PALAEOECOLOGY OF AFRICA
International Yearbook of Landscape Evolution and Palaeoenvironments

35

# Quaternary Vegetation Dynamics
## The African Pollen Database

Jürgen Runge

Guest editors
William D. Gosling
Anne-Marie Lézine
Louis Scott

CRC Press
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QUATERNARY VEGETATION DYNAMICS –
THE AFRICAN POLLEN DATABASE

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# Quaternary Vegetation Dynamics – The African Pollen Database


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# Foreword

The "Quaternary Vegetation Dynamics", and the 35th volume of *Palaeoecology of Africa* (PoA) was born out of two workshops organised to relaunch the African Pollen Database initiative in Bondy near Paris (October 2019) and Amsterdam (January 2020). These workshops brought together researchers from around the world to showcase their work from across the African continent and to train them in data management. The training at the workshop was led by the late Eric Grimm who sadly passed away in November 2020. We hope that Eric's enthusiasm for collating, standardising, and disseminating palaeoecologicial data is captured in this volume.

In total this volume of PoA, that for the first time is available as an OPEN ACCESS publication, contains twenty-four papers and is organised regionally following the format of the first meeting: western Africa (chapters 3–6), eastern Africa and Arabia (chapters 7–11), central Africa (chapters 12–13), southern Africa (chapters 14–19), islands in the vicinity of Africa (chapter 20), and pan-African syntheses (chapters 21–24). With a view to stimulate primary research and mobilise open access publication of palaeoecological data two types of primary research papers are included: (i) short data papers containing descriptions of new palaeoecological data sets (chapters 9, 18, 19, 20), and (ii) longer research papers providing more in-depth analysis (chapters 3, 4, 5, 7, 8, 12, 13, 15, 16 and 17). To provide a synthetic overview of the state of research into Quaternary Vegetation Dynamics from in and around Africa we also include short perspective papers to provide insights into key regions or issues (chapters 1, 2, 14, and 24), and extensive review papers which bring together the growing body of research from around the continent to address particular scientific questions (chapters 6, 10, 11, 21, 22 and 23).

We are delighted to have been able to bring together work from all parts of Africa focused on the Quaternary. We believe that this reflects the enthusiasm and urgency for this type of palaeoecological research. As current climatic and land-use changes continue to exert pressure on the modern ecosystems, turning to the record of past environmental change to shed light on their origins, resilience and trajectories of change becomes increasingly pertinent. While the record of past change cannot be used to define how we should manage and develop ecosystems today, we hope that it can provide a frame of reference and inspiration for managers and policy makers to work with. We hope that the data, research and syntheses provided in this volume forms a solid basis for the next generation of palaeoecological researchers from Africa to provide scientifically and societally relevant information that will assist with the development of sustainable management practices.

Finally, we would like to thank all the participants in the meetings, the authors and the reviewers whose contributions have made this volume possible. We would like to also thank the French Agence Nationale pour la Recherche and the Belmont-Forum (VULPES: ANR-15-MASC-0003 and ACCEDE: 18 BELM 0001 05) who have provided financial support for the meetings and publication of this volume. We also take this opportunity to place on record our gratitude to Senior Publisher Janjaap Blom and his team from Routledge/Taylor & Francis/CRC Press for the continuous support to PoA.

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## CHAPTER 1

# Rise of the Palaeoecology of Africa series

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ABSTRACT: The *Palaeoecology of Africa* series was founded by E.M. van Zinderen Bakker, a biologist and palynologist who emigrated from Europe to South Africa. Ever since its origin during the nineteen-sixties, it gave a reflection of the history and development of palaeoscience in connection with the African continent and played a role in promoting international collaboration with multidisciplinary reports, conference proceedings and other papers in this field.

### 1.1 INTRODUCTION

*Palaeoecology of Africa* (PoA) of which this is the 35th volume, is a series traditionally focusing on multi-disciplinary studies on palaeoenvironments of Africa, especially on more recent parts of geological time like the Neogene and Quaternary. The early PoA volumes reveal the development history of these palaeoscience aspects in Africa. Thanks to the pioneering and visionary efforts of Eduard Meine van Zinderen Bakker and the publisher A. A. Balkema, the early volumes of PoA was a unique academic initiative out of Africa in the nineteen sixties. The series served as a mouth piece for an international group of specialists at a time when the important role palaeoenvironmental changes did not yet receive as much attention as today. Palaeoscience was then, a little-known discipline for the continent except for a rich heritage of Palaoeozoic fossils and a few important hominid cranial finds such as at such as Taung, Florisbad and a few other sites (e.g. Dart 1925; Dryer 1935).

### 1.2 ORIGIN

PoA had its humble origins in the late nineteen-fifties and early sixties when van Zinderen Bakker, a Dutch naturalist who immigrated to South Africa in 1947 (Meadows 2015; Neumann and Scott 2018) started lecturing at the University of the Orange Free State in Bloemfontein (now shortened to University of the Free State). Here, he formed the Palynological Research Unit that was sponsored by the South African Council for Scientific and Industrial Research, and by the 1950's he was already involved in some of the first palynogical research projects in Africa, including modern pollen surveys in Southern Africa (Coetzee and van Zinderen Bakker 1952) and analysis of the hominin-bearing spring deposits of Florisbad near Bloemfontein (Dreyer 1935; van Zinderen Bakker 1957).

PoA started as eight soft-cover reports on pollen analysis entitled 'Palynology of Africa' in which van Zinderen Bakker reported on research news and activities in palynology and related aspects of palaeosciences in Africa covering the period of 1950–1963 (referenced in Neumann and Scott 2018). They were later re-published by Balkema, Cape Town in 1966 in book form as Volume 1 of *Palaeoecology of Africa* with the sub-title *and the Surrounding Islands &*

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*Antarctica* (Van Zinderen Bakker 1966). The sub-title reflected van Zinderen Bakker's wide multi-disciplinary interests, which included biological and palynological research at the Marion and Prince Edward Islands, *c*. 2000 km south east of Cape Town in the Southern Ocean, to which he organized the first biological and geological research expedition in 1965 (van Zinderen Bakker 1976a; Van Zinderen Bakker *et al.* 1971). PoA Volume 1 (Van Zinderen Bakker 1966) included accounts of activities of several well-known international scientist at the time like D.A. Livingstone, L.S.B. Leakey, J.D. Clarke, R.J. Mason, C.K. Brain, W.W. Bishop, A.R.H. Martin, M. van Campo, E.P. Plumstead, H. Rakotoarivelo, H. Straka, O. Hedberg, R.E. Moreau, W.F. Libby, and others.

Volume 2, 4 and 6 followed basically the same format as Volume 1, but contained chapters under specific topics as short reports by various authors (Van Zinderen Bakker 1966, 1967b, 1972). The chapter topics included climatology and palaeoclimatology, geology and palaeontology, archaeology, biogeography, palynology in Africa, Antarctica and the Southern Ocean, isotope dates and morphology of microfossils, periglacial evidence, sea-levels, and oceanography.

The third volume of Palaeoecology of Africa contained the doctoral thesis of Joey Coetzee (Coetzee 1967), which is a landmark publication for Quaternary palynology in Africa (Meadows 2007). The early volumes also included additional lists with researcher's addresses and publications.

Maintaining the wide multi-disciplinary character from an international group of palaeo-scientists, subsequent volumes of PoA began to include separately authored papers, e.g., Volume 7 that included an extended study of 106 pages by A.C. Hamilton on palynology in Uganda (Hamilton 1972).

## 1.3 EDITORIAL CHANGES

Over the years the series eventually changed editors or were assisted by guest editors especially in the case of conference proceedings. Volume 18 was edited by Joey Coetzee and served as a dedication to the work of van Zinderen Bakker (Table S1).

Klaus Heine of Regensburg took over as editor for Volumes 19-27, of which Volume 27 was co-edited by Jürgen Runge (Frankfurt) who took over the duties for the rest of the volumes. After 1999, CRC Press (Taylor & Francis Group/'A Balkema Book') became the publisher and introduced the new current enlarged layout format and new series sub-title, *Landscape evolution and Palaeoenvironments* since 2007 (Volumes 28–34).

## 1.4 CONFERENCE PROCEEDINGS

With the appearance of Volume 22 in 1991, the following seven of eleven conference proceedings, were already published in PoA of which four represented meetings of the Southern African Society for Quaternary Research (SASQUA) (see Table S1 for the full list):

(1) Volume 5, Scientific Committee on Antarctic Research (SCAR) of the International Council of Scientific Unions (ICSU) Cambridge in 1968 (Van Zinderen Bakker 1969). This was later followed up by Volume 8 (Van Zinderen Bakker 1973), which did not cover the proceedings of a specific event but expanded the topic and inspired further interest in history of Antarctica.
(2) Volume 12, Sahara and Surrounding Seas held in Mainz in 1979 under the auspices of the *Akademie der Wissenschaften und der Literatur*, guest edited by M. Sarnthein, E. Siebold and P. Rognon, (Van Zinderen Bakker and Coetzee 1979).
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**CHAPTER 2**

# The African Pollen Database (APD) and tracing environmental change: State of the Art

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ABSTRACT: The African Pollen Database is a scientific network with the objective of providing the international scientific community with data and tools to develop palaeoenvironmental studies in sub-Saharan Africa and to provide the basis for understanding the vulnerability of ecosystems to climate change. This network was developed between 1996 and 2007. It promoted the collection, homogenization and validation of pollen data from modern (trap, soils, lake and river mud) and fossil materials (Quaternary sites) and developed a tool to determine pollen grains using digital photographs from international herbaria. Discontinued in 2007 due to a lack of funding, this network now resumes its activity in close collaboration with international databases: Neotoma, USA, Pangaea, DE, and the Institut Pierre Simon Laplace, FR.

## 2.1 INTRODUCTION

International cooperation in research and decision-making is critical for solving global environmental problems linked to climate and/or human impact on ecosystems, particularly at regional level. These environmental problems include forest degradation, accelerating loss of biodiversity and water resources, instability of transitional ecological domains, and change in coastal zones. Tropical ecosystems are especially at risk as future states are likely to be beyond the range of observations, yet their preservation is of crucial importance for the maintenance of the Earth's biosphere and climate. For example, the role of the equatorial and tropical forests

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in global exchanges, such as the global carbon cycle, is widely recognised (Detwiler and Hall 1988). Research developed within the general framework of international scientific programmes (e.g., the International Geosphere Biosphere Programme, IGBP – http://www.igbp.net/) have long highlighted the need to provide quantitative understanding of the Earth's past environment in order to define the envelope of natural environmental variability within which we can assess anthropogenic impact on the Earth's biosphere, geosphere and atmosphere. Following these recommendations, the scientific community has developed a set of analytical techniques to recover high-resolution environmental and ecological records from different natural archives such as tree-rings, and lake and ocean sediments, thus providing accurate scientific information for the development of predictive models of regional and global change. The use of these data to test Earth system model simulations requires the collection, assemblation, standardization and subsequently the access to the wider scientific and modelling community in the form of specific regional databases**.**

## 2.2 MAIN ACHIEVEMENTS

The African Pollen Database (APD) was first developed in 1996 in close cooperation with its European counterpart (EPD) (European Pollen Database; http://www.europeanpollendatabase.net) and the Global Pollen Database hosted at the National Oceanic and Atmospheric Administration (NOAA) Paleoclimatology Database (USA) (https://www.ncdc.noaa.gov/data-access/paleoclimatology-data). The initial workshop and subsequent work, funded by the French National Centre for Scientific Research (CNRS), the European Union (International Cooperation for development (INCO-DEV) and European network of research and innovation centres (ENRICH) programmes and the UNESCO International Geoscience Programme (PICG), established methods of collating pollen data, developed a standardized pollen nomenclature (Vincens *et al.* 2007), generated updated age models, composed images of pollen grains from internationally recognized herbaria, and created a searchable web interface. In the first stage of its development, the APD contained 288 fossil sites and 1985 modern samples (Figure 1). Among the numerous achievements of the APD one can highlight the following topics.

### 2.2.1 Pollen based biome reconstructions

Jolly *et al.* (1998) first demonstrated that the 'biomization' method for assigning pollen taxa to plant functional types and biomes was able to predict the potential natural vegetation of tropical Africa, despite uncertainty and variability of pollen production and dissemination (Ritchie 1995) of an extremely biodiverse flora (26,000 plant species; Lebrun and Stork 1991–1997). This allowed palaeoecologists working in Africa to participate in the 'BIOME 6000' project sponsored by IGBP (Prentice and Webb 1998). This project aimed to use palaeoecological data from the mid-Holocene as a benchmark to evaluate simulations with coupled climate-biosphere models and thus to assess the extent of biogeophysical (vegetation-atmosphere) feedbacks in the global climate system (Prentice *et al.* 2000). After the validation of the modern pollen dataset (Gajewski *et al.* 2002; Jolly *et al.* 1998), the biomization method was successfully applied to reconstruct modern (Lézine *et al.* 2009; Vincens *et al.* 2006) and past biomes for selected time periods, typically the Last Glacial Maximum (LGM) and the Holocene (Jolly *et al.* 1998; Elenga *et al.* 2000). Past biome reconstructions have also been performed for the Plio-Pleistocene (Bonnefille *et al.* 2004; Novello *et al.* 2015) and more recent time periods such as the last glacial-interglacial cycle and the Holocene (Amaral *et al.* 2013; Izumi and Lézine 2016; Lebamba *et al.* 2012; Lézine *et al.* 2019).

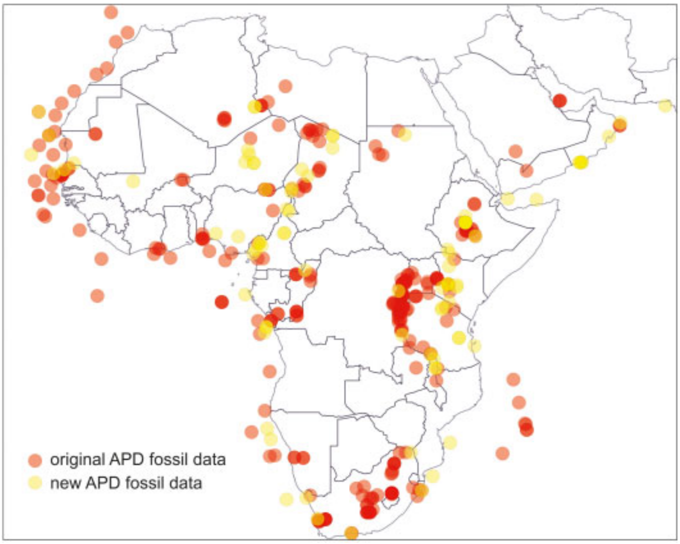


**Figure 1.** Late Quaternary African Pollen Database (APD) sites. In red: pollen data gathered during the first phase of the APD (1994–2007). In yellow: new pollen sites to be entered into the new version of APD, in construction).

### 2.2.2 Quantitative reconstructions of climate variables from pollen data

Modern-analogue, regression, and model-inversion techniques have been developed to reconstruct past climates from pollen assemblages or pollen-based reconstructed biomes worldwide. Using the APD modern pollen dataset, Peyron *et al.* (2007) provided the first quantitative pollen-based reconstruction of precipitation for all of Africa at 6000 yr BP based on the Modern Analogues Technique (MAT) and the Plant-Functional Types (PFT) climate relationships. Results were then compared with atmospheric general circulation model output and coupled ocean atmosphere-vegetation models developed in the frame of the Paleoclimate Model Intercomparison Project (PMIP) international project (Joussaume and Taylor 1995). More recently, Wu *et al.* (2007) then Izumi and Lézine (2016) developed an inverse modelling approach based on the BIOME model to quantitatively reconstruct past climates based on pollen biome scores. The advantage of this method was to provide quantitative climate reconstructions for periods when $CO_2$ concentrations were different from today. While reconstruction attempts of climate by means of pollen data in South Africa, were mostly qualitative (Scott *et al.* 2012), Chevalier and Chase (2015) applied a method that related the pollen to plant distribution data to obtain quantitative estimates.

### 2.2.3 Vegetation reconstructions from pollen data

Palaeoecological data from the APD led to a series of reconstructions of vegetation at a continental scale. Site-based global biome maps for Africa for the mid-Holocene and LGM were first completed within the framework of the ‘BIOME 6000’ project (Prentice *et al.* 2000). More recently, APD palaeoecological data was included in a global synthesis of changes in composition and structure of past vegetation since the LGM performed by Nolan *et al.* (2018). This study provided a baseline for evaluation of the magnitudes of ecosystem transformations under future emission scenarios.

At a regional scale, APD data were used to reconstruct the Green Sahara and evaluate plant migration rates during the African Humid Period (Hély *et al.* 2014; Watrin *et al.* 2009). In

East Africa, compilation of pollen and archaeological data was used to discuss the cumulative effects of climate and land-use on the environment (Marchant *et al.* 2018). Furthermore, with the increasing recognition that fossil data can improve information about fundamental climatic tolerances, modern and palaeoecological data from the APD have been included in estimates of climatic niches of at-risk plant taxa (Ivory *et al.* 2016). This information was then used to provide forecasts of future impacts to ranges under climate and land-use trajectories for the end of the 21st century (Ivory *et al.* 2019).

## 2.3 CHALLENGES AND FUTURE DEVELOPMENTS

All these realizations suffer from (1) an highly uneven geographic distribution of data. Pollen data are relatively abundant in Eastern and Southern Africa where palynological research has been ongoing since the early 1950s (Hedberg 1954; van Zinderen Bakker and Coetzee 1952). In the former region, the abundance of lakes and swamps also provides favourable conditions for pollen preservation and long-time series. In North and Central Africa, on the other hand, data are less numerous and often discontinuous in time. The drying out of Holocene lakes in the Sahara, the difficulties of access to the sites, and their rarity are all limitations to regional geographical reconstructions; (2) the scarcity of long time series beyond the LGM (Ivory *et al.* 2017; Lézine *et al.* 2019; Miller and Gosling 2014; Scott 2016), and therefore long-term vegetation changes are mostly derived from marine cores (e.g., Dupont and Kuhlmann 2017; Hessler *et al.* 2010).

Thanks to a recent funding from the Belmont Forum for Science-driven e-infrastructure innovation for the project 'Abrupt Change in Climate and Ecosystems: Where are the Tipping points?', the APD is now being relaunched and developing further collaborations with international databases ('NEOTOMA', 'PANGAEA') and the French Institute Pierre Simon Laplace (IPSL). One of the priorities is to gather and validate data published since 2007, the date of the closure of the French data centre Medias-France where APD was stored. Today, 67 new late Quaternary, 17 Plio-Pleistocene and 20 marine new pollen series have been collated. Strong links are being developed with NEOTOMA (https://www.neotomadb.org/) and PANGAEA (https://pangaea.de/) databases.

These new datasets benefit from improved dating techniques and age modelling methods. The result of which is that newly acquired pollen series have reduced temporal uncertainty and improved resolution, allowing to more precision in interpretation of local and regional ecosystem dynamics and climate-vegetation interactions. All this allows to envisage new scientific developments of which one can cite three examples here:

### 2.3.1 Better understanding of ecosystem-human interactions

The identification and quantification of human-induced alterations to the Earth's surface are critical to understand the role of land-use change on ecosystems and climate. The Land Cover 6k (6000 yrs BP) project of IGBP PAGES (http://www.pastglobalchanges.org/science/wg/landcover6k) described in Gaillard *et al.* (2018) is a unique opportunity to develop a methodological approach to carefully reconstruct land cover change from pollen data and evaluate anthropogenic land-cover change scenarios for palaeoclimate modelling. The major limitation of such a quantification in tropical Africa is that 'with very few exceptions, tropical trees have zoophilous pollinating systems and relatively low pollen productivity' (Ritchie 1995; p. 487). The relationship between pollen percentages in diagrams and actual vegetation cover is thus extremely difficult to assess. Within the equatorial forest for instance, many tree taxa are under-represented or even absent from the pollen assemblages.

The reliability of any landscape reconstruction requires the spatial scale represented by the pollen assemblage to be carefully taken into account. This requires the most accurate possible evaluation of pollen productivity of species and pollen-rain settling time. Following the work of Duffin and Bunting (2008) in South Africa, Gaillard and colleagues are currently applying the LOVE (Local Vegetation Estimates) and REVEALS (Regional Estimates of VEgetation Abundance from Large Sites) models developed by Sugita (2007a,b) in Central Africa. The development of such an approach as well as the compilation of pollen and archaeological data (Marchant *et al.* 2018) can greatly improve the involvement of the palynological community in the study of land-use as a climate forcing.

### 2.3.2 Improved constraint of climate variability over the last millennia

The recent publication of Nash *et al.* (2016) within the framework of the PAGES 2ka working group (http://www.pastglobalchanges.org/science/wg/2k-network) showed that Africa is one of the world's most poorly documented regions in terms of climate reconstructions over the last millennia. Historical archives are very rare, as are natural archives with adequate temporal resolution and age control. Time frames where historical records overlap the prehistorical data are important to obtain seamless reconstructions and validate reconstructions. Improving the spatial coverage and resolution of palaeoecological records is crucial for studying natural decadal (or multi-decadal) climate variability and associated mechanisms. It is also essential to analyze the complexity of spatial hydroclimate patterns, such as that suggested for the Little Ice Age (1250–1750 CE) in Africa, for which wet or dry regions have been identified.

### 2.3.3 Understanding vegetation responses to abrupt climate change

The evolution of northern Africa from a 'Green Sahara' state to one of the most arid deserts today (Kröpelin *et al.* 2008) or the collapse of the equatorial forests (e.g., Lézine *et al.* 2013) occurred at the end of the African Humid Period. These are among the most emblematic examples of the extreme changes that can affect the global environment with dramatic consequences for human populations. The tipping points and climatic drivers between extreme states remain to be studied, as do the early warning signals of these environmental crises, which may date back several millennia, and still need to be identified. Long-term, high-resolution and evenly distributed pollen records are critical to address these questions.

## 2.4 CONCLUSION

The African Pollen Database aims at providing the scientific community, students and teachers with scientific and educational tools (pollen grain determination tools, modern and fossil data duly validated and dated, publications) to address key issues for understanding the vulnerability of ecosystems facing climate change. It ensures interoperability with international databases for multi-proxy reconstructions of the past environment. Beyond these activities, the African Pollen Database is a scientific network to develop the sharing of data and knowledge between researchers in different countries.

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**CHAPTER 3**

# Preliminary evidence for green, brown and black worlds in tropical western Africa during the Middle and Late Pleistocene

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ABSTRACT: Modern ecological studies indicate that the degree of openness in African vegetation cover is determined, in part, by the presence of herbivores and fire as consumers of vegetation. Where herbivores are the dominant consumer of vegetation the resultant open state is described as a 'brown' world. Where fire is the dominant consumer of vegetation the resultant open state is described as a 'black' world. While if neither consumer is dominant then a more closed canopy states arises that is described as a 'green' world. Here we use palaeoecological data obtained from Lake Bosumtwi (Ghana) to characterize green, brown, and black worlds during two short sections of around 1000 years each, deposited around 200,000 and 100,000 years ago (Middle and Late Pleistocene). We characterize the vegetation cover using pollen and phytoliths, herbivory using *Sporormiella* and fire using micro-charcoal. We find that during *c*. 1000 years of the Middle Pleistocene fire was the major consumer of vegetation, while during *c*. 1000 years in the Late Pleistocene herbivores were relatively more important consumers of vegetation. We therefore suggest that the Middle Pleistocene section represents a black world, while in the Late Pleistocene section we capture a combination of green, brown and black worlds. The duration of these states seems to range from centuries to millennia and transitions are observed to occur in both an abrupt and a stepwise fashion. These preliminary data demonstrate how palaeoecological information can be used to gain insights into past landscape scale processes over thousands of years. Further work is required to test the robustness of these findings and to provide a higher temporal resolution to aid the link with modern ecological studies.

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## 3.1 INTRODUCTION

The theory of 'alternative stable states' proposes that biotic and abiotic feedbacks can determine the composition and structure of an ecosystem regardless of external factors, such as climate (May 1977; Scheffer *et al.* 2001). The presence of herbivory and fire activity in African landscapes has long been suggested to be a key factor in determining the openness of the vegetation cover (Stebbing 1937). To characterize the role of herbivory and fire as mechanisms determining the degree of vegetation openness (alternative stable state) William Bond developed the concept of 'green', 'brown' and 'black' worlds (Figure 1; Bond 2005; Bond 2019). This 'multi-coloured' world model comprises three vegetation states based on differences in herbivory and fire as consumers of vegetation: (i) a 'green' world where consumers (herbivores and fires) are at sufficiently low occurrence levels as to not influence vegetation growth and consequently vegetation cover is more closed and primarily controlled by plant resource acquisition, (ii) a 'brown' world where an abundance of herbivores consuming seeds, seedlings and saplings means a more open vegetation structure, and (iii) a 'black' world where the frequent occurrence of fires consuming vegetation means a more open vegetation structure.

Modern studies in African savannas have demonstrated that herbivory and fire play an important role in the complex interactions that determine vegetation openness (Sankaran *et al.* 2008) and consequently the regulation of both are routinely used in landscape management (Roques *et al.* 2001). Evidence from modern exclosure experiments has demonstrated that the removal of animals from ecosystems can result in changes to vegetation state on timescales of years to decades (e.g. Riginos *et al.* 2012; Staver *et al.* 2009). While the manipulation of fire regimes, through experimental burns and fire suppression initiatives, have demonstrated vegetation state can also be altered through these processes on decadal timescales (e.g. Enslin *et al.* 2000; King *et al.* 1997). Over the longer-term (>100s of years) palaeoecological data have revealed that past changes in herbivory and fire activity have altered African vegetation composition and structure (e.g. Ivory and Russell 2016; Runcia *et al.* 2009; Shanahan *et al.* 2016). Palaeoecological data therefore provide an opportunity to search for evidence of the green, brown and black worlds proposed by Bond (2005), test the timescales of their stability, and discover how transitions between them occur.

Based on Bond's multi-coloured world model it can be suggested that the addition, or subtraction, of either herbivory or fire as a consumer of vegetation in a landscape would result in a shift in the degree of openness (Figure 1). Here we use palaeoecological data to parametrize vegetation openness (Poaceae pollen/phytoliths), herbivory (*Sporormiella*) and fire (charcoal) to provide 'snap shots' of vegetation states in tropical western Africa during the Middle and Late Pleistocene. We use these data to identify periods of time when consumers (both animals and fires) did, and did not, exert a dominant control over the vegetation openness.


**Figure 1.** Conceptual panorama of vegetation change across an African landscape dependent on the dominant consumer of vegetation. Green = absence of consumers. Brown = herbivores are the dominant consumers. Black = fire is the dominant consumer.

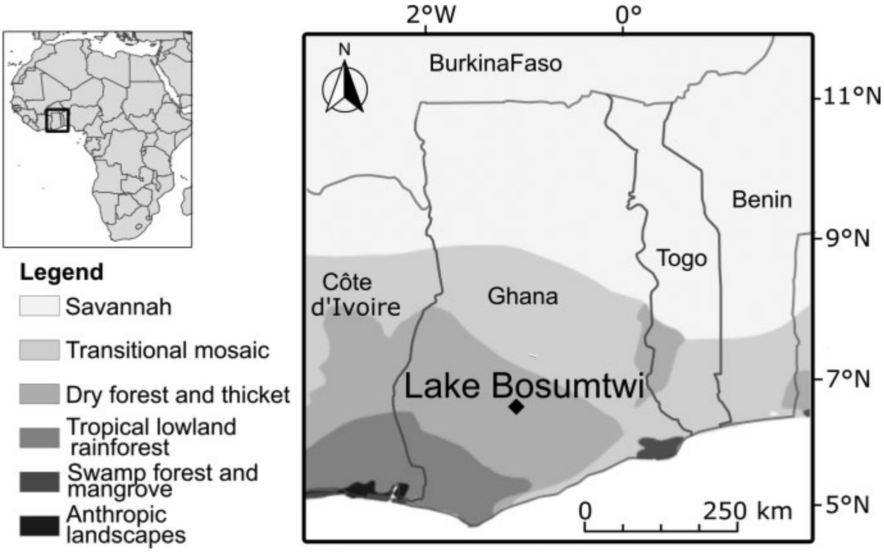


**Figure 2.** Major vegetation types of western Africa relative to Lake Bosumtwi (Ghana). Vegetation classifications follow White (1983).

## 3.2 MATERIALS AND METHODS

### 3.2.1 Study site

Lake Bosumtwi (06° 30' 06.04" N, 01° 24' 52.14" W, 97 metres above sea level; Figure 2) was formed by a meteorite impact *c*. 1 million years ago and is a hydrologically closed system (Koeberl *et al.* 1998). The International Continental Scientific Drilling Program (ICDP) Lake Bosumtwi drilling project extracted a *c*. 295 m sediment core from the centre of the basin in 2004 (named BOS04-5B) (Koeberl *et al.* 2005; Koeberl *et al.* 2007).

Lake Bosumtwi lies within the seasonal migration path of the Intertropical Convergence Zone (ITCZ) and moisture is also delivered to the site by the West African monsoon (Nicholson 2009). This climate configuration results in a strong gradient of decreasing precipitation from south to north across western Africa. Concomitant with the climate gradient is a vegetation gradient which means that today Lake Bosumtwi is surrounded by semi-deciduous forest, with evergreen forest to the south, and savanna to the north (Figure 2; White 1983). Analysis of ancient pollen contained within the BOS04-5B core revealed multiple transitions between forest and savanna vegetation during the last *c*. 520,000 years which have been linked to multi-millennial, orbitally forced, climate changes (Miller and Gosling 2014; Miller *et al.* 2016). In this study, two short (*c*. 5 m) sections of the core, in which vegetation transitions had previously been identified, were sub-sampled for further palaeoecological analysis to explore the impact of shorter-term landscape-scale process on past vegetation dynamics (Figure 3; Gosling *et al.* 2021).

### 3.2.2 Chronological control

Previously published radiometric dates indicate that the meteorite which formed Lake Bosumtwi impacted the Earth *c*. 1.07 ± 0.05 million years ago (Koeberl *et al.* 1998). Subsequent sediment

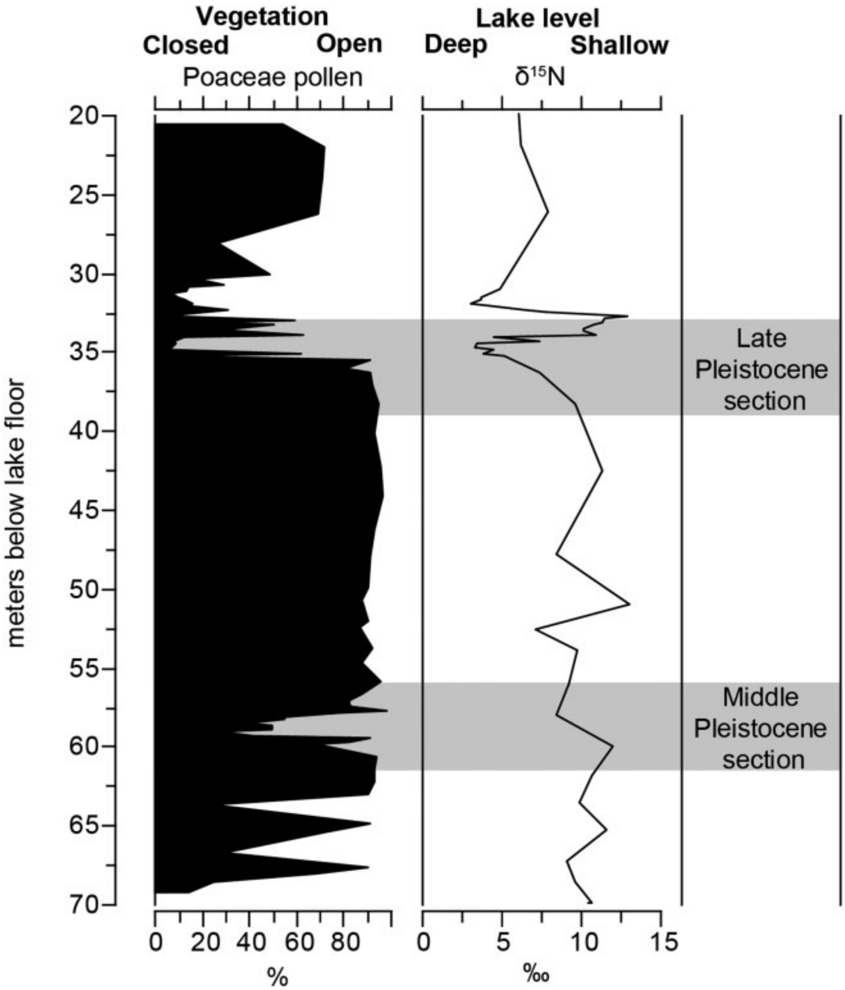


**Figure 3.** Position of the two sections focused on in this study (grey bars) from Lake Bosumtwi relative to previous palaeoecological work (modified from Miller *et al.* 2016).

accumulation through the core has been constrained by radiocarbon, U-series and optically stimulated luminance dating (Shanahan *et al.* 2013a). The two sections of the BOS04-5B core focused on here were recovered from 61.25–56.05 and 38.85–33.45 metres below lake floor (mblf) (Figure 3). Based on the radiometric dating these two sections were likely deposited during the Middle Pleistocene (*c*. 200,000 years ago) and Late Pleistocene (*c*. 100,000 years ago) respectively (Miller *et al.* 2016).

Previous studies into sediment deposition within Lake Bosumtwi indicated that the light-dark couplets of laminations within the sediments likely represent seasonal cycles (Shanahan *et al.* 2013b). Therefore, to gain a minimum estimate of the timescale over which these sections were deposited, the number of laminations within each section was counted on the basis that the sediment core images were included in the initial core descriptions.

### 3.2.3 Palaeoecological analysis

Twenty sub-samples were prepared for palaeoecological analysis across each of the two sections using standard techniques including density separation, acetolysis and sieving at 180 $\mu$m (Moore *et al.* 1991). An exotic marker (*Lycopodium*) was added to each sample to allow the concentration of microscopic remains to be calculated (Stockmarr 1971); University of Lund, batch #483216, containing 18,583 grains $\pm$ 4.1%. Each sub-sample was analysed for the concentration of Poaceae pollen, *Sporormiella*, and micro-charcoal (< 180 $\mu$m); identifications followed Gosling *et al.* (2013), van Geel and Aptroot (2006), and Whitlock and Larsen (2001) respectively. Phytoliths were also present in the prepared slides. Phytolith concentration from the same sub-samples were analysed across the Middle Pleistocene section; phytolith identifications were based on Piperno (2006).

### 3.2.4 Statistical analysis and data presentation

To assess the robustness of the palaeoecological datasets 95% confidence intervals were calculated (following Maher 1981). Bayesian Change Point (BCP) analysis (Barry and Hartigan 1993), which determines if there is a significant change in the mean of the variable at a given point in a time series, was used on: (i) *Sporormiella* (herbivore) concentration, and (ii) micro-charcoal (fire) concentration data. The posterior probabilities of the BCP analysis indicated the likelihood of significant change of those variables at each time step sampled (Barry and Hartigan 1993; Blois *et al.* 2011). Where the posterior probability of the BCP analysis exceeded 0.8 for *Sporormiella* or charcoal, a zone boundary was defined, indicating a significant change in herbivory or fire activity. Data were plotted using C2 (Juggins 2005).

## 3.3 RESULTS

Previously published radiometric dating indicates that the two sections studied here were deposited during the Middle and Late Pleistocene (Figure 3; Shanahan *et al.* 2013a). The results of the younger section are presented in the upper panel (Figure 4A) and the results of the older section are presented in the lower panel (Figure 4B).

### 3.3.1 Lamination counting

Approximately 1200 light-dark couplets of laminations were identified in the Middle Pleistocene section; however, no laminations could be identified in three parts of the section at: 60.25–59.85, 58.65–58.45, and 57.05–56.85 mblf (Figure 4B). Approximately 750 light-dark couplets of laminations were identified for the Late Pleistocene section; however, no laminations could be identified between 34.45 and 33.45 mblf (Figure 4A).

### 3.3.2 Palaeoecological analysis

For the Middle Pleistocene section two abrupt changes in vegetation consuming processes were detected by the BCP analysis at 59.25 (micro-charcoal) and 56.65 (*Sporormiella*) mblf defining three zones (Zones i, ii, and iii; Figure 4B). Within Zone i Poaceae pollen occurs in high concentrations (mean of 38,000 grains/cm$^3$), Poaceae phytoliths, tree phytoliths and micro-charcoal are ever present but are highly variable in concentration (1100–46,000 Poaceae phytoliths/cm$^3$, 28,000–240,000 tree phytoliths/cm$^3$, and 250,000–1,600,000 fragments/cm$^3$), and *Sporormiella* is absent. In Zone ii Poaceae pollen is continually present at medium concentration (mean 26,000 grains/$cm^3$), Poaceae phytoliths, tree phytoliths and micro-charcoal are usually present and highly variable in concentration (4000–127,000 Poaceae phytoliths/$cm^3$, 0–360,000 tree phytoliths/cm3, 199,000–6,194,000 fragments/$cm^3$), and *Sporormiella* is absent. In Zone iii Poaceae pollen and phytoliths occur at high concentrations (mean 35,000 grains/$cm^3$ and 34,000 phytoliths/$cm^3$ respectively), but tree phytoliths are absent; micro-charcoal is variable (395,000–978,000 fragments/$cm^3$), and *Sporormiella* is continually present (395–1133 spores/$cm^3$).

For the Late Pleistocene section two abrupt changes in vegetation consuming processes were detected by the BCP analysis at 36.45 (*Sporormiella* and micro-charcoal) and 34.25 (*Sporormiella*) mblf defining three zones (Zones I, II, and III; Figure 4A). Within Zone I Poaceae pollen (17,000 grains/$cm^3$), *Sporormiella* (mean 1200 spores/$cm^3$), and micro-charcoal (mean 291,000 particles/$cm^3$) are all relatively highly abundant within the section. In Zone II Poaceae pollen (mean 14,000 grains/$cm^3$) are abundant, while *Sporormiella* and micro-charcoal vary widely (0–8400 spores/$cm^3$ and 15,000-496,000 fragments/$cm^3$ respectively). In Zone III Poaceae pollen (mean 2700 grains/$cm^3$) and micro-charcoal (mean 4400 fragments/$cm^3$) are relatively low, while *Sporormiella* varies (0–4000 spores/$cm^3$) in concentration.

## 3.4 DISCUSSION

### 3.4.1 Timescales of deposition

Radiometric dating indicates that the Middle Pleistocene section was deposited *c*. 200,000 years ago during a period of high eccentricity in the Earth's orbital cycle (Miller *et al.* 2016). This orbital configuration of northern hemisphere insolation maximum, during a precession minimum and an eccentricity maximum, extenuates seasonal variations at Lake Bosumtwi (6°N). Therefore, this period of time likely represents ecosystem functioning under high seasonal stress, and a consistently low level of Lake Bosumtwi during this period (Figure 2). The Late Pleistocene section is indicated to have been deposited *c*. 100,000 years ago as part of the longer transition out of the last interglacial period and includes a period of relatively higher lake levels (Figure 2).

Lamination counting within the two sections revealed 1200 light-dark couplets in 5.2 m of sediment in the Middle Pleistocene section, and 750 light-dark couplets in 5.4 m in the Late Pleistocene section. These counts were derived from visual inspection of digital core scan images and consequently likely represent an under-estimate of the true number of bands present because some may not have been captured in the digital imagery of the core surface. To reveal all bands, and develop a robust internal chronology, further analysis of the sediments in thin section is required. The preliminary analysis presented here shows this is a promising line of investigation and, based on the visible bands, it can be roughly estimated that the period of deposition represented by each of these sections is more than 1000 years. The relatively higher number of bands in the older section could be related to the enhanced seasonality and lower sedimentation rates during this period.

### 3.4.2 Evidence for green, brown and black worlds

Fire (charcoal) was ever present, and highly abundant, in the Middle Pleistocene section (Zone i, ii and iii in Figure 4B), while herbivores (*Sporormiella*) only appear in the uppermost samples (Zone iii in Figure 4B). The first transition (Zone i to Zone ii) is defined by a change in fire activity that is coincident with a slight drop in the average concentration of Poaceae pollen, however, no directional change in the concentration of Poaceae or tree phytoliths is discernible at this time. This suggests that vegetation state did not change significantly. The second transition

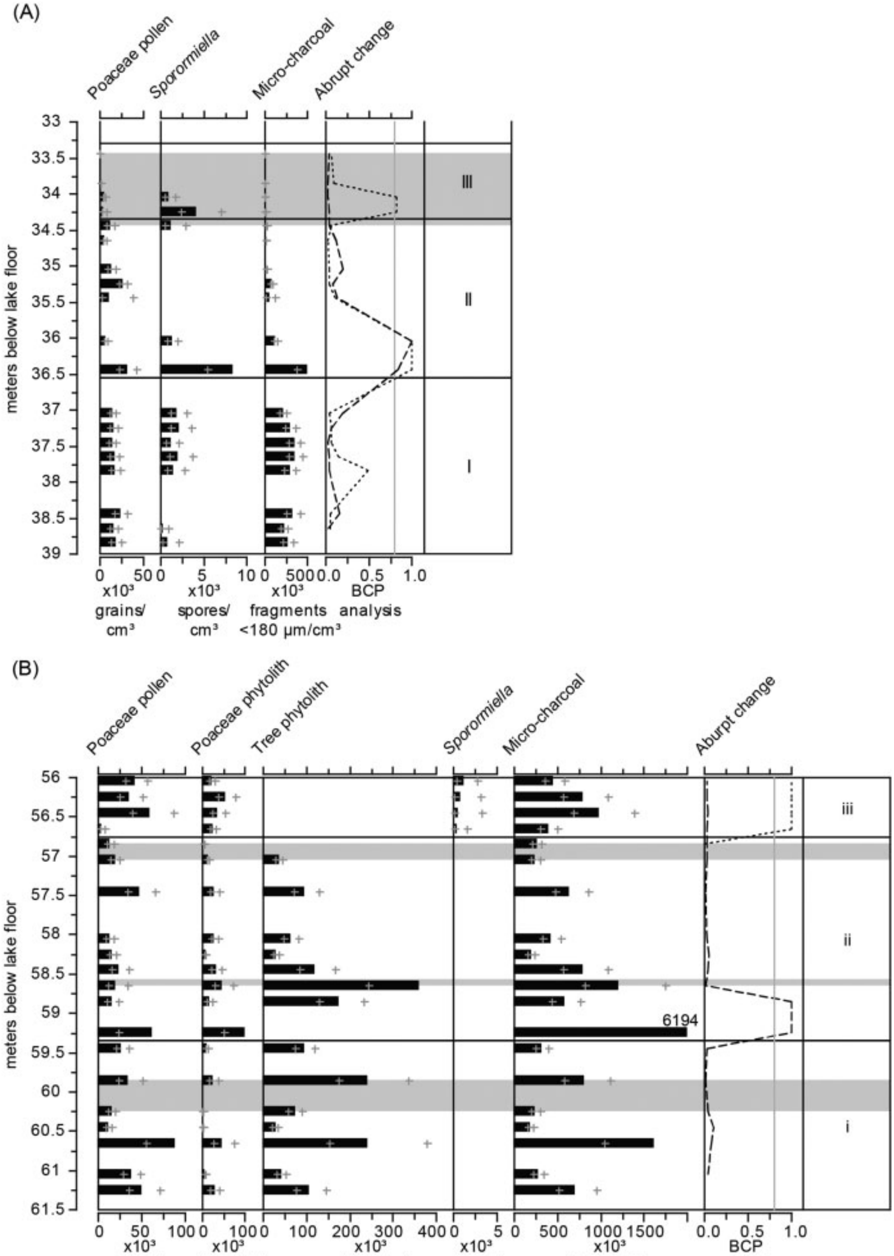


**Figure 4.** Palaeoecological diagram from two portions of the Lake Bosumtwi (BOS05-3B) sedimentary record: (A) Late Pleistocene (*c*. 39.0-33.0 mblf), and (B) Middle Pleistocene (*c*. 56.0–61.5 mblf). Dark grey plus symbols indicate upper and lower confidence intervals (95%). Horizontal light grey bands indicate portions of the sediment without laminations. For 'Abrupt change' curves: black dotted line indicates BCP analysis of *Sporormiella* concentration data, black dashed line indicated BCP analysis of micro-charcoal concentration data, vertical solid grey line indicates 0.8 significance threshold. In the case of one sample, at 59.25 mblf, the concentration of charcoal fragments exceeds the scales shown and the upper value is indicated numerically. Raw data available from Gosling *et al.* (2021).

(Zone ii to Zone iii) is defined by the appearance of herbivores, and is associated with the loss of tree phytoliths and the rise of Poaceae pollen and phytolith concentrations. This suggests that increased herbivory did diminish, or alter, the woody component of the vegetation. Throughout this section the high concentration of Poaceae (indicated by both pollen and phytoliths) with a variable woody component (indicated by the tree phytoliths) suggests that the landscape around Lake Bosumtwi during this short snapshot of the Middle Pleistocene was similar to the open vegetation found in the forest-savannah transition zone *c*. 250 km north of Lake Bosumtwi today (Julier *et al.* 2018), rather than the closed vegetation found close to the site today (Julier *et al.* 2019; Figure 1). Today in the transition zone fires during the dry season (November-March) limit juvenile establishment and sapling recruitment (Armani *et al.* 2018). The enhanced seasonality during this part of the Middle Pleistocene likely resulted in two prolonged and intense dry seasons during which burning could have occurred. The enhanced seasonality likely meant that fire was an even greater consumer of vegetation then than it is today in the transition zone, suggesting that this entire section likely represents 'black' world open vegetation.

Fire activity and herbivory both change through the Late Pleistocene section (Figure 4A). The first transition (Zone I to II) sees first a spike and then a persistent decline in both herbivory and fire activity. Prior to the spike (Zone I) herbivory levels and fire activity are relatively high and stable, and this is mirrored in the Poaceae concentration. After the spike (Zone II) herbivory and fire activity fluctuate, and are periodically absent, which is coincident with a slight drop in Poaceae concentration. *Sporormiella* and micro-charcoal concentrations relative to the Middle Pleistocene 'black' world section are higher and lower respectively. This suggests that in the Late Pleistocene section herbivores likely played a relatively more important role in determining vegetation structure. Therefore, it can be tentatively suggested that where *Sporormiella* is abundant a 'brown' world persisted. Although it should be noted that both herbivory and fires were clearly present and no doubt both helped to maintain the vegetation openness. Furthermore, it seems that the role of both herbivory and fire as consumers of vegetation (promoting higher Poaceae concentration and inferred openness) is diminishing through Zones I and II. The concomitant decline in consumers and Poaceae perhaps suggests a move from a consumer controlled stable state, towards a more closed canopy 'green(er)' world. The second transition (Zone II to III) is defined by a rise in herbivory, and is coincident with a drop (to near absence) in fire activity, low concentrations of Poaceae pollen, a sedimentological change (loss of laminations), and a drop in lake level (Figure 2). It is consequently unclear if the lower Poaceae pollen concentration (and inferred decreased openness) observed in Zone III are a direct result of diminishing numbers of herbivores and fire activity leading us into a 'green' world, or if other, possibly climatological or taphonomic controls are responsible.

### 3.4.3 Insights into past vegetation states in tropical western Africa

The preliminary data from the two sections examined here provide evidence for the presence of, and switches between, green, brown and black worlds in tropical western Africa during the Middle and Late Pleistocene. It is also apparent that different combinations of herbivores and fire in the landscape resulted in different degrees of openness (stable states) persisting. It seems likely that the background climatic configuration and seasonality played a significant role in determining the relative importance of these processes; an observation that aligns with modern studies which indicate that fire prevalence is most strongly linked to previous years' rainfall (van Wilgen *et al.* 2004). The presence of both herbivores and fire within the landscape is coincident with elevated concentration of Poaceae pollen and phytoliths in line with expectations from modern studies that suggest these vegetation consumers promote more open ecosystems (Bond 2005; Bond 2019; Warman and Moles 2009). The timescales over which the green, brown and black alternative 'stable states' persisted appears to be at least on the order of centuries to millennia.

It can be tentatively suggested that transitions between green, brown and black worlds occur over decades to centuries; however, it should also be noted that both gradual transitions seem to exist (i.e. in the Late Pleistocene section herbivory, fire activity and Poaceae all decline in a step wise fashion) as well as abrupt shifts (i.e. in the Middle Pleistocene section herbivory appears and tree phytoliths disappear at the same time). The different modes of transition suggest a complex series of interactions are responsible for initiating and driving vegetation dynamics during both time windows. This finding is in line with more recent data from savanna in eastern African that suggest that over the last 1400 years periodic fluctuations in woody cover driven by landscape processes are the rule, not the exception (Gillson 2004). Complex landscape scale processes have also been observed to be important over longer timescales during the transition out of the last interglacial period at Lake Bosumtwi (Shanahan *et al.* 2016) and over shorter timescales in the modern forest-savanna transition zone to the north (Ametsitsi *et al.* 2020). These findings emphasize the need for further empirical data to contextualize the role of processes, such as herbivory and fire activity, in determining vegetation states in Africa across space and through time.

### 3.4.4 Future perspectives

To determine the relative importance of herbivory and fire as consumers of vegetation, and how this changes through time, at Lake Bosumtwi further research is required. Firstly, a robust internal chronology should be established through detailed examination of the nature and frequency of the laminations, and secondly further details should be extracted from the palaeoecological and palaeoclimatic record. Specifically, detailed pollen and phytolith analyses are required at a higher temporal resolution to characterize trajectories of vegetation change. These vegetation data need to be supported by: (i) further charcoal analyses (micro- and macro-charcoal and charcoal chemistry) to reveal the biomass consumption and temperature of burning (Gosling *et al.* 2019; Whitlock and Larsen 2001), (ii) examination of a full suite of coprophilous fungal spores (not just *Sporormiella*) to provide insights into changing animal assemblages (Loughlin *et al.* 2018; van Geel and Aptroot 2006), and (iii) further independent evidence for climatic change should be sought, including further $\delta^{15}N$ analysis to determine changes in moisture balance (Talbot 2001; Talbot and Johannessen 1992), and pollen chemical analysis to identify fluctuations in solar irradiance (Jardine *et al.* 2016; Jardine *et al.* 2021).

## 3.5 CONCLUSIONS

The examination of Middle and Late Pleistocene sections of the Lake Bosumtwi sediment core provide evidence for, and switches between, ‘green’, ‘brown’ and ‘black’ worlds. The different coloured worlds (alternative stable states) each seem to persist for hundreds to thousands of years. The addition, and subtraction, of herbivory and fire activity from the landscape around Lake Bosumtwi seems to have resulted in vegetation change occurring in both an abrupt and complex gradual fashion over decades to centuries. Although the mechanisms behind the changes in herbivory and fire activity remain largely ambiguous, it seems likely that seasonality modulated by orbital forcing plays a strong role in governing fire activity. To further our understanding of the persistence of, and transition between, alternative stable states around Lake Bosumtwi we now need to improve the chronological control, enhance our sampling resolution, and expand the range of proxies analysed to provide a comprehensive insight into past ecosystem dynamics. Armed with these data we will be able to better anticipate the impact of projected climate changes for tropical western Africa.

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## DATA AVALIABILITY

All data presented in this manuscript can be downloaded from DOI: 10.6084/m9.figshare.127 38131

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