Park, Namibia

Adele C.M. Julier [a,b,*], Glynis J. Humphrey [b,d], Caitlin Dixon [c], Lindsey Gillson [b]

[a] School of Biological Sciences, University of Portsmouth, Portsmouth, United Kingdom
[b] Plant Conservation Unit, University of Cape Town, Cape Town 7701, South Africa
[c] Division of Epidemiology and Biostatistics, School of Public Health, University of the Witwatersrand, Johannesburg 2193, South Africa
[d] African Climate and Development Initiative, University of Cape Town, Cape Town 7701, South Africa

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ABSTRACT

The relationships between woody vegetation cover and fire, climate, herbivory, and human activities in African savanna ecosystems are complex. Fire has been managed by humans for thousands of years, but post 1800, fire suppression was implemented in many areas. The impact of these policies are largely unknown, due to a lack of long-term records extending from before, during and after their implementation.

Here, we present two ~1000-year pollen, dung fungal spore and charcoal records from a savanna ecosystem in Bwabwata National Park, in north-east Namibia, an area that had a fire suppression policy in place from 1888 to 2005. Proxies from both cores (Jackalberry and Mukolo) show similar trends. Both records show higher tree abundance during a wetter period early in the record. No evidence of fire suppression or enhanced tree recruitment is seen in the charcoal and pollen data from the period post 1888. The results imply that the policy of fire suppression was ineffective, and did not lead to noticeable decreases in fire and associated enhancement of tree recruitment. The results are consistent with the knowledge that fire is an integral component of this ecosystem, and that fire occurrence in savanna ecosystems is more closely linked to climate than management. Therefore, fire management should adapt to rainfall variability as well as integrating customs of early dry season burning that benefit both biodiversity and livelihoods. Our results show how long-term datasets can be used to assess the impacts of fire suppression and inform present-day management decisions.

1. Introduction

African savanna ecosystems are important for biodiversity, tourism and livelihoods, and have been managed extensively by humans for millennia (Twine, 2019). The co-existence of trees and grasses in savannas is maintained by a combination of fire and vegetation feedbacks, alongside herbivory, which together allow heterogeneous ecosystems dominated by C_4 grasses to persist throughout most of sub-Saharan Africa, even in areas where rainfall is high enough to support forest (Bond et al., 2005).

There are interactions between fire, climate, herbivory and vegetation that affect the density of woody vegetation over time and space (Archibald et al., 2019; Bond, 2008; Bond and Midgley, 2000; Sankaran et al., 2004, 2005, 2008; Staver et al., 2011). Higher rainfall is generally associated with higher tree density, and it is fire that maintains the co-existence of trees and grasses in savannas (Bond and Midgley, 2012; Sankaran et al., 2004). Fire is a key factor in savanna ecosystems and occurs naturally as well as due to human ignitions (Archibald et al., 2012). Frequent fire in savannas effectively stunts savanna trees in a "fire trap", restricting them to the herbaceous layer and preventing them recruiting to larger size classes (Bond and van Wilgen, 1996; Hoffmann et al., 2020; Ribeiro et al., 2019). On the other hand, higher rainfall in savannas leads to higher grass biomass and therefore higher fire occurrence, because grass biomass is the main source of fuel in savanna fires (van Wilgen et al., 2004). If fire is suppressed, however, tree recruitment can increase, shading out grasses and reducing fire frequency (Charles-Dominique et al., 2018). The process of 'woody thickening' is sped up in high CO_2 conditions which facilitate rapid tree and shrub growth, helping them to escape the "fire trap" (Bond and Midgley, 2000; Midgley and Bond, 2015). This is because CO_2 benefits C_3 trees and shrubs more than C_4 grasses (Bond and Midgley, 2012). Herbivores also contribute to the balance between trees and grasses with mega-herbivores such as elephant (*Loxodonta africana*) being particularly important for limiting tree cover and maintaining landscape heterogeneity (Staver and Bond, 2014; Waldram et al., 2008).

The fact that local and landscape drivers such as fire and herbivory

* Corresponding author.
E-mail address: adele.julier@port.ac.uk (A.C.M. Julier).

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can mediate the effects of regional and global drivers such as rainfall and CO_2, provides opportunities for people to manage savanna vegetation structure to their benefit (Whitlock et al., 2010). Humans have manipulated fire in savannas for a range of reasons including managing of grazing resources, facilitating hunting, managing livestock diseases and protecting important plant food resources in the landscape (Humphrey et al., 2021b; Laris, 2002, 2011). Burning early in the dry season, when most vegetation still has high water content, can lead to patchy fires that create a heterogenous mosaic of post-fire ages and in turn limit the spread of late season wildfires (Laris, 2002; Parr and Andersen, 2006). These landscape mosaics provide a wide range of biodiversity habitat and are favoured by many communities for the wide range of ecosystem services that they provide (Humphrey et al., 2021b; Laris, 2011). In contrast, late dry season burns tend to be hotter and more likely to homogenise vegetation (Laris, 2011).

Fire regimes and traditional management of fire in many African savannas were disrupted by European settlement, when many colonial governments instigated policies of fire suppression (Archibald, 2016; Meyer, 1984; Moura et al., 2019; O'Connor et al., 2014). The effect of such policies is largely unknown, however, since the details of past fire regimes and fire management practices before European settlement are not always readily available. Furthermore, high resolution charcoal records are scarce in savannas, and those that exist are usually interpreted in terms of climatic rather than anthropogenic drivers of fire regimes (Ekblom and Gillson, 2010; Gillson and Duffin, 2007; Gillson and Ekblom, 2009; Scott, 2016). It is therefore often difficult to determine how policies of fire suppression affected savanna landscapes on historical and longer term timescales (Bond, 2008; Sankaran et al., 2005) and to design fire management policies which reflect the longer-term history of landscapes (Bowman et al., 2011; Gillson et al., 2019). In some areas, policies of fire suppression still persist, but in others there has been a shift towards fire management policy that includes a recognition of both the ecological and cultural values of fire in ecosystems (Mistry et al., 2019; Russell-Smith et al., 2013; Ryan et al., 2013). Even in strictly protected areas, there are some attempts to mimic traditional fire management which tends to focus on early dry season burning and the creation of landscape mosaics (Humphrey et al., 2021b). In moving away from policies of fire suppression, a long-term perspective is needed to investigate how policies of colonial fire suppression affected fire, and if so whether there were associated effects on vegetation structure, for example through enhanced tree recruitment (Archibald, 2016; Meyer, 1984; Moura et al., 2019; O'Connor et al., 2014). Furthermore, data from past millennia illuminate the effects of customary fire management and potentially reflect transitions in livelihood and subsistence strategies (Razanatsoa et al., 2021a, 2021b; Williams et al., 2015).

In Namibia, there is a long history of fire management by communities who live in savanna ecosystems. For millennia, the Khwe San, former hunter-gatherers, used fire to facilitate new growth of grass to attract animals for hunting purposes and to encourage the growth of favoured veld foods (i.e., important plant foods), and they still do so today (Humphrey et al., 2021b; Lee and DeVore, 1976; Schapera, 1930; Trollope and Trollope, 1999). From around 200 years ago, agro-pastoralists, the Mbukushu people, used fire to stimulate grazing resources for their livestock and later also to clear land for crops (Tinley, 1966). The German colonial government instigated a policy of fire suppression from 1888, which was maintained after independence (1990) and persisted until 2005 (Humphrey et al., 2021b). In Bwabwata National Park, fire suppression was replaced by a policy of early dry season burning in 2006.

It is not clear whether the suppression policy was effective and if so, whether the suppression of fires led to anomalously high tree recruitment, as has been observed in other savanna systems (Geiger et al., 2011; Kraaij and Ward, 2006). This has implications for current management of vegetation and fire, especially given recent trends of shrub encroachment in the park (Eastment et al., 2022; Humphrey et al., 2021a).

This study uses palaeoecological data from two sediment cores from Bwabwata National Park in north-east Namibia. Fossil pollen and charcoal were used to assess vegetation and fire changes over the past c. 1000 years. The data are used to test the hypothesis that a policy of fire-suppression between 1888 and 2005 reduced fire occurrence and caused an increase in woody vegetation cover. Secondly, the data sets provide an opportunity to explore the relative effects of climatic and anthropogenic drivers on fire and long-term vegetation change. The data provide additional insights that could help to inform management that restores the historical range of variability and ecological character of the Bwabwata National Park landscape, by exploring the range of variability in fire and tree cover before, during and after a period of fire suppression. The information could inform current fire management and in considering future environmental change.

2. Methods

2.1. Study area

The study area is Bwabwata National Park (BNP; 18.1157° S, 21.6696° E) in north-east Namibia within the Zambezi and Kavango East Regions, an area of land that borders both Angola to the north and Botswana to the south. The park is an elongated strip of land that stretches broadly East–West for approximately 200 km between the Okavango and Kwando River systems, and is 30 km in width from north to south. Bwabwata National Park is situated within the centre of the Kavango Zambezi-Transfrontier Conservation Area (KAZA-TFCA) where Angola, Botswana, Namibia, Zambia, and Zimbabwe converge and is one of the world's largest transfrontier conservation areas (Fig. 1). The KAZA-TFCA and BNP are major tourism destinations owing to the concentration and diversity of wildlife.

The region receives an average annual rainfall of average 650 mm (Tinley, 1966), largely falling between November and February, with small amounts sometimes falling in October and September (Mendelsohn and Roberts, 1997). Rainfall varies across the park, being slightly higher in the east, and considerably from year to year, but is the highest in the country and is sufficient to support semi-tropical vegetation types. BNP lies within the Zambezian domain of the Sudano-Zambezian Floristic region (White et al., 1983) and falls within the southern limit of the broadleaved tree-shrub savanna biome of the Miombo eco-region due to the high species diversity, endemism and endangered species in the area (Timberlake and Chidumayo, 2011). The vegetation of BNP is amongst the most diverse in the country, due to its higher rainfall, relative higher landscape heterogeneity and nutrient rich sediments from flooding of its rivers.

The BNP landscape is characterised by SE-NW oriented palaeo dunes and ancient river valleys that are now stabilised by vegetation (McFarlane and Eckardt, 2007). The valley grasslands (known locally as orimamba (plural)) and dune crest woodlands together form the heterogenous savanna mosaic of BNP known as Kalahari woodland (Mendelsohn and Roberts, 1997). Characteristic species in the savanna-woodlands include *Burkea Africana* Hook., *Baikiaea plurijuga* Harms, *Guibourtia coleosperma* (Benth.) J.Léonard, *Ochna pulchra* Hook., *Terminalia sericea, Erythrophleum africanum* (Benth.) Harms, *Combretum hereroense* Schinz, *Combretum collinum* Fresen., *Schinziophyton rautanenii* (Schinz) Radcl.-Sm. and *Pterocarpus angolensis* DC (Tinley, 1966). There is an absence of Miombo genera in the study area (i.e., *Brachystegia, Julbernadia* and *Isoberlinia*). Some tropical taxa are found here, at the extreme south or west of their distributions (e.g. *Commiphora mossambicensis* (Oliv.) Engl. and *Boscia integrifolia* J.St.-Hil. (Curtis and Mannheimer, 2005). Woody vegetation has been increasing in recent decades (Eastment et al., 2022; Humphrey et al., 2021b) as has been observed in many sub-Saharan African savannas (O'Connor and Stevens, 2017; Stevens et al., 2017; Wigley et al., 2009).

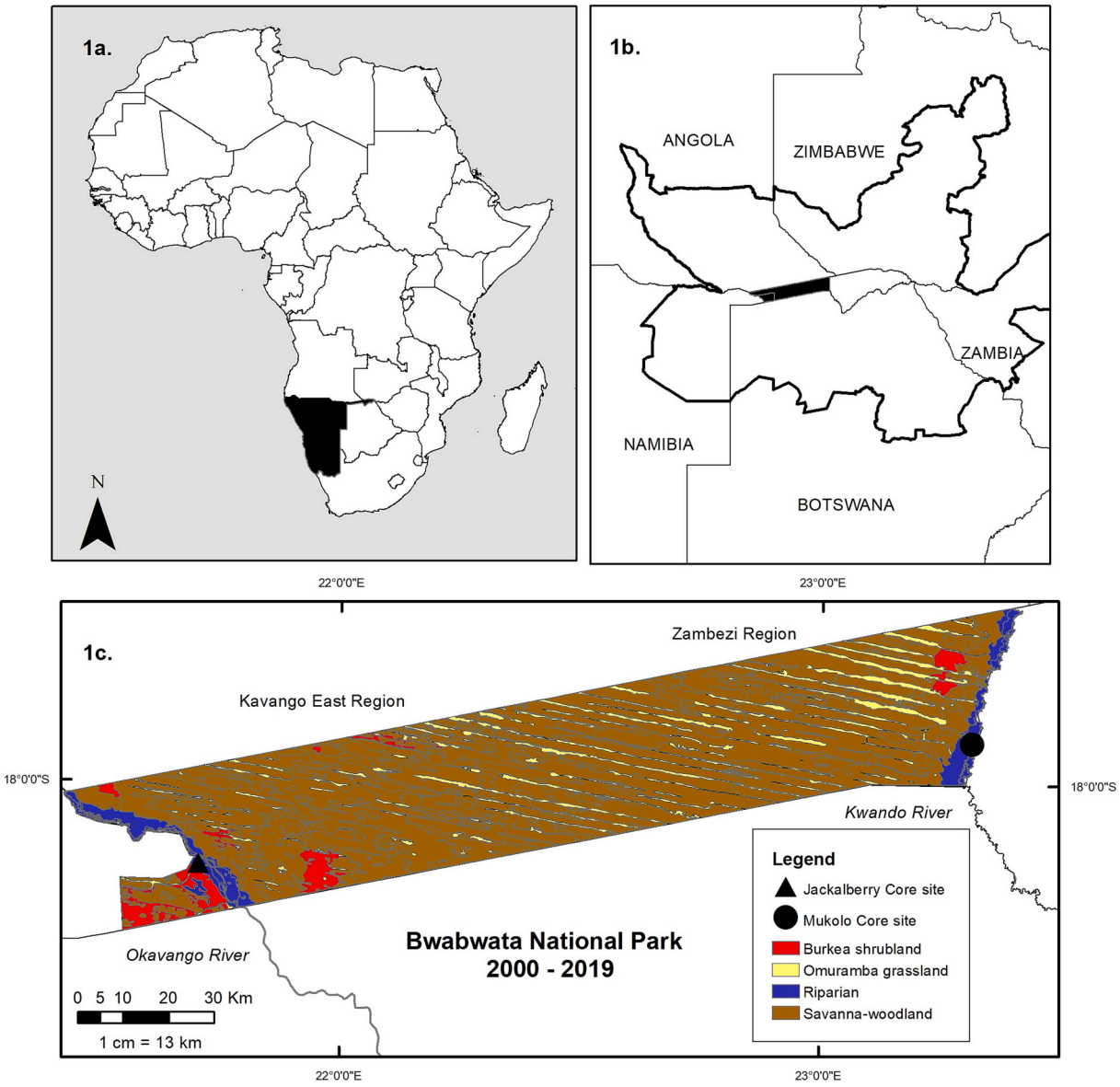


Fig. 1. Map of Africa showing the location of Bwabwata National Park in north-east Namibia (1a) and within the Kavango Zambezi-Transfrontier Conservation Area (KAZA-TFCA) (1b) and the location of the sediment cores in the east (Mukolo) on the Kwando river and Jackalberry in the west on the Okavango River together with the four dominant vegetation types in the park (1c).

2.2. Collection of sediment cores

Two sediment cores were collected in October 2014, using a Russian corer, from the flood plains of the Okavango River (Jackalberry; in the west of BNP) and the Kwando River (Mukolo; in the east of BNP, a wetter area) (Fig. 1b and Table 1). Cores were recovered from wet, muddy areas on the edges of the wetlands adjacent to respective riverine areas and coring was undertaken in the dry season, ensuring that areas cored were perennially wet. The accumulation of sediments in these areas is therefore likely to have been affected by flooding of the rivers rather than continuously, which would disrupt its continuity.

2.3. Chronologies

Radiocarbon dates were obtained on bulk organic sediment samples from the cores. The basal radiocarbon dates for the cores from Mukolo and Jackalberry were analysed by Chrono, Queen's University Belfast, Northern Ireland. Other dates from the Mukolo core were measured at

Table 1
Table summarising details of the two sediment cores taken from Bwabwata National Park, north-east Namibia.

Location (region)	Core name	Vegetation community	Average annual rainfall (mm)	Latitude	Longitude	Depth of core (cm)	Estimated basin size (m/diam)
Zambezi	Mukolo	Floodplain/Riverine woodland	600	−17.877598	23.341643	87	80
Kavango East	Jackalberry	Floodplain/Riverine woodland	550–600	−18.152061	21.712346	76	100

the iThemba Labs, Somerset West, South Africa. Further samples from both cores were sent to Beta Analytic Inc., Miami, Florida.

Age-depth models were developed using Bayesian statistics in the R "rbacon" package (Blaauw et al., 2021) and are presented in Supplementary Fig. 1 and 2. The SHCal20 radiocarbon calibration curve was used (Hogg et al., 2020).

2.4. Loss on ignition (LOI)

LOI was used to determine total carbon content (TOC) and total inorganic carbon content (TIC). Samples (1.5–2 cm^3) were placed in pre-weighed porcelain crucibles, weighed, dried overnight at 100 °C, and weighed again. The samples were then heated to 550 °C in a muffle furnace for four hours, left to cool, and weighed to determine TOC as a percentage of dry weight. The samples were then heated to 950 °C for two hours to determine TIC as a percentage of dry weight (Heiri et al., 2001).

2.5. Isotope analysis

Dried samples were ground into a fine powder, and weighed into tin cups to an accuracy of 1 μg. Samples were combusted in a FLASH™ 2000 organic element analyser and the gases passed to a DELTA V™ Plus isotope ratio mass spectrometer via a ConFlo IV gas control unit. The in-house standards used were "Australian National University (ANU)" sucrose (approx. -10.6 $\delta^{13}C:^{12}C$), Nastd (dried *Tropaeolum* sp. Leaves) (approx. -28.6 $\delta^{13}C:^{12}C$, and Acacia (dried *Acacia saligna* (Labill.) H.L. Wendl. (approx. -27.8 $\delta^{13}C:^{12}C$) leaves). These internal standards are regularly calibrated against international standards. Samples were not treated with hydrochloric acid to remove carbonates as LOI (see above) showed low levels of carbonates in the samples (2.5% or less in all samples). Analyses were performed at the Stable Light Isotope Laboratory at the Department of Archaeology, University of Cape Town.

Less negative $\delta^{13}C$ values are interpreted as indicating a more C_4 plant dominated (i.e. grassy) landscape due to the fact that C_4 plants discriminate less against ^{13}C than C_3 plants (Lane et al., 2004). The C:N values (between 11 and 19) from both cores indicate primarily terrestrial rather than aquatic origin of the material measured (Herczeg et al., 2001; Meyers, 1994; Thevenon et al., 2012).

2.6. Pollen and Charcoal analysis

Samples were processed for pollen analysis as outlined in Bennett and Willis (2001) by treatment with HCl to remove carbonates, NaOH to remove humic acids, sieving at 150 μm, using Hydrofluoric acid to dissolve siliceous material, sodium pyrophosphate to de-flocculate clay, and mounting samples in glycerol. In a modification of standard palynological preparations, acetolysis was not needed due to the low levels of organic material in sediments. *Lycopodium* tablets (batch no. 100320201 and 3862) were added in order to be able to calculate pollen concentrations. At least 300 terrestrial pollen grains were counted for each sample. Cyperaceae were not included in the terrestrial pollen sum as they likely primarily wetland or marginal plants in this environment and do not reflect changes in the wider terrestrial landscape. Pollen diagrams were plotted in R statistical software using the rioja package (Juggins, 2015; R Core Team, 2016). Pollen was identified using reference material from the Plant Conservation Unit at the University of Cape Town, and reference guides (Riollet and Bonnefille, 1980). Constrained hierarchical cluster analyses were performed on terrestrial pollen assemblage using the 'coniss' algorithm within the 'chclust' function in the rioja package (Juggins, 2015).

Charcoal was counted in two fractions; microcharcoal (<150 μm) and macrocharcoal (>150 μm). Microcharcoal was counted in pollen slides relative to Lycopodium and a total of at least 300 objects (Lycopodium spores and microcharcoal fragments) were counted per sample. Every macrocharcoal fragment from each 1cm^3 sample was counted.

3. Results

3.1. Chronologies

Details of radiocarbon dates obtained on bulk sediment are presented in Table 2. Visual representations of chronologies are presented in Supplementary Figs. 1 and 2.

Wetlands adjacent to riverine area are typically episodic depositional environments and not isotaphonomic which can make the production of high precision age-depth models challenging. Here radiocarbon dates were obtained on bulk organic sediment samples from the cores as no macrofossils suitable for dating were found. The basal radiocarbon dates for the cores from Mukolo and Jackalberry were analysed by Chrono, Queen's University Belfast, Northern Ireland. Other dates from the Mukolo core were measured at the iThemba Labs, Somerset West, South Africa. Further samples from both cores were sent to Beta Analytic Inc., Miami, Florida.

No age reversals were present (when considering the full calibrated age range) and age-depth models could be developed using Bayesian statistics in the R "rbacon" package (Blaauw et al., 2021) The SHCal20 radiocarbon calibration curve was used (Hogg et al., 2020). The full age-depth models vs depth are presented in the Supplementary files. These are presented in Supplementary Figs. 1 and 2. From these it can be seen that there appears to be a faster sedimentation rate in both cores below ~40 cm. Mukolo has a more robust age-depth model due to having a greater density of radiocarbon dates available, however it is clear non-trivial age uncertainties are present in both cores. Jackalberry has an uncertainty of ±100 years until below 65 cm where this reduces to ±75 years to base. Similarly, Mukolo has an uncertainty of ±100 years until below 40 cm where this reduces to ±50 years. To help the reader understand these uncertainties a min and max age are given in the text alongside the mean age.

3.2. Jackalberry

3.2.1. Chronology, pollen, charcoal and spores

The Jackalberry core is dominated by Poaceae pollen, which accounts for between 71 and 92% of terrestrial pollen counts. Combretaceae is the second most abundant taxon, accounting for 0.3–6% of terrestrial pollen grains. The Cyperaceae are abundant with 4.6–30.5% relative to the terrestrial pollen sum (calculated outside of the terrestrial sum).

Although the core does not show dramatic shifts in pollen assemblages, a cluster analysis split it into three sections: a lower section (1) from c. 1080 (range 1010–1180) to 1400 (range 1260–1540) CE, a middle section (2) from 1400 (range 1260–1540) to 1800 (range 1640–1960) CE and a top section (3) from 1800 (range 1640–1960) – 2014 CE (Fig. 2).

The lower section (1) from c. 1080 (range 1010–1180) to 1400 (range 1260–1540) has 9 levels. This section has relatively lower Poaceae abundance (71–86%) and higher Tree/Shrub pollen (2.6–12.5%).

Table 2
Details of radiocarbon dates on cores. In Sample Ref. column, IT refers to iThemba lab, BETA to Beta Analytic, UBA to Chrono.

Site	Sample Ref.	Material	Depth	Age BP	Error
Mukolo	IT-C-1386	Organic sediment	10	410	68
Mukolo	BETA-577526	Organic sediment	20	360	30
Mukolo	BETA-525651	Organic sediment	46	620	30
Mukolo	IT-C-1384	Organic sediment	50	570	72
Mukolo	BETA-525652	Organic sediment	60	590	30
Mukolo	UBA30919	Organic sediment	87	654	28
Jackalberry	BETA-577527	Organic sediment	20	Modern	NA
Jackalberry	BETA-525657	Organic sediment	40	970	30
Jackalberry	BETA-525656	Organic sediment	67	890	30
Jackalberry	UBA-30920	Organic sediment	76	1090	24

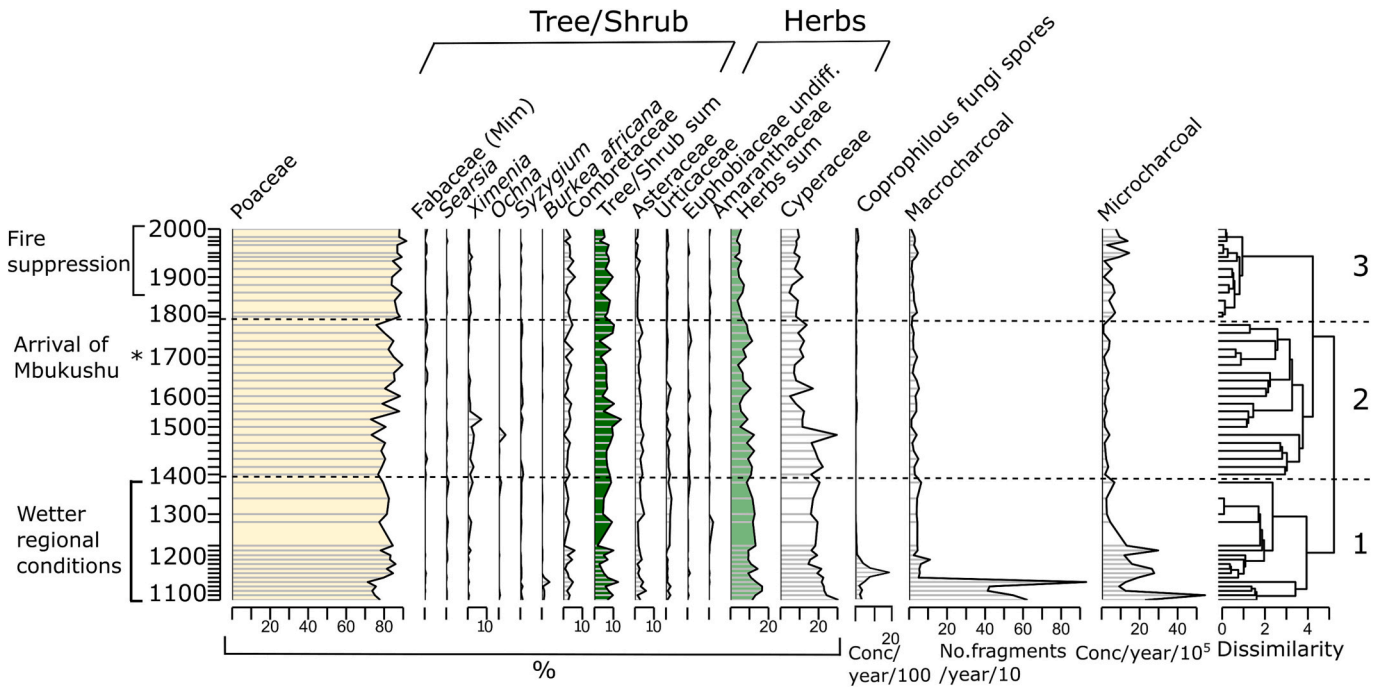


Fig. 2. Summary pollen diagram for the Jackalberry core located in the west of Bwabwata National Park. The clusters segregated into three zones (1, 2 and 3) and distinguished by dashed horizontal lines.

The highest values of the species *Burkea africana* also occur in this section of the core. Macrocharcoal and microcharcoal values are higher than in the upper sections of the core, with a particularly large pulse in microcharcoal at around 1100 (range 1040–1210) CE and in microcharcoal until 1150 (range 1070–1270) CE, as is the occurrence of coprophilous fungi spores.

The middle section (2) from 1400 (range 1260–1540) to 1800 (range 1640–1960) has 20 levels. This section of the core has marginally higher percentages of Poaceae than the lower section (73–90%) and variable Tree/Shrub percentages of 1.6–14.0%. This section has the highest values of *Ximenia* and *Ochna* pollen (up to 7.1 and 3.6% respectively). There are low levels of coprophilous spores and consistent presence of microcharcoal and microcharcoal, not showing any major fluctuations.

The upper section (3) from 1800 (range 1640–1960) – 2014 (range 2013–2014) CE) has 13 levels. This section has the highest percentages of Poaceae (84–92%), relatively low levels of pollen from herbaceous

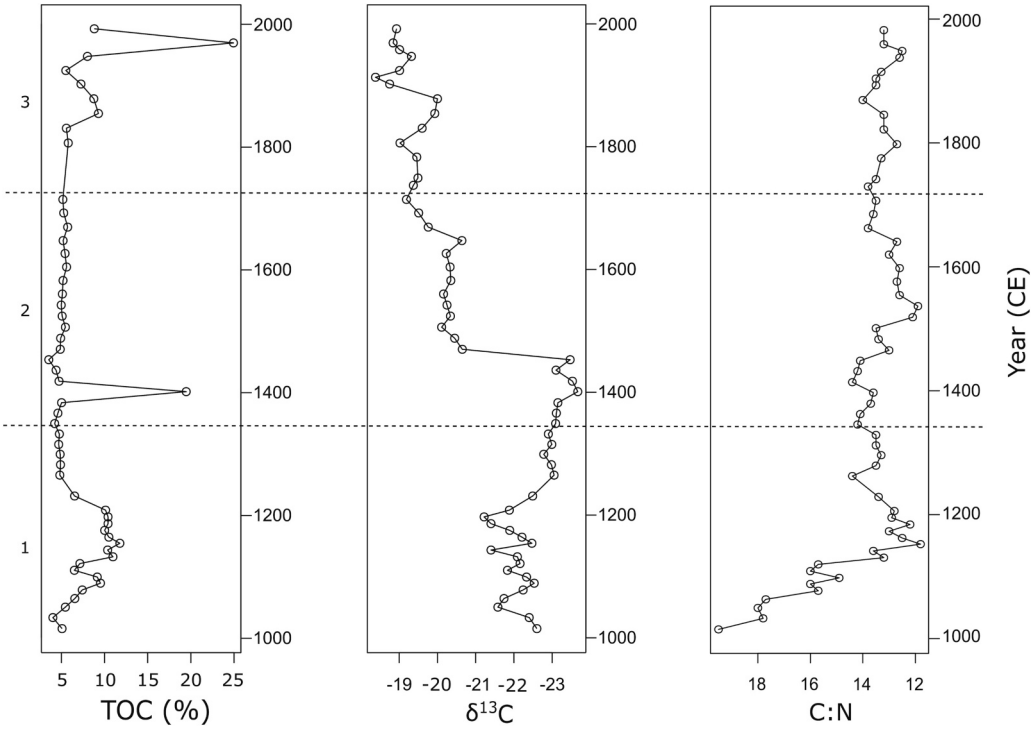


Fig. 3. TOC, Carbon isotope and C:N plots for the Jackalberry core located in the west of Bwabwata National Park. Zones indicated are as for pollen diagram (Fig. 2).

plants and Tree/Shrub pollen of 3.0–9.7%. Coprophilous fungi spores prevalence is low. There is an increase in microcharcoal concentrations towards the top of the section, but macrocharcoal concentrations remain consistently low in comparison to lower sections.

3.2.2. Loss on Ignition, $\delta^{13}C$ and C: N ratios

TOC for Jackalberry varies between 3.5–25% across the core, but most values are up to around 10%, with just 2 being higher than 12%; at 1400 (range 1260–1540) and in the late 1900s (see Fig. 3). These anomalous samples could be due to a piece of root or other organic material being present in the samples.

$\delta^{13}C$ values for Jackalberry are around −21 to −23‰ until 1450 (range 1300–1570), at which point there is a sudden shift to higher values of −19 to −20‰, with some increase towards the top of the core.

C:N ratios decrease from around 19 at the base of the core to 12 in around 1200 (range 1130–1370). From this point they fluctuate between 12 and 14 until the top of the core.

3.3. Mukolo

3.3.1. Chronology, pollen, charcoal and spores

The Mukolo core can be split into three sections (see Supp. Fig. 2 for chronology), as shown by the cluster analysis in Fig. 4. The lower section (1) is from 1330 (range 1280–1370) to 1420 (range 1380–1460) CE, the middle section (2) from 1430 (range 1390–1480) to 1740 (range 1590–1930) CE and the top section (3) from 1780 (range 1600–1950) to 1990 (range 1951–2012) CE.

There are high percentages of Poaceae (79–91%) throughout the core (Fig. 4). The second most abundant terrestrial taxon is Combretaceae (2.3–8.4%). Cyperaceae pollen is also abundant but variable across the core (4.5–64%).

The lower section of the core (1) (1330 (range 1280–1370) to 1420 (range 1380–1460) CE - 1420 CE) has 8 levels. This section has Poaceae abundances of 80–86% and relatively higher Tree/Shrub pollen (5.6–11%). This section of the core also shows high levels of coprophilous fungi spores. Microcharcoal and macrocharcoal are low relative to the rest of the core.

The middle section of the core (2) (1430 (range 1390–1480) to 1740 (range 1590–1930)has 16 levels. This section has Poaceae abundances between 85 and 89% and Tree/Shrub pollen abundance of between 5.0–8.6%. Coprophilous fungi spore levels are low, and there are relatively low microcharcoal and macrocharcoal levels.

The upper section of Mukolo (3) (1780 (range 1600–1950) to 1990 (range 1951–2012) CE has, 10 levels. This section has Poaceae levels between 82 and 91% and Tree/Shrub percentages of 4.6–9.0%. Coprophilous spore percentages variable in this section of the core but slightly higher than the middle section. Microcharcoal concentrations in the upper section of the core are higher than in the lower sections, but macrocharcoal concentrations are lower.

3.3.2. Loss on Ignition, $\delta^{13}C$ and C:N ratios

$\Delta^{13}C$ values for Mukolo vary between −22.0 and − 26.9‰ across the core (see Fig. 5). At the base of the core, $\delta^{13}C$ values are between −22 and − 25‰ but variable until around 1500 (range 1440–1600) CE. From 1500 CE until 1800 (range 1600–1960) CE values were between −23 and − 24‰. At the top of the core the values became less negative from the 1800 onwards to the top of the core. TOC in the core varies between 0.2–17%. From the base of the core until around 1500, TOC is stable at around 5%. From 1500 until 1800 there is an increase in TOC to 17%, after which point it decreases until the mid-1900s, after which they increase again. C:N ratios broadly decrease from the bottom to the top of the core, from 16 to 13.

4. Discussion

4.1. Jackalberry

The lower section (1) from c. 1080 (range 1010–1180) to 1400 (range 1260–1540), in which there is relatively lower grass pollen, relatively higher abundance of tree and shrub pollen, higher microcharcoal and macrocharcoal abundances and coprophilous fungal spores is consistent with wetter regional conditions during this time, as suggested in the regional climate record and coincident with the Medieval Climate Anomaly (MCA) (Holmgren and Öberg, 2006). The more wooded landscape combined with higher fire in the Jackalberry core suggests greater grass biomass productivity, which is also consistent

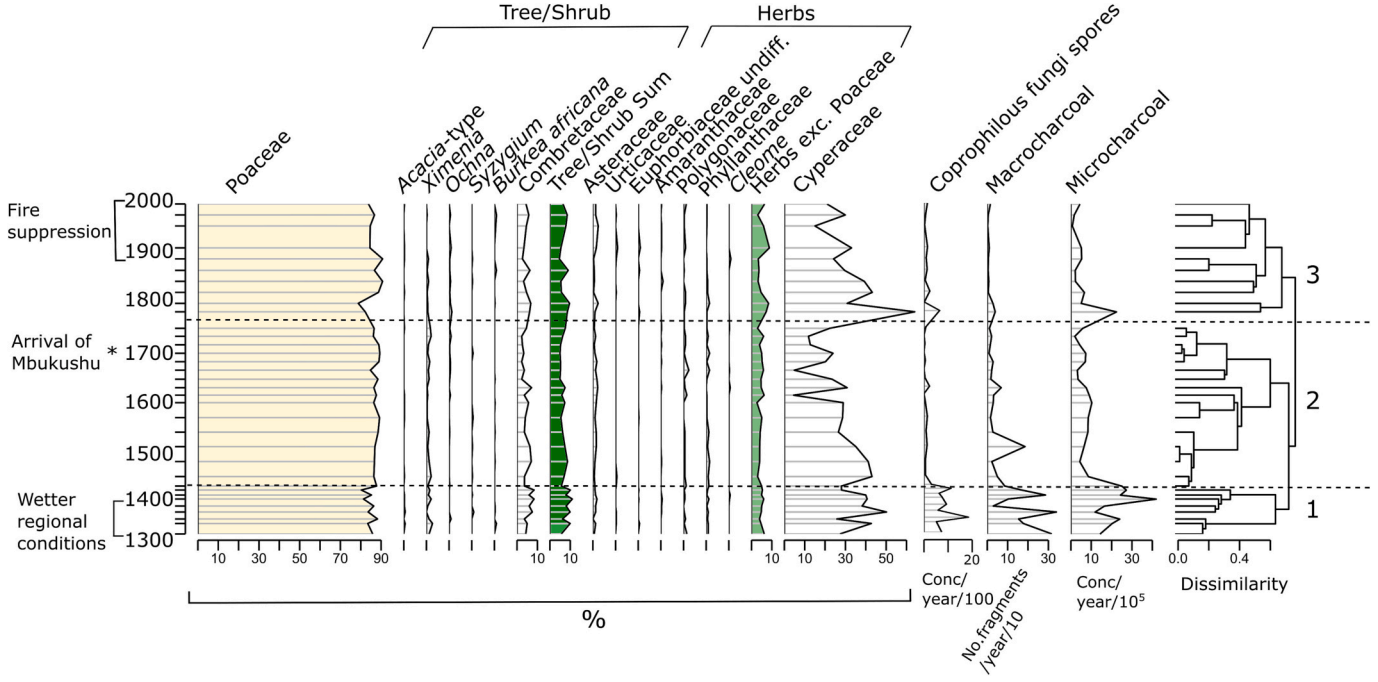


Fig. 4. Summary pollen diagram for the Mukolo core located in the east of Bwabwata National Park.

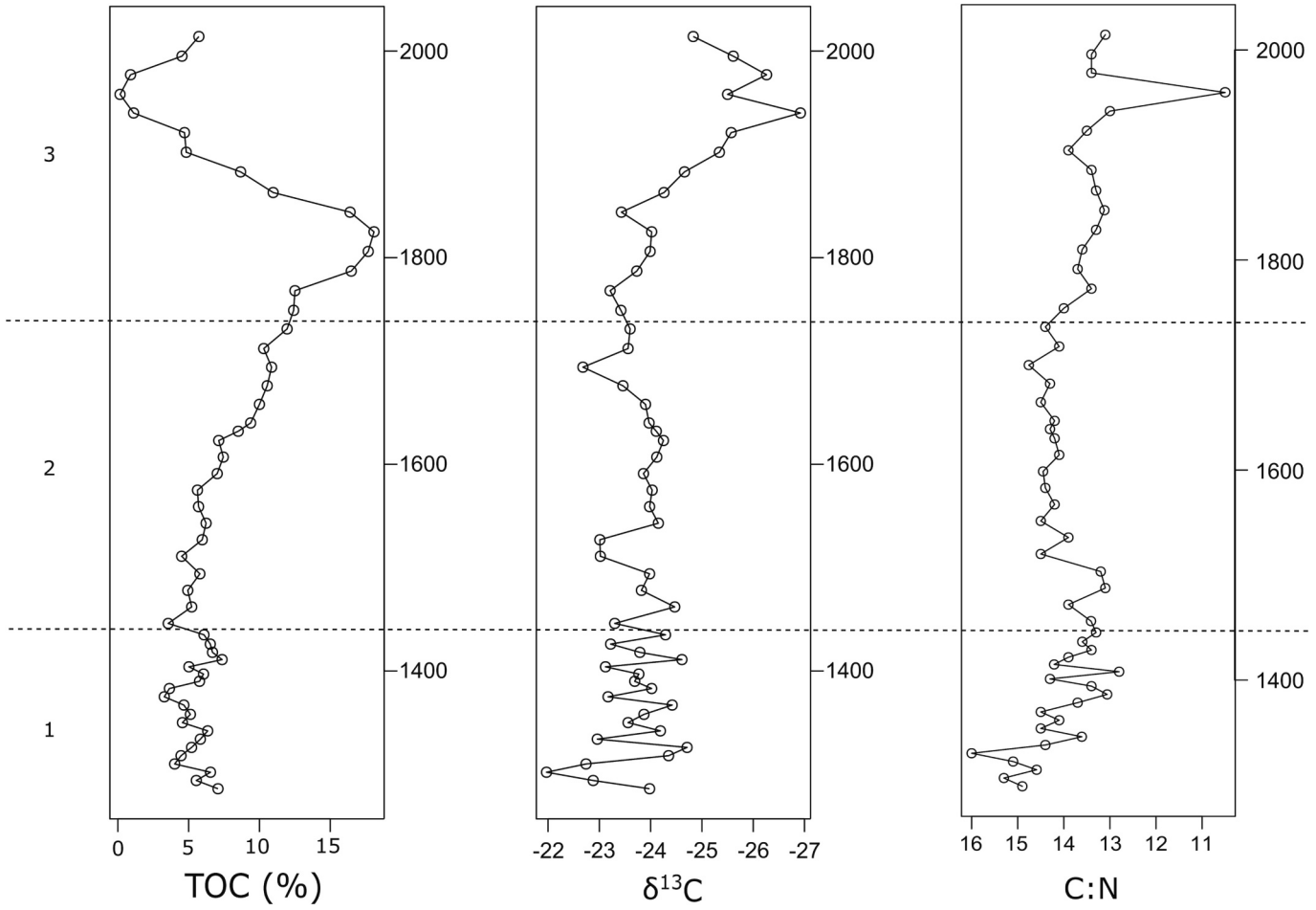


Fig. 5. TOC, Carbon isotope and C:N plots for the Mukolo core located in the east of Bwabwata National Park. Zones indicated are as for pollen diagram (Fig. 4).

with wetter conditions that would favour higher carrying capacity for herbivores, as indicated by higher abundance of coprophilous spores.

The middle section of the core (2) from 1400 (range 1260–1540) to 1800 (range 1640–1960) CE, suggests a slight decline in woody vegetation cover, associated with lower microcharcoal and macrocharcoal levels, and lower abundance of coprophilous fungal spores. These results are consistent with a drier, cooler period, consistent with the regional climate record (Holmgren and Öberg, 2006) and associated with less biomass productivity and associated fire and herbivory. The shift in $\delta^{13}C$ towards a C_4 signal during this time period may also indicate a vegetation shift towards a more C_4-grass dominated ecosystem.

The top section of the Jackalberry core, from around 1800 (range 1640 to 1960) CE (onwards shows a slight increase in grass pollen (and relatively lower levels of other herbaceous taxa. The increase in grass and microcharcoal is likely correlated with the arrival of the Mbukushu people into the area during this time when they settled on the Okavango River prior to colonial administration (Fisch, 1999; Tinley, 1966). The Mbukushu people used late dry season fires to clear land for agriculture as well as early season fires to generate herbage for their livestock herds (Humphrey et al., 2021b). There is also an increase in microcharcoal at the top of this section, indicating higher levels of regional burning, potentially linked to military activity in the region (South African Border War 1966–1989). Macrocharcoal levels, which can indicate more local burning, remained fairly constant through this time period, perhaps reflecting that land clearance for cultivation was not happening directly adjacent to the river.

There is no clear signal in the pollen or charcoal record of the fire suppression policy that was enacted in the area by German colonial administration from 1888 and by the South African administration from 1914 to 1989, and there was no corresponding increase in tree recruitment visible in the pollen record. Similarly, the relinquishment of this policy in recent years is not reflected by higher charcoal abundance and furthermore the pollen record does not indicate recent increases in woody vegetation. It is unclear, however, whether the top of the core represents the present day. During coring, unconsolidated sediment at the top of the core may be lost due to local disturbance factors (e.g., trampling by herbivores), meaning that the more recent years or even decades are not shown. Nevertheless, the timespan and resolution of the core are sufficient samples that the effects of fire suppression over 100 year should be detectable.

4.2. Mukolo

The lower section of the Mukolo core (1330 (range 1280–1370) to 1420 (range 1380–1460) CE), with slightly lower Poaceae pollen abundance, high Tree/Shrub levels and higher coprophilous fungi spores likely captures the end of the wetter period in the MCA also seen in the Jackalberry core, again consistent with regional climate records (Holmgren and Öberg, 2006).

The middle section of the core (1430 (range 1390–1480) to 1740 (range 1590–1930)) is also consistent with the Jackalberry core, showing consistent, high Poaceae levels and a low abundance of coprophilous dung fungi, with consistent but relatively low presence of microcharcoal and macrocharcoal. This is likely due to regionally cool, dry conditions associated with changes in the position of the Intertropical Convergence Zone and fluctuations of the El Niño Southern Oscillation (Holmgren and Öberg, 2006; Russell and Johnson, 2007). The dry conditions would have reduced biomass production leading to

less fire activity and fewer herbivores.

The top section of the core (1780 (range 1600–1950) to 1990 (range 1951–2012) CE)shows some increase in microcharcoal and, similarly to Jackalberry, does not demonstrate an increase in macrocharcoal. It does, however, see a small increase in coprophilous fungal spores, potentially indicating an expansion of farming consistent with the arrival of the Mbukushu people and their cattle into the area in the late 1700s (Fisch, 1999; Tinley, 1966). This area, being wetter, was likely more favoured by agropastoralists than the western, drier area (Humphrey et al., 2021a).

There is no evidence of a marked shift in vegetation or fire following the 1888 fire suppression policy in the pollen record, suggesting that the policy did not have a significant effect on fire or woody cover. As in the Jackalberry record, the recent increase in woody vegetation is not apparent in the pollen record.

5. Synthesis and management implications

The results presented in this study indicate that the landscape in BNP has been grass dominated and experienced fire consistently for at least the past 1000 years, despite changing environmental conditions and different human impacts during that time. Neither core supports the hypothesis that the policy of fire suppression affected fire frequency or tree recruitment. The period of fire suppression (1888–2005) does not appear to have led to dramatic changes in tree cover. This period is represented by seven levels at Jackalberry and five levels at Mukolo. Therefore, even though annual resolution is not possible with these cores, the century long-policy should be detectable in our two records.

Both sites retained an open landscape, dominated by Poaceae, throughout the period of fire suppression. There is therefore no evidence from these cores that the policy of fire suppression prevented fires occurring or caused anomalously high tree recruitment. The results suggest that vegetation maintains stability through feedbacks between fire, grass abundance and tree recruitment despite climatic fluctuation and changes in fire management policy. These feedbacks between vegetation (specifically grass biomass) and fire are important in maintaining open savanna landscapes and help maintain the co-existence of trees and grasses in areas that have high enough rainfall to support closed canopy forest (Bond et al., 2003, 2005; Bond and Keeley, 2005; Bond and Midgley, 2012). The results suggest that the feedbacks between vegetation and fire confer resilience to open savanna landscapes, in that they persisted despite evidence of changes in rainfall, fire management policy, and herbivory. Here, resilience is defined as the ability of a system to withstand or recover from disturbance without changing to an alternate stable state (Holling, 1996; Oliver et al., 2015).

Despite this resilience, proxies from both cores pick up an increase in woody vegetation cover associated with wetter conditions prior to 1400. Furthermore, the drier period from 1400 to 1700 was associated with a lack of coprophilous fungal spores, indicating lower herbivore abundance, and lower charcoal levels, indicating less biomass available for burning. These findings suggest that broad-scale climatic trends are important in determining changes in tree cover. Such changes may be subtle or more marked than indicated by the pollen record due to under-representation of tree pollen compared with grasses.

Recent calibration work has shown that even small changes in the abundance of savanna tree pollen can represent relatively large changes in woody vegetation cover, whereas changes in grass pollen abundance is less reliable as an indicator of landscape openness (Tabares, 2021; Tabares et al., 2018). This is because grass pollen is abundant and well dispersed, whereas the abundance of tree pollen is much more tightly associated with vegetation cover at local – landscape scales (Tabares, 2021). Further calibration work would be needed to interpret the results quantitatively in terms of changes in tree cover, rather than changes in arboreal pollen abundance (Gillson and Duffin, 2007; Julier et al., 2021).

The present study confirms the futility of attempts to prevent fire in savannas, a fire-maintained ecosystem, and highlights the importance of fire management strategies that work with rather than against prevailing ecological processes. Similar results have been found in the Kruger National Park, South Africa, for example, where rainfall rather than fire management policy is the major driver of fire regimes (van Wilgen et al., 2004). More specifically, rainfall in the preceding 6 months frequently correlates with burn area (Alvarado et al., 2020). In this case, a linear relationship between burn area and antecedent rainfall was apparent, regardless of transitions in fire management policy from fire suppression, to prescribed burning to unmanaged fires (van Wilgen et al., 2004).

Despite the overriding role of climate as a driver of landscape dynamics, there is evidence of interactions with human activities. For example, the arrival of the Mbukushu people into the area in the late 1700s, likely coupled with a shift towards a warmer, wetter climate, was accompanied in the records by an increase in coprophilous fungal spores and microcharcoal in Mukolo, and an increase in microcharcoal in Jackalberry. Furthermore, it is well known that people can manipulate fire through burning early in the dry season, in order to favour a more heterogenous landscape with a wider range of ecosystem services, compared with landscapes where large, intense fires occur mainly in the late dry season (Laris, 2002).

In contrast, disruption of traditional fire management practices (specifically early-season burning) (Humphrey et al., 2021a) alongside rising CO_2 levels (Bond and Midgley, 2000; Midgley and Bond, 2015) might have contributed to the encroachment of shrubs that has been observed in the park in recent decades (Eastment et al., 2022; Humphrey et al., 2021a). This increase in shrubs reported in Bwabwata and other southern Africa savannas is not apparent in either record in the current study. This is likely because bioturbation blurred the signal from the last few decades. The effect of bioturbation is to mix layers of sediment, which effectively smooths out extreme events and masks more subtle changes in the sedimentological record. Such sediment records are therefore likely rather conservative in their estimation of change. An additional factor might be the lack of consolidation at the top of the core, which can lead to the last few years or decades being absent. Furthermore, the over-production to grass pollen relative to other taxa may further mask changes meaning that changes in tree cover are conservatively estimated (Tabares et al., 2020).

Careful monitoring of woody vegetation cover and an adaptative fire management approach should be implemented to avoid reaching ecological thresholds where species adapted to open habitats are disadvantaged by the encroaching shrub layer, which shades out the herbaceous layer and suppresses fire (Scholes, 2003; Smit, 2004). Maintaining structural and spatial heterogeneity in the vegetation cover will be essential to maintaining biodiversity and game viewing potential. Early season burning is generally considered beneficial in discouraging hot late season fires, that can homogenise landscapes. However, if tree cover increases to the point where grassy elements of the landscape are lost, late season, intense burns might be needed to curb woody vegetation recruitment, especially as rising CO_2 continues to promote fast tree growth and enhance the chances of escape from the fire trap (Higgins and Scheiter, 2012; Midgley and Bond, 2015). Thus, an adaptive strategy is needed which a) links burn area to antecedent rainfall (Archibald et al., 2010) and b) adjusts fire seasonality (and hence intensity) in relation to woody vegetation cover and the desired level of tree cover as defined by stakeholders including local communities, conservation managers and tourists.

6. Conclusions

This paper used palaeoecological data from two cores taken from the Bwabwata National Park, north-east Namibia explore the relative effects of climatic and anthropogenic drivers at a local and landscape scales. We used fossil pollen and charcoal data covering the past c1000 years to test the test the hypothesis that a policy of fire-suppression between 1888 and 2005 reduced fire occurrence, and caused an increase in woody

vegetation cover, compared with pre-colonial times. The fossil pollen and charcoal data showed no evidence that this was the case. Fire did not appear to decline during the period of fire suppression and this is consistent with studies elsewhere that show that fire mainly responds to rainfall in the preceding year, as this determines grass biomass (Archibald et al., 2010; Batista et al., 2018; Smit et al., 2013; van Wilgen et al., 2004). Attempts to prevent fires in such landscapes are often ineffective.

The stability of the pollen record despite changing management and land-use is consistent with the interpretation of a resilient savanna system, where feedbacks between fire and vegetation buffer the ecosystem and allow the co-existence of trees and grasses (Bond and van Wilgen, 1996). However, there was some evidence of response to increased rainfall, which enhanced tree recruitment during the MCA.

Furthermore, the data provide additional insights that could help to inform management that maintains the ecological character of the Bwabwata landscapes, by exploring the range of historical variability in fire and tree cover before, during and after a period of fire suppression and concerning future environmental change. The increases in woody vegetation cover, especially in smaller size classes that have been observed in the park (Eastment et al., 2022; Humphrey et al., 2021b), represent a departure from the historical range of variability. Though this was not apparent in the pollen record, possibly due to lack of chronological resolution and/or lack of consolidation in the uppermost section of the core. Nevertheless, the observation highlights the uneasy co-existence of trees and grasses, with CO_2 increases and disruption of traditional fire management possibly playing a role in recent woody plant thickening (Bond and Midgley, 2012). The implementation of early season burning in Bwabwata National Park represents a return to traditional fire management, but may need to be supplemented by intense, late season burns if shrub encroachment threatens open areas, grazing fauna and associated ecosystem services.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be uploaded to neotoma prior to publication

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2023.105002.

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