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The modern pollen–vegetation relationships of a tropical forest–savannah mosaic landscape, Ghana, West Africa

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ABSTRACT

Transitions between forest and savannah vegetation types in fossil pollen records are often poorly understood due to over-production by taxa such as Poaceae and a lack of modern pollen-vegetation studies. Here, modern pollen assemblages from within a forest-savannah transition in West Africa are presented and compared, their characteristic taxa discussed, and implications for the fossil record considered. Fifteen artificial pollen traps were deployed for 1 year, to collect pollen rain from three vegetation plots within the forest-savannah transition in Ghana. High percentages of Poaceae and Melastomataceae/Combretaceae were recorded in all three plots. *Erythrophleum suaveolens* characterised the forest plot, *Manilkara obovata* the transition plot and *Terminalia* the savannah plot. The results indicate that Poaceae pollen influx rates provide the best representation of the forest-savannah gradient, and that a Poaceae abundance of >40% should be considered as indicative of savannah-type vegetation in the fossil record.

KEYWORDS

pollen; transitions; Poaceae; savannah; Ghana; palaeoecology; Bosumtwi

1. Introduction

The transition between closed-canopy forest and open-canopy savannah vegetation is one that can be observed at the present day along climate gradients, and in the fossil record during periods of climatic change (Mayle et al. 2007; Azihou et al. 2013; Miller & Gosling 2014; Miller et al. 2016). The transition between forest and savannah is, however, not always stable or clear cut (Cardoso et al. 2016), with large areas of land being classified as mosaics of forest and savannah (e.g. White et al. 1983; Torello-Raventos et al. 2013). Transitional ecosystems are today recognised as having conservation value in their own right, due to their ability to provide habitats for organisms from different ecosystems, and the potential for them to be especially sensitive to climate change (JNCC 2010; Ibie et al. 2016; Joyce et al. 2016). The identification of transitional ecosystems in the fossil record may be crucial in providing evidence to support efforts to conserve biodiversity, especially if the persistence of these transitional areas can be demonstrated over long time scales.

Projections of future environmental change suggest that modern forest–savannah boundaries will be altered, and transitional zones shift (Niang et al. 2014), but little is known about what this change will look like in terms of vegetation composition (Cramer et al. 2001). Fossil pollen records of forest-to-savannah transitions can serve as a guide to the likely future vegetation response; however, it has been difficult to observe forest-to-savannah transitions in the fossil pollen record because of a poor understanding of how they are represented. The relationship between taxa represented in the vegetation and in the pollen rain is known not to be directly proportional (Davis 1963). Anemophilous taxa, and zoophilous taxa with 'messy' pollination syndromes (open flowers with extruded anthers) are generally over-represented relative to their abundance in the vegetation, whereas those zoophilous taxa with more closed floral morphologies are more often under-represented or palynologically silent (present in vegetation but not pollen assemblages) (Bush & Rivera 2001).

To facilitate a better understanding of transitional periods in fossil pollen records, this study has explored modern pollen–vegetation relationships on a landscape scale (plots within 10 km of one another) within the forest–savannah transition zone in tropical West Africa. Data from pollen traps were used to characterise the modern pollen rain produced by three vegetation types (forest, transition and savannah) during 1 year. Modern pollen data were then compared with vegetation inventories, and an assessment was made as to whether it is possible to differentiate between forest, transition and savannah vegetation on the basis of the pollen assemblage alone. The implications of this modern study for identification of past forest–savannah transitions in the fossil pollen record are then discussed.

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1.1. Vegetation at the forest–savannah transition

The transition between forest and savannah ecosystems, on both spatial and temporal scales, is one that has been of interest to biogeographers, ecologists and palaeoecologists for decades (Beard 1953; Aubréville 1966; Ybert 1975). Although the botanical composition of savannah-type ecosystems on different continents has been shown to vary widely, it can, along with the height and canopy cover, be used in their classification (Torello-Raventos et al. 2013). The shift from forest to savannah is controlled on a macro-scale (100s of km) by climatic gradients, primarily rainfall (Swaine 1992; Lehmann et al. 2011), but on smaller scales other factors such as soil type and herbivory are also important. Where mean annual precipitation (MAP) is less than 650 mm, savannahs form because water availability limits tree growth and, consequently, forest cover (Sankaran et al. 2005). At precipitation levels of more than 650 mm MAP, savannahs can occur when other factors such as fire and herbivory inhibit the growth or enhance the mortality of trees (Swaine et al. 1992; Higgins et al. 2012; Dexter et al. 2015). Edaphic factors such as soil type and fertility may also influence local vegetation dynamics, resulting in the formation of a mosaic of forest and savannah within regions that experience a more or less uniform climate (Lehmann et al. 2011).

1.2. Pollen at the forest–savannah transition

On a large scale, pollen production by modern ecosystems in Africa has been found to differ between vegetation types (Gajewski et al. 2002; Lézine et al. 2009). For example, an extensive study of modern pollen–vegetation relationships in central Africa demonstrated that it is possible to differentiate broad vegetation types, such as tropical forest and tropical seasonal forest, using the pollen signal, although difficulties were encountered in areas that were considered transitional (Lebamba et al. 2009). Within the forest–savannah transition zone of Cameroon, it is possible to identify different vegetation types by their modern pollen rain, although the characteristic pollen and vegetation taxa are different due to sampling bias towards larger woody plants in the botanical inventories, and pollen from entomophilous taxa being under-represented (Vincens et al. 2000). The forest–savannah transition has also been shown, in Côte d'Ivoire, to produce distinct pollen assemblages depending on the vegetation, with *Hewittia malabarica* L. (Suresh) indicating the forest edge, and savannah being characterised by Poaceae pollen percentages of $>$ 40% (Ybert 1975). Studies of the Sudanian and Sahelian regions have shown that it is possible to differentiate between these regions by their pollen signals, and to also differentiate smaller scale vegetation types within them (e.g. *Isoberlinia* dry forest and dry or wet Combretaceae forest) (Lézine & Edorh 1991; El Ghazali & Moore 1998), although the arboreal pollen signal is often overwhelmed by very high ($>$ 90%) Poaceae abundances.

1.3. Forest–savannah transitions through time

Transitions between forest and savannah have been tracked through the last c. 1 Ma in tropical West Africa by 15 offshore pollen records (Sowunmi 1981; Dupont et al. 1989; Bengo & Maley 1991; Lézine 1991; Dupont & Agwu 1992; Lézine & Vergnaud-Grazzini 1993; Frédoux 1994; Dupont & Weinelt 1996; Shi & Dupont 1997; Dupont et al. 1998; Jahns et al. 1998; Shi et al. 2001; Marret et al. 2013; Dalibard et al. 2014; Vallé et al. 2014) and several terrestrial records (Maley 1991; Elenga et al. 1994; Maley & Brenac 1998; Salzmann et al. 2002) of which only one record is older than 35 ka BP (Lake Bosumtwi, Ghana). The fossil pollen record obtained from Lake Bosumtwi is unique to tropical West Africa, and to date covers the last c. 500,000 years of the 1 Ma sediment core that was recovered (Koeberl et al. 2007; Miller & Gosling 2014; Miller et al. 2016). Pollen from offshore and terrestrial records identifies shifts in the vegetation correlating with climatic changes that broadly relate to orbital (glacial–interglacial) cycles during the Quaternary (Miller et al. 2016). The vegetation shifts observed are thought to be a consequence of the north- to southwards movement of the tropical rain belt, and the intensity of the African Monsoon (Shanahan et al. 2015; Miller et al. 2016). The shifts between wetter forest and drier savannah ecosystems are recorded in the pollen record of Lake Bosumtwi by fluxes in the Poaceae abundance, which varies from 0 to 90% of the terrestrial pollen sum; interpretations of the Lake Bosumtwi fossil pollen record placed the transition between forested and savannah vegetation types at 55% Poaceae (Miller et al. 2016).

2. Study region

2.1. Tropical West Africa

The vegetation of tropical West Africa has been classified into two main biomes – the 'Guineo–Congolian regional centre of endemism' and, farther north, the 'Sudanian regional centre of endemism' – which are distinct because of their endemic flora. The transition between the two is primarily driven by decreasing precipitation from south to north (White, 1983). The Guineo–Congolian region comprises areas of wet and semi-deciduous forests, transitional rainforests, secondary grassland and mosaics, while the Sudanian region contains drier woodland and more open savannah vegetation types (Supplemental data).

At around 8°N there is a band of vegetation known as the 'Guineo–Congolian/Sudanian transition zone' (White 1983), which is between 100 and 500 km wide and runs approximately east–west across the West African countries, including Ghana (Gautier & Spichiger 2004). The transition zone comprises a patchwork of forest and savannah vegetation types and can be considered the boundary between the wet Guineo–Congolian forest types of the south and the drier Sudanian savannah regions of the north. It is within this transition zone that the Kogyae Strict Nature Reserve is situated, in which the plots for this study are located (Figure 1).

2.2. Kogyae strict nature reserve

In 2012, three permanent vegetation study plots (KOG02, 'Forest'; KOG04, 'Transition'; and KOG05, 'Savannah' (see sections 2.3.1–2.3.3 for further details) were established in the Kogyae Strict Nature Reserve (Ghana) at the transition between the Guineo–Congolian and Sudanian biomes, to characterise the vegetation and monitor environmental changes at the ecotone (Figure 1). The Kogyae vegetation study plots were set up as part of the

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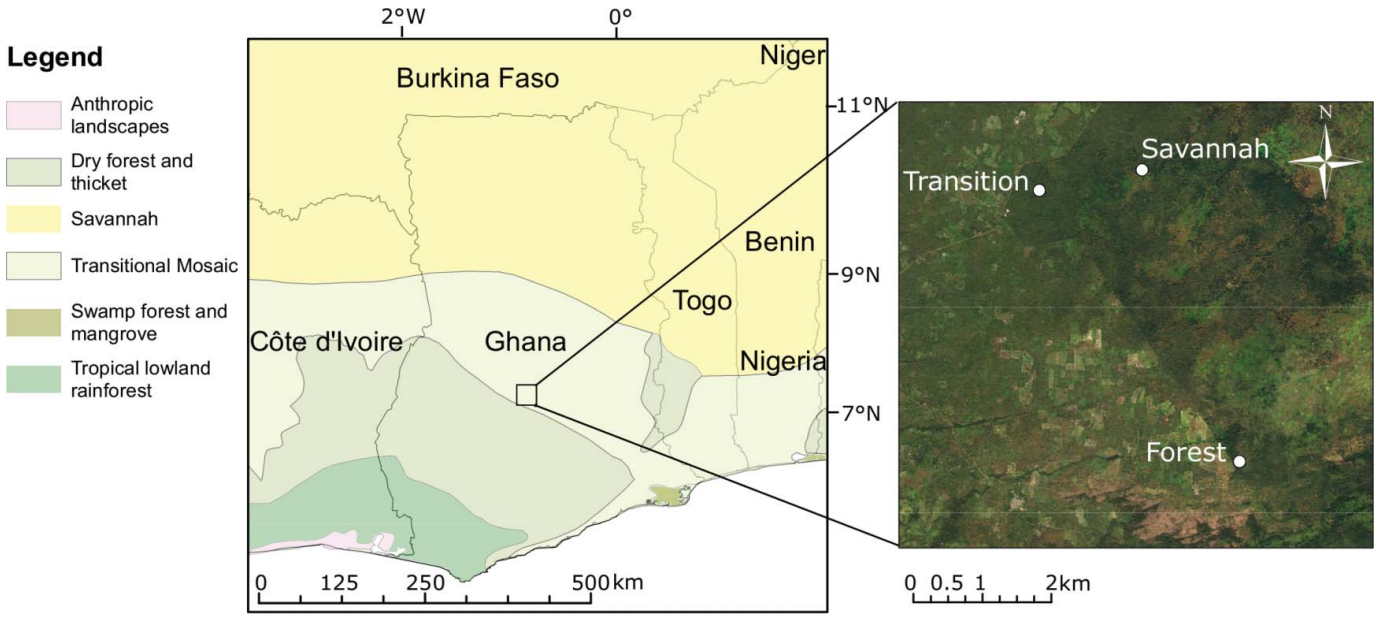


Figure 1. Location of the field study site in Ghana as a whole, relative to vegetation types (left), and location of vegetation plots relative to one another (right) (Source of map/satellite image).

Global Ecosystem Monitoring (GEM) network (http://gem.tropicalforests.ox.ac.uk/) and are also part of the African Tropical Rainforest Observation Network (AfriTRON) (Lewis et al. 2013). Vegetation data from these plots are available at http://www.forestplots.net (Lopez-Gonzalez et al. 2011). The Kogyae Strict Nature Reserve contains a mosaic of ecosystems which differ in their floristic composition, tree cover, canopy height and density, and understory vegetation. The Kogyae region typically receives around 1000 mm of rain/year, and experiences a dry season between October and April of each year (weather data from the weather station at the Kogyae Field Station). During the dry season the savannah vegetation in Kogyae usually burns, typically during February. The three vegetation study plots were established in three distinct vegetation types within Kogyae, but experience similar climatic conditions due to their close proximity; they are within 10 km of one another (Figure 1).

The soils present in the Kogyae Strict Nature Reserve are shallow and prone to drying out, and overlie horizontally bedded sandstones that are part of the Voltarian Group; however, depth and composition of soils differs between forested and savannah areas (Wildlife Department, Accra 1994). Animals present in the reserve that may exert grazing or browsing pressure include buffalo, baboons, antelopes, five species of monkey and domestic cattle (Danquah & Owusu 2015).

2.3. Vegetation of study plots

The Forest (KOG02), Transition (KOG04) and Savannah (KOG05) vegetation study plots are each 1 hectare and were established following the standard GEM protocols (Marthews et al. 2014). As part of the GEM programme a vegetation inventory was generated for each plot, and a programme of yearly measurements of all trees > 10 cm in diameter at breast height (DBH) was established measuring DBH, height and yearly growth. Two genera occur only in the Forest plot (*Cola* and *Dacryoides*) and two genera occur only in the Savannah plot (*Trichilia* and *Uapaca*) (Supplemental data). The Transition plot includes six genera which occur across all three plots (*Ficus*, *Anogeissus*, *Lannea*, *Margaritaria*, *Sterculia* and *Pterocarpus*) and shares multiple genera with both the Forest and Savannah plots, but does not contain any unique genera.

2.3.1. Forest (KOG02)

The centre of the Forest plot is located at 7°15′41.9″N, 1°09″00.2″W, 197 m above sea level (asl) (Figures 1 and 2). Thirty-seven species were recorded in the Forest plot with DBH > 10 cm, with nine taxa occurring at > 3% abundance (Supplemental data), the most abundant, by percentage of stems, being *Cola gigantea* A.Chev. (12.3%), *Sterculia tragacantha* Lindl. (10.7%) and *Dacryodes klaineana* (Pierre) H.J.Lam (9.6%). There are also understory monocotyledonous plant taxa, e.g. Zingiberaceae, Costaceae and Marantaceae, although the abundance of these taxa was not quantitatively assessed, as they are herbaceous and therefore were not included in the vegetation surveys. The taxa in the Forest plot fall largely into 'drier peripheral semi-evergreen rainforest' (seven taxa), or 'Guineo-Congolian transition woodland' (six taxa), but with some 'Sudanian transitional woodland' elements (five taxa), including *Ceiba pentandra* (see Supplemental data and Figure 3). The average tree height is 20.8 m. The diversity (Shannon index) of the Forest plot is 3.11.

2.3.2. Transition (KOG04)

The centre of the Transition plot is located at 7°18'07.7"N, 1°10′50.2″W and 190 m asl. There are 34 species recorded with >10 cm DBH, with nine taxa occurring at > 3% abundance (Supplemental data), the most abundant of which, by percentage of stems, are *Sterculia tragacantha* (26.9%), *Pterocarpus erinaceus* Poir (10.7%) and *Maranthes polyandra* (Benth.) Prance (6.8%). When compared to White (1983), the taxa in the plot are those characteristic of 'Guineo–Congolian transition woodland' (12 taxa) and 'Sudanian Woodland' (11 taxa), with some

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Figure 2. Photographs of the vegetation in the three plots; (a) Forest (KOG02) 7°15'41.9"N, 1°09'00.2"W, 197 m asl; (b) Transition (KOG04) 7°18'07.7" N, 1°10'50.2"W and 190 m asl; and (c) Savannah (KOG05) 7°18'04.1" N, 1°09'53.8"W and 186 m asl.

'Guineo–Congolian secondary grassland and wooded grassland' taxa (eight). The average tree height is 12.1 m. The diversity (Shannon index) of the Transition plot is 2.82.

2.3.3. *Savannah (KOG05)*

The Savannah plot is located at 7°18'04.1"N, 1°09'53.8"W and 186 m asl. There are 26 recorded species with > 10 cm DBH, of which eight occur at > 3% (Supplemental data), the most abundant of which, by percentage of stems, are *Bridelia ferruginea* Benth. (27.7%), *Pterocarpus erinaceus* (10.7%) and *Uapaca togoensis* Pax (8.1%). The vegetation types of White (1983) are represented by 'Sudanian woodland' (13 taxa) and 'Guineo-Congolian secondary grassland and wooded grassland' (11 taxa). The understory consists mainly of tall (>1 m in height) grasses, with other herbaceous taxa such as members of the Asteraceae. The average tree height is estimated to be between 10 and 12 m. The diversity (Shannon index) of the Savannah plot is 2.56.

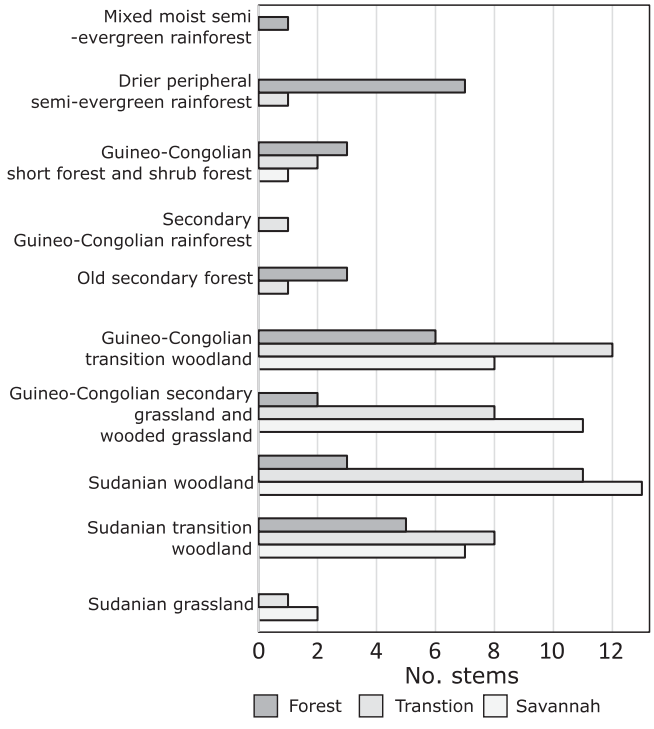


Figure 3. Bar chart showing the vegetation types, as outlined by White (1983), to which the species in the three plots belong.

3. Methods

3.1. *Field methods*

Modern pollen rain was collected using pollen traps, composed of a plastic funnel (diameter 140 mm), glass fibre filter paper affixed to the funnel using bathroom sealant, and cotton wool fibre filling the rest of the funnel, held in place with plastic netting secured around the funnel using plastic-coated wire, following (Gosling et al. 2003).

A total of 30 traps, 10 per vegetation plot (1 ha; 100 m × 100 m) were deployed, along the 40-m line (i.e. a 100-m-long transect across the plot, at the point 40 m along from the 0 m/0 m point of the plot; Figure 4). All traps were positioned at approximately 50 cm above ground level to reduce risk of inundation and to ensure standard height of sampling across this study. The traps were affixed to stakes hammered firmly into the ground or, in cases where that was not possible, to trees. The distance from each trap to the closest large tree (> 10 cm DBH) was recorded for all sites, and the tag numbers of these trees noted. Upon collection, traps were emptied of their

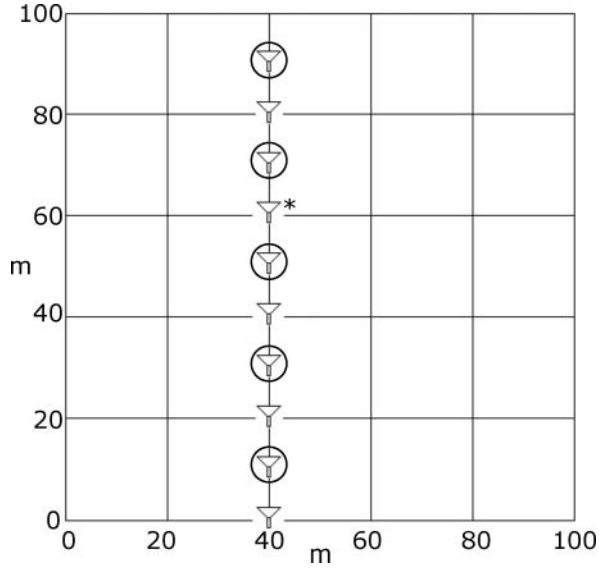


Figure 4. Diagram showing layout of pollen traps (represented by triangle symbols) within vegetation survey plots. Circled traps indicate those processed and counted, which was every other trap in the Savannah and Transition plots (odd numbers). Asterisk indicates Trap 76 in the Forest plot, which was sampled instead of Trap 75, due to poor condition of Trap 75.

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contents, which were placed into sealed plastic bags and stored in a refrigerator.

The traps were in the field between October 2013 and October 2014, except for a short period in February during which all scientific equipment was removed from the plots to avoid destruction in the annual burn; equipment in the plots was removed and re-deployed by researchers from the Forestry Institute of Ghana (FORIG).

3.2. Laboratory methods

Five traps per plot were processed and counted, to provide good statistical coverage of the plot whilst avoiding unnecessary effort (Gosling et al. 2005). Samples were processed following the method for cotton wool-based traps from Gosling et al. (2003), in which cotton wool is removed by acetolysis and filter paper removed using hydrofluoric acid. Eight *Lycopodium* tablets per trap were added as an exotic marker to enable the calculation of pollen concentrations (Stockmarr 1971); University of Lund batch number 124961, containing 12,542 $\pm$ 931 spores per tablet. Samples were mounted in glycerol and counted at 400$\times$ magnification using a Nikon Eclipse 50i microscope. Pollen taxa were identified using atlases relating to tropical West Africa (van Campo 1974; Ybert 1979; Riollet & Bonnefille 1980; Gosling et al. 2013) and the African Pollen Database (Vincens et al. 2007).

3.3. Statistical methods

Pollen counts were recorded digitally (Valencia 2014), and sample-specific estimate count sizes required to capture the major features of pollen rain were generated (Keen et al. 2014), which returned count sizes that varied between 300 and 800 grains per sample. Data were visualised in the plotting programme C2 (Juggins 2007). Pollen types were allocated numbers sequentially from 1 upwards during counting, and taxonomic information was later assigned to these types. Pollen type information can be found in Julier and Gosling (2017).

The relationship between pollen and vegetation abundance was calculated by dividing average percentage abundance of pollen in each trap by percentage basal area of the corresponding taxon in the vegetation plot; the degree of under- or over-representation is then expressed as an 'R-rel value' following Gosling et al. (2017), i.e. values $>$ 1 indicate a taxon is over-represented in the pollen relative to the vegetation. Characteristic taxa were designated as those that occurred in at least four out of five samples from a plot, and at $\geq$ 3% abundance in one sample or more. These conditions were chosen as they ensure that the taxa designated as characteristic are well-represented spatially in the plot (present in at least four of five traps) and represented by enough pollen grains (minimum of nine grains in smallest count of 300) to decrease the chance that they were anomalous or from far outside the bounds of the plots.

Non-metric multidimensional scaling (NMDS) using the Bray–Curtis distance metric was used to ordinate the data. Wisconsin double-standardisation, which standardises taxon counts to their taxon maxima and sample counts to their sample size, was used to minimise the effect of rare and very abundant taxa, and to reduce the effect of sample size. Singletons (taxa that only occur in one sample and as such provide no useful grouping information) were removed. NMDS is considered an appropriate ordination technique for count data as it is non-parametric (Oksanen et al. 2015) and has previously been used to analyse fossil and modern pollen assemblages (Jardine & Harrington 2008; Schüler et al. 2014). The Shannon index was used to calculate diversity, as this metric has been shown to give equal weight to rare and abundant taxa (Morris et al. 2014). All statistical analyses were conducted using R statistical software (R Core Team 2016) with R Studio (RStudio 2012) and with the package Vegan (Oksanen et al. 2015). Code for all analyses run in this section may be found in the Supplemental data.

4. Results

4.1. Modern pollen rain

Of the 30 traps deployed in Kogyae, 30 were recovered and every other trap (i.e. odd numbers) was processed and counted, to give five traps from each plot and an even coverage of the plot. Two taxa from Kogyae had mean abundances of $>$ 10.0%: Poaceae (minimum 17.0%, maximum 60.9%, mean 28.8%) and Melastomataceae/Combretaceae (minimum 1.0%, maximum 72.7%, mean 18.8%), and four taxa were present in all traps: *Celtis*, *Alchornea*, Poaceae and Melastomataceae/Combretaceae (Figure 5). In total, 121 pollen taxa were defined in Kogyae, of which 37 were assigned botanical affinities.

4.1.1. Forest

The Forest traps displayed broadly similar pollen assemblages, with Poaceae accounting for 19.0–25.0% of grains, and with a consistent presence of *Alchornea* (7.4–12.6%) and *Erythrophleum* (1.0–38.0%). Melastomataceae/Combretaceae was present in all traps, but varied in abundance from 3.6 to 23.0%. *Celtis*, although present in all of the traps, varied from 0.5 to 4.0% of the assemblage. Both Asteraceae types (Asteraceae 1 and Asteraceae 2) were present in four out of the five Forest traps, albeit in low abundances (1.8–5.8%). *Milicia* was present in three of the traps, from 0.3 to 7.0%. Nine taxa were identified in both the pollen and vegetation assemblages; these were *Afzelia africana* (R-rel = 0.02), *Bombax* (R-rel = 0.02), *Celtis* (R-rel = 1.44), *Erythrophleum suaveolens,* (R-rel = 3.64), *Ficus* (R-rel = 0.24), *Lannea* (R-rel = 0.05), *Manilkara obovata* (R-rel = 0.61), Melastomataceae/Combretaceae (R-rel = 6.37) and *Milicia* (R-rel = 0.89) (Table 1; Figures 6 and 7). Within the Forest plot, 37 vegetation and 86 pollen taxa were identified, with nine taxa identified in both. The influx rates in this plot varied between 85 grains/cm^2/month and 258 grains/cm^2/month, with an average of 154 grains/cm^2/month, and the diversity of the samples ranged from 2.0 to 2.9, with a mean of 2.5 (Figure 8).

4.1.2. Transition

Poaceae pollen was present in all the Transition traps, accounting for at least 19.0% and at most 60.0% of the pollen sum. *Alchornea* was present in abundances of 2.0–7.0%. *Erythrophleum* was present in three traps, in abundances of $<$ 5%. The Melastomataceae/Combretaceae signal ranged from 0.9 to 31.5% among the five traps. The two Asteraceae types accounted for up to 5.0% each of the pollen sum, but with

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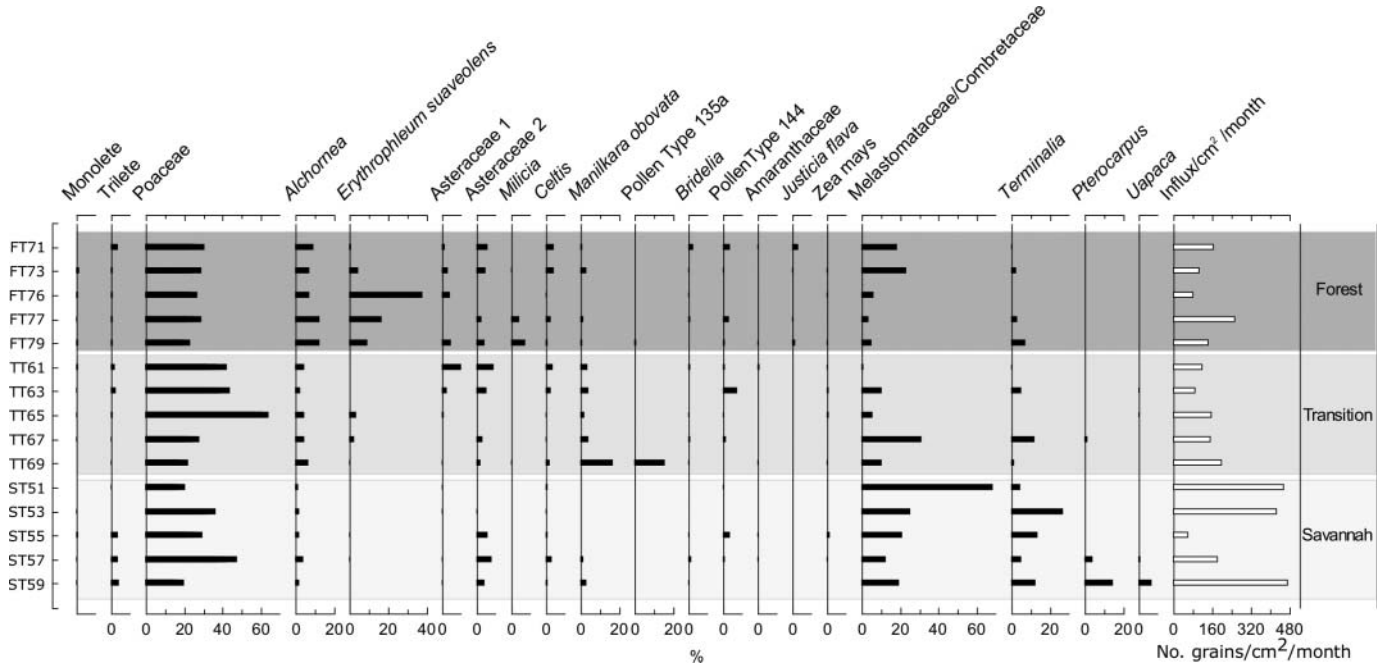


Figure 5. Pollen diagram showing pollen assemblages from each plot, along with total influx values for each trap. Forest traps begin 'FT', Transition traps 'TT' and Savannah traps 'ST'.

variable percentage abundances (1.2–10.0%), and with neither being present in all five traps. *Manilkara obovata* accounted for between 2.3 and 4.5% of the pollen sum in four traps, but 16.9% in the fifth. 'Pollen type 135a' was only present in Trap 69, at 15.5%. Seven taxa that were present in both the vegetation and pollen assemblages were *Afzelia africana* (R-rel = 0.06), *Ceiba* (R-rel = 0.08), *Erythrophleum suaveolens* (R-rel = 0.39), *Lannea* (R-rel = 0.05), *Manilkara obovata* (R-rel = 0.80), Melastomataceae/Combretaceae (R-rel = 5.18), *Moraceae* (R-rel = 0.15) and *Terminalia* (R-rel = 0.34) (Table 2; Figures 6 and 7). Within the Transition plot, 34 vegetation and 71 pollen taxa were identified, with eight taxa identified in both. Influx rates in this plot varied from 92 to 204 grains/cm^2/month, with an average of 146 grains/cm^2/month, and diversity of the traps ranged from 1.8 to 2.5, with an average of 2.3 (Figure 8).

4.1.3. Savannah

The traps exhibited largely similar pollen assemblages, with Poaceae and Melastomataceae/Combretaceae contributing more grains than any other taxa. Poaceae percentages were between 17.0 and 42.4%, and Melastomataceae/Combretaceae grains contributed 12.5–68.1%. *Alchornea* was present in all traps, but at $<$ 3.0% in four. Asteraceae 2 was present in three

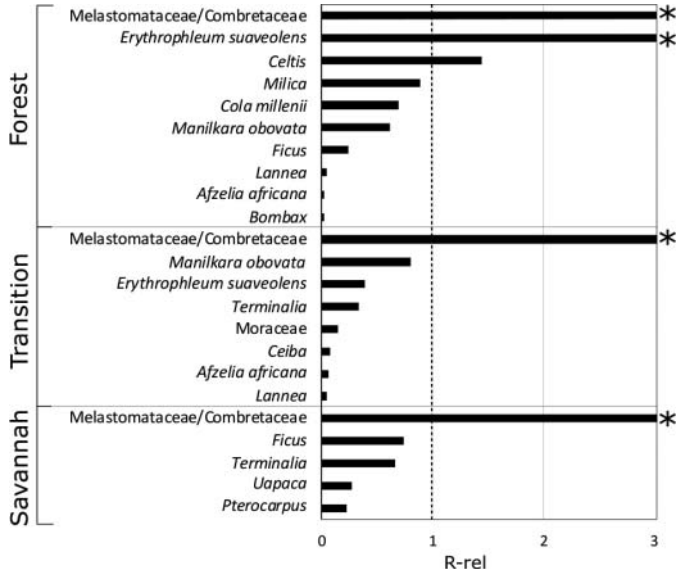


Figure 6. Bar chart showing R-rel values of taxa represented in both pollen and vegetation, where p = average % abundance of a taxon and v = total basal area of taxon in the vegetation. Asterisks indicate that the R-rel values were too high to show on the figure; Forest Melastomataceae/Combretaceae R-rel = 6.37 and *Erythrophleum suaveolens* R-rel = 3.64. Transition Melastomataceae/Combretaceae R-rel = 5.18, and Savannah Melastomataceae/Combretaceae R-rel = 3.53.

Table 1. Taxa that occur in both pollen assemblages and vegetation survey for the Forest plot, their abundances in the data set and their R-rel values (average pollen abundance in samples/% basal area of plot covered by vegetation taxon).

Taxon	No. stems ≥ 10 cm DBH	Stems in vegetation (%)	Basal area (% of plot area)	Average pollen abundance (%)	R-rel (average pollen abundance/basal area)
Afzelia africana	7	3.6	5.84	0.12	0.02
Bombax	4	2.0	2.56	0.05	0.02
Celtis	5	2.7	1.58	2.28	1.44
Erythrophleum suaveolens	9	4.8	4.42	16.10	3.64
Ficus	2	1.0	0.46	0.11	0.24
Lannea	5	2.7	2.19	0.10	0.05
Manilkara obovata	3	1.5	2.04	1.25	0.61
Melastomataceae/Combretaceae	2	1.1	1.67	10.64	6.37
Milica	2	1.0	2.62	2.33	0.89

DBH, diameter at breast height.

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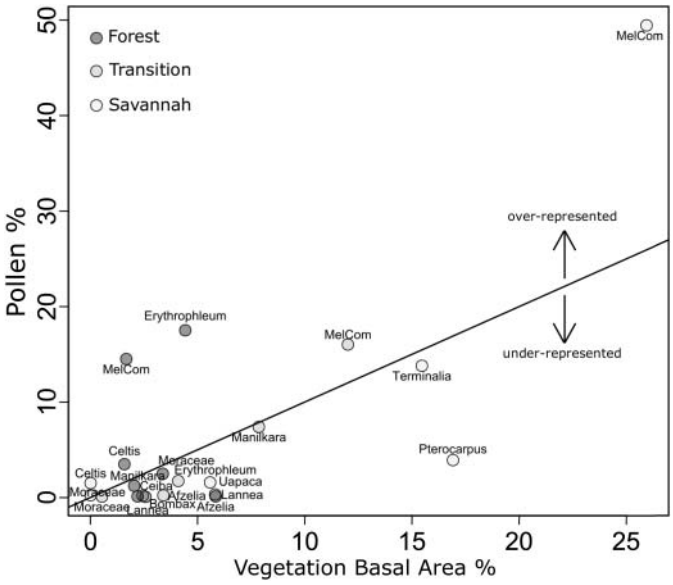


Figure 7. Scatter plot of vegetation basal area % against pollen abundance %. Taxon names are as in the text, except Melastomataceae/Combretaceae, which is abbreviated to 'MelCom'. The R-rel = 1 line is added to illustrate those taxa that are over-represented in the pollen compared to the vegetation (above the line), against those which are under-represented (below the line).

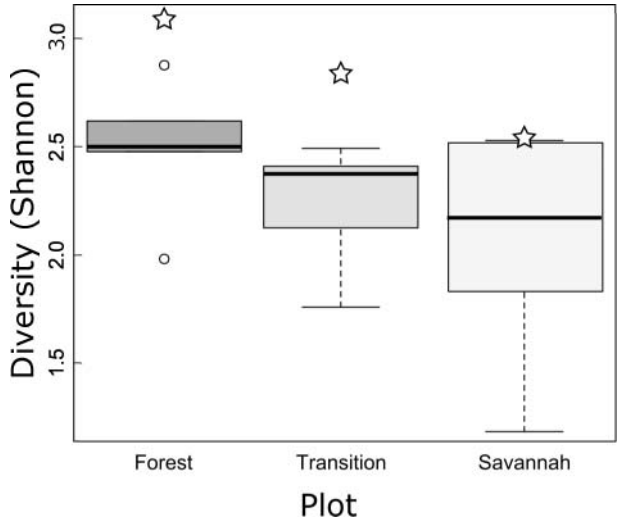


Figure 8. Diversity of the pollen assemblages (box and whisker plots) and the vegetation diversity of the plots (star symbols). Boxes show 25th and 75th percentiles of data; bars near the middle of the boxes show the median value; and ends of whiskers show the extremes of the data, as long as those are not more than 1.5 inter-quartile ranges from the 25th and 75th percentiles. For 'Forest' the diversity data are not very variable, leading to its whiskers being short, and its outlying values not being joined by a whisker.

traps at percentages of > 3.0%, but not in the other two. *Celtis* was present in four out of the five traps, but at abundances of < 3.0%. *Pterocarpus* pollen was found at 4.3 and 14.9% in two traps. *Uapaca* was present in the same two traps (57 and 59) as *Pterocarpus*, at 0.9 and 6.5%, respectively. *Terminalia* was present in all of the Savannah traps, from 4.6 to 27.1%. Five taxa were present in both the vegetation and pollen assemblages: *Ficus* (R-rel = 0.74), Melastomataceae/Combretaceae (R-rel = 3.53), *Pterocarpus* (R-rel = 0.22), *Terminalia* (R-rel = 0.66) and *Uapaca* (R-rel = 0.27) (Table 3; Figures 6 and 7). Within the Savannah plot, 26 vegetation and 67 pollen taxa were identified, with five taxa identified in both. Influx rates for Savannah traps varied from 61 to 478 grains/cm^2/month (Trap 55 had an unusually low influx rate compared to the other traps) with an average of 322 grains/cm^2/month, and the diversity of the traps ranged from 1.2 to 2.6, with an average of 2.1 (Figure 8).

4.2. Multivariate analysis

The NMDS plot (Figure 9) shows the distribution of the samples (each indicated by black, capital letters, e.g. 'FT71' = Forest, Trap 71) in ordination space. The Forest and Savannah samples form two distinct groups in ordination space, separated on NMDS 2. The Transition samples cluster on NMDS 1, but are distributed widely over NMDS 2, and overlap with the ordination space occupied by Savannah samples. Abundant pollen taxa from the plots fall out with their parent vegetation types, such as *Erythrophleum suaveolens* with the Forest traps, *Manilkara*

Table 2. Taxa that occur in both pollen assemblages and vegetation survey for the Transition plot, their abundances in the data set and their R-rel values (average pollen abundance in samples/% basal area of plot covered by vegetation taxon).

Taxon	No. stems ≥ 10 cm DBH	Stems in vegetation (%)	Basal area (% of plot area)	Average pollen abundance (%)	R-rel (average pollen abundance/basal area)
Afzelia africana	3	1.3	3.39	0.20	0.06
Ceiba	2	0.9	2.34	0.18	0.08
Erythrophleum suavolens	6	2.6	4.09	1.60	0.39
Lannea	10	4.3	5.81	0.28	0.05
Manilkara obovata	14	6.0	7.85	6.31	0.80
Melastomataceae/Combretaceae	4	1.7	2.25	11.65	5.18
Moraceae	2	0.9	0.53	0.08	0.15
Terminalia	24	10.2	9.70	3.28	0.34

DBH, diameter at breast height.

Table 3. Taxa that occur in both pollen assemblages and vegetation survey for the Savannah plot, their abundances in the data set and their R-rel values (average pollen abundance in samples/% basal area of plot covered by vegetation taxon).

Taxon	No. stems ≥ 10 cm DBH	Stems in vegetation (%)	Basal area (% of plot area)	Average pollen abundance (%)	R-rel (average pollen abundance/ basal area)
Ficus	1	0.5	0.23	0.17	0.74
Melastomataceae/Combretaceae	11	6.0	10.40	36.70	3.53
Pterocarpus	24	13.0	16.70	3.74	0.22
Terminalia	23	12.5	14.80	9.80	0.66
Uapaca	15	7.8	5.44	1.49	0.27

DBH, diameter at breast height.

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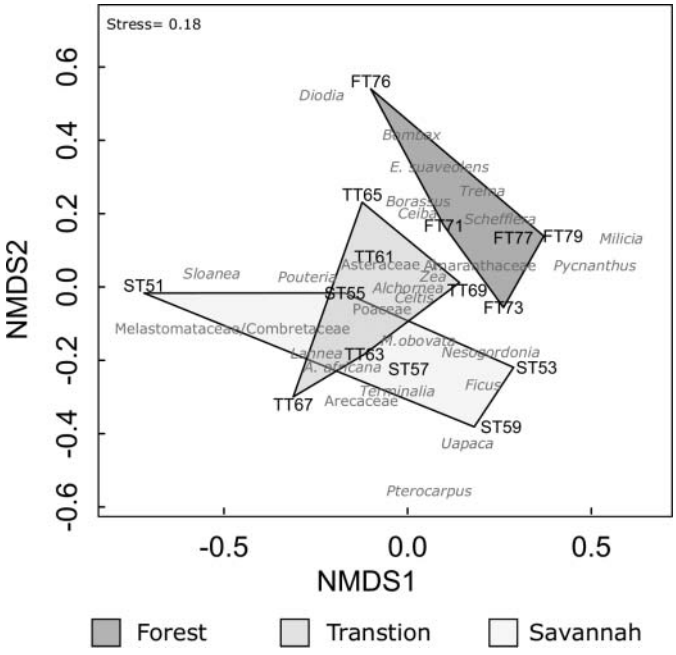


Figure 9. Non-metric multidimensional scaling (NMDS) plot of pollen trap assemblages. Forest traps begin 'FT', Transition traps 'TT' and Savannah Traps 'ST'. Polygons encompass all traps of each plot. Named taxa are included in grey. Unidentified pollen taxa were used in the analysis but are not shown in the figure.

obovata with the Transition traps and *Uapaca* with the Savannah traps. Poaceae is positioned roughly centrally to the distribution of all of the samples.

5. Discussion

The data presented here suggest that it is possible to differentiate between vegetation types within a forest–savannah transition zone using their pollen assemblages. Here, characteristic pollen taxa from each plot are defined, along with more minor elements of the pollen rain which do not meet the definition of 'characteristic' but still merit discussion based on their low abundance in a high number of traps, or high abundance in a small number of traps. Plate 1 shows characteristic pollen taxa from the plots. Pollen–vegetation relationships are then discussed, the three plots are compared and the implications of these data for interpreting the fossil pollen record are considered, particularly with reference to the fossil pollen record of Lake Bosumtwi, Ghana (Miller & Gosling 2014; Miller et al. 2016).

5.1. Characterisation of vegetation plots by their modern pollen rain

5.1.1. Forest

The Forest traps are relatively homogeneous in terms of pollen assemblage, influx values and diversity (Figures 5 and 8). The characteristic pollen taxa in the Forest plot were Poaceae, *Alchornea*, *Erythrophleum suaveolens* and Melastomataceae/Combretaceae (Figure 5). Of these characteristic taxa, *Erythrophleum suaveolens* (1.0–38.0% of the pollen sum) and Melastomataceae/Combretaceae (3.6–23.2% of the pollen sum) exhibited the most variation between traps. The other characteristic taxa had less variable signals, with Poaceae accounting for between 19.1 and 26.0% and *Alchornea* between 7.4 and 12.6% of the pollen sum.

Only one of the taxa that accounts for more than 3% of stems in the vegetation inventory was identified in the pollen signal as characteristic: *Erythrophleum suaveolens*. *Erythrophleum suaveolens* is widespread across tropical Africa (Hawthorne & Jongkind 2006), but is predominantly a tree of dry semi-deciduous Guineo–Congolian forest (Gorel et al. 2015), and as such provides a useful indicator of the Forest plot in this study. It is also strongly over-represented in this plot, with a R-rel ratio of 3.64.

Melastomataceae/Combretaceae was a characteristic pollen taxon (up to 38.0% of the pollen sum). It did not, however, account for a large component of the vegetation inventory, comprising just 1.6% of the basal area of the plot. Consequently, the R-rel value for this group was 6.37. This large R-rel value could be due to the over-production of pollen by Combretaceae, in which andromonoecious inflorescences are known to occur (Watson & Dallwitz 1992). There are no woody Melastomataceae recorded in the Forest plot, but there may be understory plants which contribute to the pollen signal. Any herbaceous Melastomataceae would likely, however, contribute only a small amount of pollen, as many Melastomataceae are buzz-pollinated, meaning that their pollen is not freely released into the air (Jones & Little 1983).

Together, the Asteraceae pollen types are characteristic of the Forest plot, although Asteraceae is absent from the vegetation survey. The absence of Asteraceae in the vegetation survey is likely due to it being represented by herbaceous taxa which were not recorded in the inventory, potentially including the invasive Asteraceae *Chromolaena odorata* (L.) King and Robinson which has been reported widely in Ghana and in the Kogyae Strict Nature Reserve (Castel 2012).

One of the characteristic pollen taxa of the Forest plot is *Alchornea*, which occurs in all traps at percentages of up to 12.6%. This taxon is not, however, present in the vegetation survey for the plot. This could be due to one of several factors: (i) that *Alchornea* is genuinely not present in the vegetation plot, but is present in the surrounding vegetation; (ii) that the pollen grain identified as *Alchornea* is a misidentification and originates from a different plant; or (iii) that the *Alchornea* plants contributing to the signal possess stems that are too small to be included in the vegetation surveys, which only record plants of $>$ 10 cm DBH. It is likely that the latter is true of *Alchornea cordifolia* (Schumach. & Thonn.) Müll.Arg, which is a commonly recorded species in Guineo–Congolian Transition woodland and exhibits a scandent habit, making it likely that it could have been excluded from surveys and therefore account for the apparently orphan *Alchornea* pollen.

Taxa that occurred at $>$ 3% but in less than four traps included *Milicia* and *Celtis*. *Milicia* accounted for $>$ 3% of the pollen sum in two traps, although it was present in three, and *Celtis* only occurred at $>$ 3% in two traps, although was present in four. The low abundances of *Milicia* and *Celtis* mirror their abundance in the vegetation, which is surprising, as both the Moraceae (the family to which *Milicia* belongs) and *Celtis* have previously been found to be over-represented in pollen rain (Gosling et al. 2005; Bush et al. 2011). Possible reasons for their relatively low representation compared to similar studies could

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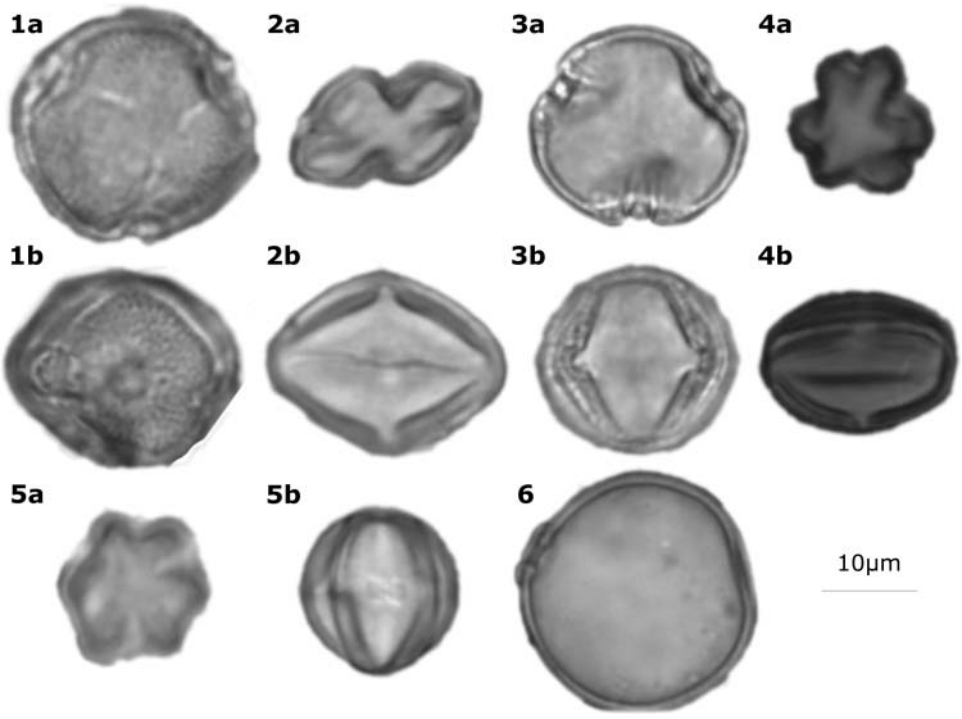


Plate 1. Characteristic taxa from all plots. 1 = *Erythrophleum suaveolens*, 2 = *Manilkara obovata*, 3 = *Alchornea*, 4 = Melastomataceae/Combretaceae, 5 = *Terminalia* sp., 6 = Poaceae sp. Letters 'a' and 'b' denote polar and equatorial views of the same grain.

relate to over-production by Melastomataceae/Combretaceae and Poaceae swamping the traps. It is also possible that due to only 1 year of data being available, the climatic conditions may not have favoured flowering that year, or a biological factor such as a fungal infection or pest could have prevented the *Celtis* individuals from producing as much pollen as usual.

There were 27 vegetation taxa whose pollen was not identified in the pollen assemblages, including all but two of the most abundant species recorded in the vegetation surveys (*Erythrophleum suaveolens* and *Afzelia africana*). This abundance of palynologically silent taxa could be due to their entomophilous pollination syndromes (Supplemental data), climatic conditions not favouring flowering in the year 2013–2014, or the individuals of those taxa being located in the plot in such a way as to make pollen deposition unlikely. Although the main over-producing taxa such as Poaceae and Melastomataceae/Combretaceae may have 'messy' or anemophilous pollination syndromes, there does not seem to be a clear link between taxa that are entomophilous or zoophilous and absent from the pollen assemblages in this system, despite this having been shown to be the case in other studies of modern pollen rain (Bush & Rivera 2001; Gosling et al. 2005).

5.1.2. Transition

Characteristic taxa for the Transition plot were Poaceae, *Alchornea*, Melastomataceae/Combretaceae and *Manilkara obovata*. The percentage abundances of Poaceae (19.1–61.1%), Melastomataceae/Combretaceae (1.0–31.5%) and *Manilkara obovata* (2.3–16.9%) vary considerably between traps. *Alchornea* (2.7–6.8%) does not exhibit such variability.

Melastomatacee/Combretaceae were over-represented (R-rel = 5.18), likely due to over-production by Combretaceae. All other taxa identified in both pollen and vegetation in this plot, besides Poaceae, were under-represented. *Manilkara obovata* exhibits the closest ratio to 1:1 in this plot, at 0.8 (Figure 6). Although *Manilkara obovata* is primarily a forest species (White et al. 1983), it is characteristic of this particular plot's pollen assemblage. It has entomophilous, hermaphroditic flowers whose anthers protrude from the perianth, potentially allowing pollen to be released more freely than from a closed flower and resulting in a higher R-rel value of this taxon than might be expected for an entomophilous taxon.

Four taxa are present at percentages of $>$ 10% in only one trap. These are Asteraceae types 1 and 2, Type 135a and *Terminalia*. *Terminalia* accounts for 10.2% of the stems in this plot, but does not contribute a characteristic level of pollen to the assemblages, instead being under-represented (R-rel = 0.34).

The Moraceae in the Transition plot were under-represented (R-rel = 0.15), as were *Ceiba* (R-rel = 0.08), *Afzelia africana* (R-rel = 0.06) and *Lannea* (R-rel = 0.05). Of these, the Moraceae, *Ceiba* and *Afzelia africana* were all only represented by a small number of individuals (two, two and three individuals, respectively), meaning that pollen production may have been genuinely low for these taxa. *Lannea* is represented by 10 individuals, however, and has the lowest R-rel ratio (0.05), indicating that it is the most under-represented. These taxa are all monoecious or hermaphroditic, and insect pollinated, leading to no clear explanation of why they might be under-represented to different extents.

Alchornea and *Celtis* were present in the pollen (2.5–6.7% and 0.7–3.8% of the pollen sum, respectively) but not in the vegetation. As *Celtis* pollen was present in all three plots, but only in one of the vegetation surveys (Forest), this could be the result of transport of pollen from outside the plot.

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5.1.3. Savannah

The characteristic pollen taxa of the Savannah plot were Poaceae (14.1–42.4%), Melastomataceae/Combretaceae (12.5–68.1%), *Terminalia* (4.6–27.1%) and *Alchornea* (1.8–4.4%). *Celtis* (0.6–2.9%) was present in at least four out of five of the traps, but did not account for more than 3% of the pollen sum in any trap. Taxa that accounted for > 3% in at least one trap but were not present in at least four included *Pterocarpus* (0.0–14.9%) and *Uapaca* (0.0–6.6%).

The pollen assemblage in the Savannah plot exhibited an over-representation of Melastomataceae/Combretaceae (R-rel = 3.53). Under-represented taxa were *Pterocarpus* (R-rel = 0.22), *Terminalia* (R-rel = 0.66) and *Uapaca* (R-rel = 0.27). *Pterocarpus*, although not a characteristic pollen type of the Savannah pollen assemblage, is a genus of the Sudanian woodland (Novinyo et al. 2014). *Uapaca* is also a genus of wooded Savannah ecosystems, but is dioecious, and the genders of the trees in the Savannah plot are unknown, meaning that this could be a reason for its under-representation despite its abundance in the vegetation.

One trap (Trap 55) was found to have a low pollen accumulation rate (62 grains/cm^2/month) in comparison to the other Savannah plot traps, which exhibited concentrations of between 187 and 475 grains/cm^2/month. Despite its low pollen accumulation rate, Trap 55 did not contain an anomalous pollen assemblage, with similar percentages of abundant taxa to the other traps, and a high diversity. It is possible that it was covered by a leaf or other debris for part of the year, leading to less pollen accumulating in this trap than the other traps. We decided, however, to include Trap 55 in the analysis despite its anomalously low pollen accumulation rate, as we consider that it represents the pollen assemblage in a similar way to its sister traps.

The Savannah plot contains low levels of *Alchornea* (1.7–4.4%), despite none being present in the vegetation survey of the site. *Celtis* was present in the pollen assemblages at low abundance (present in one trap at 2.9%) but was not recorded in the vegetation, and therefore possibly represents transport from outside the plot.

5.2. Differentiation of vegetation plots within a forest–Savannah mosaic

Despite their close geographical proximity within the forest–Savannah mosaic, the plots give rise to different palynological assemblages, in both the relative abundances of common taxa and the presence or absence of rarer taxa. The pollen assemblages differ in abundance of dominant, over-producing taxa, such as Poaceae and Melastomataceae/Combretaceae, but there are also differences in the less abundant components of the assemblages such as *Erythrophleum suaveolens* in the Forest plot, *Manilkara obovata* in the Transition, and *Pterocarpus* in the Savannah plot. The differences in pollen assemblage composition reflect the unique vegetation assemblage in each plot. The R-rel values for taxa are often not consistent across plots; although Melastomataceae/Combretaceae is consistently over-represented in the pollen sum, the degree of over-representation varies widely (Figures 6 and 7).

Erythrophleum suaveolens, whilst over-represented in the Forest plot (R-rel = 3.64), is under-represented in the Transition plot (R-rel = 0.39). As there are relatively few individuals in each plot (nine in the Forest and six in the Transition), this discrepancy in representation may be due to factors such as tree location in the plot, wind direction, tree height or openness. Although there are fewer individuals of *Erythrophleum suaveolens* in the Transition plot, they account for a similar total percentage of the basal area as in the Forest plot, indicating that the Transition plot individuals may be larger – a factor which does not appear to have influenced their representation in the pollen rain.

Terminalia is under-represented in both the Transition and Savannah pollen assemblages, but has a lower R-rel value in the Transition plot (R-rel = 0.34) than in the Savannah plot (R-rel = 0.66). This is despite it being more vegetatively abundant in the Transition plot than it is in the Savannah plot (24 stems in Transition, 23 in Savannah). *Terminalia* does account for a greater percentage of total stems and has a larger basal area percentage coverage in the Savannah plot than in the Transition plot, however, suggesting that *Terminalia* trees in the Savannah plot may be larger than those of the Transition plot.

Alchornea is 'characteristic' of all plots in this study, as it is present in the majority of traps and occurs at above 3% in at least one trap in each plot. *Alchornea* is, however, a wind-pollinated taxon that is widely distributed across tropical Africa (Watrin et al. 2007). Anemophily, and its prevalence in all plots, means it is not a useful taxon when distinguishing between vegetation types within a Forest–Savannah transitional mosaic.

Poaceae, one of the most abundant taxa in all three plots, does not display an increase in percentage abundance from Forest to Savannah (Figure 5). Its influx values, however, increase along the gradient with the Forest having an average of 36 grains/cm^2/month, the Transition traps 51 grains/cm^2/month and the Savannah traps 79 grains/cm^2/month. Melastomataceae/Combretaceae pollen shows an increase in percentage abundance along the Forest–Transition–Savannah gradient, but also displays very high influx values in the Savannah plot (an average of 54 grains/cm^2/month) compared to the other two plots (an average of 8 grains/cm^2/month in the Forest plot, and 9 grains/cm^2/month in the Transition). This very high Melastomataceae/Combretaceae influx effectively masks the Poaceae signal in the Savannah plot and accounts for its similarity to the Transition and Forest plots in the percentage data. The absence of a clear differentiating signal from Poaceae percentage abundance in this study is illustrated both by its lack of clear increase from Forest to Savannah (Figure 5), and by its position in the ordination roughly centrally to all three plots (Figure 9). The absence of variation in the Poaceae signal differs from the findings of Vincens (Vincens et al. 2000) and Ybert (Ybert 1975), who both observed a strong increase in the percentage abundance of Poaceae pollen along the Forest–Savannah gradient in Cameroon and Côte d'Ivoire, respectively. The discrepancy between this study and previous studies could be due to the swamping of pollen counts in previous studies by arboreal taxa such as *Celtis*, and a lack of Melastomataceae/Combretaceae-type pollen. The studies by Vincens (2000) and Ybert (1975) encompass wider vegetational gradients than the plots used in this study, with samples

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encompassing swamp wet Forest types. Vincens (2000) used soil samples, meaning that their results may be representative of a longer time period than ours. The clear increase in the absolute abundance of Poaceae pollen from Forest to Savannah observed in this study may, however, indicate that concentration data might be able to provide a more accurate representation of grass-dominated pollen assemblages than percentage data alone (Supplemental data).

In this dataset there are 67 pollen taxa whose abundance is low enough (< 3% in any trap) that it would not be informative or practical to include them in a pollen diagram, but whose presence may nevertheless contribute to the separation of the plots palynologically. The differences between the pollen assemblages of the plots are highlighted by the fact that the Forest and Savannah samples form two clearly separate groups in ordination space, with Transition traps overlapping with the Savannah (Figure 9). There were, however, a variety of pollen taxa which contributed to the spread of the data but which are not recorded in the vegetation plots, including *Borassus*, *Schefflera*, *Sloanea*, *Diodia*, *Trema*, *Nesogordonia* and *Pycnanthus*, as well as multiple distinctive pollen morphotypes. These taxa may represent extra-plot pollen, or may have been present in the plot but not recorded due to being too small (< 10 cm DBH).

5.3. Pollen and vegetation diversity

In comparison to the diversity of the vegetation plots, the pollen assemblage diversity indices were lower: Forest pollen 2.7 against vegetation 3.1, Transition pollen 2.4 against vegetation 2.8, and Savannah pollen 2.2 against vegetation 2.6. The diversity data show a trend of increasing pollen diversity with increasing vegetation diversity (Figure 8), with the Forest traps showing less variation than the Transition traps, which in turn showed less than the Savannah traps. The large variability in the diversity of the Savannah plot pollen traps could have been due to a more open canopy, allowing for more extra-plot components to feature in the pollen rain. Statistical tests of this relationship were not attempted due to the small number of vegetation diversity measures (three) available. The positive relationship between vegetation and pollen diversity has been demonstrated in modern pollen traps (Jantz et al. 2014), and in lake sediments (dependent on the situation of the lake in question) (Felde et al. 2016), although there are difficulties involved with using these data to interpret fossil pollen assemblages due to features of depositional environments that may affect the relationship between pollen and parent vegetation in the fossil record (Odgaard 1999).

5.4. Implications for the Lake Bosumtwi fossil pollen record

In Lake Bosumtwi, shifts from Forested to grassland ecosystems have been inferred from high levels (> 55% abundance) of Poaceae in fossil samples (Miller & Gosling 2014; Miller et al. 2016). If this criterion were applied to the data presented here, just one of the traps would be considered grassland (Transition trap 65).

The palynological over-production of Poaceae likely accounts for the very high percentages of pollen observed during 'Savannah' periods of the Bosumtwi record, as opposed to these representing an ecosystem that is more grass dominated and open than the Savannah plot of this study. If these periods were representative of a more grass dominated landscape, it might be expected that Sahelian elements would be observed within these, which is not the case (Miller & Gosling 2014). Determining which grass taxa contribute to the signal of sections of the Bosumtwi record that are very high in Poaceae may help to improve the interpretation of the parent vegetation; although Poaceae pollen is very difficult to identify to below the family level using light microscopy, techniques are now being developed which may allow this analysis to be undertaken (Mander et al. 2013; Julier et al. 2016).

Even with the strong bias towards anemophilous taxa displayed in the fossil record, the Forest stages identified in the Lake Bosumtwi record have higher Moraceae abundances than the traps in this study, indicating that the inference of some form of wooded environment is well justified. However, in the Forest zones of the Lake Bosumtwi record, taxa used to indicate a moist, broadleaf Forest vegetation type include *Uapaca*, *Alchornea* and *Celtis*. *Uapaca*, in the samples analysed here, is only present in the Savannah plot (although it is not a characteristic taxon of this plot). *Alchornea* and *Celtis* are present in the pollen rain of the majority of trap samples from all three plots, at similar abundances to those observed in the Bosumtwi record. Melastomataceae/Combretaceae, along with Poaceae percentages of up to 40%, are used to indicate a moist, rainForest environment in the Bosumtwi record, but here are indicative of the Savannah plot. It is possible, therefore, that the ecosystems characterised in the Bosumtwi record as 'moist broadleaf Forest' may represent drier vegetation types (the inferred rainfall of the Bosumtwi Forest zones was 1000–3300 mm/year, whereas the rainfall at Kogyae and within the transitional zone in general is 900–1200 mm/year) (Miller & Gosling 2014). The Forest zone may include the transitional mosaic explored here, an observation that could have implications for the reconstruction of past climate change.

Data obtained from an artificial pollen trap (diameter 140 mm) and a lake such as Lake Bosumtwi (radius 4 km) will vary considerably, with the former likely capturing a very local signal (within tens of metres of the trap), but the latter a heavily regional signal (likely 90% or more of regional pollen) (Jacobson & Bradshaw 1981; Sugita 1994). The individual source areas for the traps in this study are likely to have varied, depending on the structure of the vegetation immediately surrounding them. Traps can, therefore, be considered to capture a 'snapshot' of the pollen produced by a specific vegetation type, as opposed to the regional, time-averaged signal captured by large lakes (Kidwell & Flessa 1995). The spatial and temporal differences in the pollen signal obtained from traps and lakes should be taken into consideration when interpreting fossil records.

The observation that the Poaceae percentages in this study differ from those of the fossil record is not, alone, an indication that the interpretation of the fossil record needs to be re-examined. Poaceae is wind dispersed, highly productive, and therefore more likely to appear in high percentages in the sediment record as opposed to traps under the canopy, in relation to other entomophilous or zoophilous taxa. When treated alone,

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Poaceae is an unreliable indictor taxon (Bush 2002). It is therefore sensible to use other taxa along with Poaceae to distinguish between vegetation types; the taxa outlined here may help to provide better constraints on the interpretation of transitional zones within pollen records.

6. Conclusions

This work has demonstrated that by using modern pollen traps deployed within vegetation plots, differences can be identified between the pollen assemblages produced by three vegetation types within a Forest–Savannah transitional mosaic landscape. Although there is not a straightforward relationship between pollen and vegetation assemblages, certain taxa can be used to indicate the different vegetation types, such as *Erythrophleum suaveolens* for the Forest, *Manilkara obovata* for the Transition, and *Pterocarpus* and *Uapaca* for the Savannah vegetation types. These taxa, and many other rarer taxa, contribute to the plots, producing pollen assemblages that can be separated using multivariate methods, and to the biodiversity of the pollen assemblages reflecting that of the vegetation. The plots also differ in their percentage and influx values of Poaceae, with the influx of Poaceae better reflecting the gradient of Forest to Savannah than percentage data, a finding that has implications for the interpretation of the fossil record. Based on the insights gained from the modern pollen data, a re-examination of the fossil pollen record from Lake Bosumtwi may benefit from a lower threshold of Poaceae pollen to categorise an assemblage as being from a Savannah or transitional ecosystem. Depending on other taxa present, this threshold could be as low as 40%. Future high-resolution sampling of the Lake Bosumtwi record, from periods of Transition between Forest and Savannah, may benefit from the results outlined in this study, thereby improving knowledge of how vegetation responds to climate fluctuations in the past and helping to shape predictions of how ecosystems might respond to climate change in the future.

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No potential conflict of interest was reported by the authors.

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