| 1 | The modern pollen-vegetation relationships of a tropical forest-savannah mosaic |
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| 2 | landscape, Ghana, West Africa. |
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The modern pollen-vegetation relationships of a tropical forest-savannah mosaic landscape, Ghana, West Africa

20 1 Abstract

21 Transitions between forest and savannah vegetation types in fossil pollen records are often 22 poorly understood due to over-production by taxa such as Poaceae and a lack of modern 23 pollen-vegetation studies. Here, modern pollen assemblages from within a forest-savannah 24 transition in West Africa are presented and compared, their characteristic taxa discussed, and 25 implications for the fossil record considered. Fifteen artificial pollen traps were deployed for 26 1 year, to collect pollen rain from three vegetation plots within the forest-savannah transition 27 in Ghana. High percentages of Poaceae and Melastomataceae/Combretaceae were recorded in 28 all three plots. Erythrophleum suaveolens characterised the forest plot, Manilkara obovata 29 the transition plot and *Terminalia* the savannah plot. The results indicate that Poaceae pollen 30 influx rates provide the best representation of the forest-savannah gradient, and that a 31 Poaceae abundance of > 40 % should be considered as indicative of savannah-type vegetation 32 in the fossil record.

33 Keywords: Pollen; Transitions; Poaceae; Savannah; Ghana; Palaeoecology; Bosumtwi

34 2 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 41 ecosystems are today recognised as having conservation value in their own right, due to their
42 ability to provide habitats for organisms from different ecosystems, and the potential for them
43 to be especially sensitive to climate change (JNCC 2010; Ibie et al. 2016; Joyce et al. 2016).
44 The identification of transitional ecosystems in the fossil record may be crucial in providing
45 evidence to support efforts to conserve biodiversity, especially if the persistence of these
46 transitional areas can be demonstrated over long time scales.

Projections of future environmental change suggest that modern forest-savannah 47 48 boundaries will alter, and transitional zones shift (Niang et al. 2014), but little is known about 49 what this change will look like in terms of vegetation composition (Cramer et al. 2001). 50 Fossil pollen records of forest to savannah transitions can serve as a guide to the likely future 51 vegetation response; however, it has been difficult to observe forest to savannah transitions in 52 the fossil pollen record because of a poor understanding of how they are represented. The 53 relationship between taxa represented in the vegetation and in the pollen rain is known not to 54 be directly proportional (Davis 1963). Anemophilous taxa, and zoophilous taxa with 'messy' 55 pollination syndromes (open flowers with extruded anthers) are generally over-represented 56 relative to their abundance in the vegetation, whereas those zoophilous taxa with more closed 57 floral morphologies are more often under-represented or palynologically silent (present in vegetation but not pollen assemblages) (Bush & Rivera 2001). 58

59 To facilitate a better understanding of transitional periods in fossil pollen records, this 60 study has explored modern pollen-vegetation relationships on a landscape scale (plots within 61 10 km of one another) within the forest-savannah transition zone in tropical West Africa. 62 Data from pollen traps has been used to characterise the modern pollen rain produced by 63 three vegetation types (forest, transition, and savannah) during one year. Modern pollen data 64 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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69

2.1 Vegetation at the forest-savannah transition

70 The transition between forest and savannah ecosystems, on both spatial and temporal 71 scales, is one that has been of interest to biogeographers, ecologists and palaeoecologists for 72 decades (Beard 1953; Aubréville 1966; Ybert 1975). Although the botanical composition of 73 savannah-type ecosystems on different continents has been shown to vary widely, it can, 74 along with the height and canopy cover, be used in their classification (Torello-Raventos et 75 al. 2013). The shift from forest to savannah is controlled on a macro-scale (100s of km) by 76 climatic gradients, primarily rainfall (Swaine 1992; Lehmann et al. 2011), but on smaller 77 scales other factors such as soil type and herbivory are also important. Where mean annual 78 precipitation (MAP) is less than 650 mm, savannahs form because water availability limits 79 tree growth and, consequently, forest cover (Sankaran et al. 2005). At precipitation levels of 80 more than 650 mm MAP, savannahs can occur when other factors such as fire and herbivory 81 inhibit the growth or enhance the mortality of trees (Swaine et al. 1992; Higgins et al. 2012; 82 Dexter et al. 2015). Edaphic factors such as soil type and fertility may also influence local 83 vegetation dynamics, resulting in the formation of a mosaic of forest and savannah within 84 regions that experience a more or less uniform climate.

85 2.2 Pollen at the forest-savannah transition

86 On a large scale, pollen production by modern ecosystems in Africa has been found to
87 differ between vegetation types (Gajewski et al. 2002; Lézine et al. 2009). For example, an

88 extensive study of modern pollen-vegetation relationships in central Africa demonstrated that 89 it is possible to differentiate broad vegetation types, such as tropical forest and tropical 90 seasonal forest using the pollen signal, although difficulties were encountered in areas that 91 were considered transitional (Lebamba et al. 2009). Within the forest-savannah transition 92 zone of Cameroon, it is possible to identify different vegetation types by their modern pollen 93 rain, although the characteristic pollen and vegetation taxa are different due to sampling bias 94 towards larger woody plants in the botanical inventories, and pollen from entomophilous taxa 95 being under-represented (Vincens et al. 2000). The forest-savannah transition has also been 96 shown, in Côte d'Ivoire, to produce distinct pollen assemblages depending on the vegetation, 97 with *Hewittia malabarica* L. (Suresh) indicating the forest-edge, and savannah being 98 characterised by Poaceae pollen percentages of >40% (Ybert 1975). Studies of the Sudanian 99 and Sahelian regions have shown that it is possible to differentiate between these regions by 100 their pollen signals, and to also differentiate smaller scale vegetation types within them (e.g. 101 Isoberlinia dry forest and dry or wet Combretaceae forest) (Lézine & Edorh 1991; El Ghazali 102 & Moore 1998), although the arboreal pollen signal is often overwhelmed by very high 103 (>90%) Poaceae abundances.

104

105 2.3 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

111 several terrestrial records (Maley 1991; Elenga et al. 1994; Maley & Brenac 1998; Salzmann 112 et al. 2002) of which only one record is older than 35 ka BP(Lake Bosumtwi, Ghana). The 113 fossil pollen record obtained from Lake Bosumtwi is unique to tropical West Africa, and to 114 date covers the last c. 500,000 years of the 1Ma sediment core that was recovered (Koeberl et al. 2007; Miller & Gosling 2014; Miller et al. 2016).Pollen from off-shore and terrestrial 115 116 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 117 118 vegetation shifts observed are thought to be a consequence of the north- to south-wards 119 movement of the tropical rain belt, and the intensity of the African Monsoon (Shanahan et al. 120 2015; Miller et al. 2016). The shifts between wetter forest and drier savannah ecosystems are 121 recorded in the pollen record of Lake Bosumtwi by fluxes in the Poaceae abundance, that 122 varies from 0% to 90% of the terrestrial pollen sum; interpretations of the Lake Bosumtwi 123 fossil pollen record placed the transition between forested and savannah vegetation types at 124 55% Poaceae (Miller et al. 2016).

125

126 **3** Study region

127 3.1 Tropical West Africa

128 The vegetation of tropical West Africa has been classified into two main biomes; the 129 'Guineo-Congolian regional centre of endemism' and, further north, the 'Sudanian regional 130 centre of endemism', that are distinct because of their endemic flora. The transition between 131 the two is primarily driven by decreasing precipitation from south to north (White, 1983). 132 The Guineo-Congolian region comprises areas of wet and semi-deciduous forests, transitional rainforests, secondary grassland and mosaics, while the Sudanian region contains drierwoodland and more open savannah vegetation types (Supp. Mat.).

135 At around 8°N there is a band of vegetation known as the 'Guineo-136 Congolian/Sudanian transition zone' (White 1983), that is between 100 and 500 km wide and runs approximately West-East across the West African countries, including Ghana (Gautier & 137 138 Spichiger 2004). The transition zone comprises a patchwork of forest and savannah 139 vegetation types and can be considered as the boundary between the wet Guineo-Congolian 140 forest types of the south and the drier Sudanian savannah regions of the north. It is within this 141 transition zone that the Kogyae Strict Nature Reserve is situated, in which the plots for this 142 study are located (Figure 1).

143

144 3.2 Kogyae Strict Nature Reserve

145 In 2012, three permanent vegetation study plots (KOG02 'Forest', KOG04 146 'Transition' and KOG05 'Savannah' see 3.3.1-3 for further details) were established in the 147 Kogyae Strict Nature Reserve (Ghana) at the transition between the Guineo-Congolian and 148 Sudanian biomes, to characterise the vegetation and monitor environmental changes at the 149 ecotone (Figure 1). The Kogyae vegetation study plots were set up as part of the Global 150 Ecosystem Monitoring (GEM) network (http://gem.tropicalforests.ox.ac.uk/) and are also part 151 of the African Tropical Rainforest Observation Network (AfriTRON) (Lewis et al. 2013). 152 Vegetation data from these plots are available at http://www.forestplots.net(Lopez-Gonzalez 153 et al. 2011). The Kogyae Strict Nature Reserve contains a mosaic of ecosystems which differ 154 in their floristic composition, tree cover, canopy height and density, and understorey vegetation. The Kogyae region typically receives around 1000 mm of rain/year, and 155

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; within 10 km of one another (Figure 1).

161 The soils present in the Kogyae Strict Nature Reserve are shallow, prone to drying 162 out and overlie horizontally bedded sandstones that are part of the Voltarian Group, however, 163 depth and composition of soils differs between forested and savannah areas (Wildlife 164 Department, Accra 1994). Animals present in the reserve that may exert grazing or browsing 165 pressure include buffalo, baboons, antelopes, five species of monkey and domestic cattle 166 (Danguah & Owusu 2015).

167

168 3.3 Vegetation of study plots

169 The Forest (KOG02), Transition (KOG04), and Savannah (KOG05) vegetation study 170 plots are each one hectare and were established following the standard GEM protocols 171 (Marthews et al. 2014). As part of the GEM programme a vegetation inventory was generated 172 for each plot, and a programme of yearly measurements of all trees >10 cm Diameter at 173 Breast Height (DBH) was established measuring DBH, height, and yearly growth. Two 174 genera occur only in the Forest plot (Cola and Dacryoides) and two genera occur only in the 175 Savannah plot (*Trichilia* and *Uapaca*) (Supp. Mat.). The transition plot includes six genera 176 which occur across all three plots (Ficus, Anogeissus, Lannea, Margaritaria, Sterculia, and 177 Pterocarpus) and shares multiple genera with both the Forest and Savannah plots, but does 178 not contain any unique genera.

180 3.3.1 Forest (KOG02)

181 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) (Figure 1 and Figure 2). Thirty-seven species have been recorded in the Forest plot 182 183 with DBH >10 cm, with nine taxa occurring at >3% abundance (Supp. Mat.), the most 184 abundant, by percentage of stems, being Cola gigantea A.Chev. (12.3%), Sterculia 185 tragacantha Lindl. (10.7%) and Dacryodes klaineana (Pierre) H.J.Lam (9.6%). There are 186 also understory monocotyledonous plant taxa, e.g. Zingiberaceae, Costaceae and 187 Marantaceae, although the abundance of these taxa was not quantitatively assessed, as they 188 are herbaceous and therefore were not included in the vegetation surveys. The taxa in the 189 Forest plot fall largely into "Drier peripheral semi-evergreen rainforest" (seven taxa), or 190 "Guineo-Congolian transition woodland" (six taxa), but with some "Sudanian transitional 191 woodland" elements (five taxa), including *Ceiba pentandra* (see Supp. Mat. and Figure 3). 192 The average tree height is 20.8m. The diversity (Shannon index) of the Forest plot is 3.11.

193

194 *3.3.2 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 (Supp. Mat.), the most abundant, by percentage of stems, of which 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),

| 201 | with some "Guineo-Congolian secondary grassland and wooded grassland" taxa (eight). The |
|-----|--|
| 202 | average tree height is 12.1 m. The diversity (Shannon index) of the Transition plot is 2.82. |
| 203 | |
| 204 | 3.3.3 Savannah (KOG05) |

205 The Savannah plot is located 7°18'04.1"N, 1°09'53.8"W and 186 m asl. There are 26 206 recorded species with >10 cm DBH, of which eight occur at >3% (Supp. Mat.), the most 207 abundant of which, by percentage of stems are Bridelia ferruginea Benth.(27.7%), 208 Pterocarpus erinaceus (10.7%) and Uapaca togoensis Pax (8.1%). The vegetation types of 209 White (1983) are represented by 'Sudanian woodland' (13 taxa) and 'Guineo-Congolian 210 secondary grassland and wooded grassland' (11 taxa). The understorey consists mainly of tall 211 (>1 m in height) grasses, with other herbaceous taxa such as members of the Asteraceae. The average tree height is estimated to be between 10-12 m. The diversity (Shannon index) of the 212 213 Savannah plot is 2.56.

214

215 **4 Methods**

216 4.1 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). 221 A total of 30 traps, 10 per vegetation plot (1 ha; 100 m x 100 m) were deployed, along 222 the 40 m line (i.e. a 100 m long transect across the plot, at the point 40 m along from the 0 m 223 0 m point of the plot) (Figure 4). All traps were positioned at approximately 50 cm above 224 ground level to reduce risk of inundation and to ensure standard height of sampling across 225 this study. The traps were affixed to stakes hammered firmly into the ground or, in cases 226 where that is not possible, to trees. The distance from each trap to the closest large tree (>10 227 cm DBH) was recorded for all sites, and the tag number of these trees noted. Upon collection, 228 traps were emptied of their contents, which was placed into sealed plastic bags and stored in a 229 refrigerator.

The traps were in the field between October 2013 and October 2014, except for a short period during 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 redeployed by researchers from the Forestry Institute of Ghana (FORIG).

234

235 4.2 Laboratory Methods

236 Five traps per plot were processed and counted, to provide good statistical coverage of 237 the plot whilst avoiding unnecessary effort (Gosling et al. 2005). Samples were processed 238 following the method for cotton wool based traps from Gosling et al. (2003), in which cotton 239 wool is removed by acetolysis and filter paper removed using hydrofluoric acid. Eight 240 Lycopodium tablets per trap were added as an exotic marker to enable the calculation of 241 pollen concentrations (Stockmarr 1971); University of Lund batch number 124961, 242 containing 12542 +/- 931 spores per tablet. Samples were mounted in glycerol and counted at 243 x400 magnification using a Nikon Eclipse 50i microscope. Pollen taxa were identified using

| 244 | atlases relating to tropical West Africa (van Campo 1974; Ybert 1979; Riollet & Bonnefille |
|-----|--|
| 245 | 1980; Gosling et al. 2013) and the African Pollen Database (Vincens et al. 2007). |

247 4.3 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 300-800 grains per sample. Data were visualised in 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).

254 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 255 256 corresponding taxon in the vegetation plot; the degree of under- or over-representation is then 257 expressed as a "R-rel value" following Gosling (2009), i.e. values >1 indicate a taxon is over-258 represented in the pollen relative to the vegetation. Characteristic taxa were designated as 259 taxa that occurred in at least four out of five samples from a plot, and at ≥ 3 % abundance in 260 one sample or more. These conditions were chosen as they ensure that the taxa designated as 261 characteristic are well-represented spatially in the plot (present in at least four of five traps) 262 and represented by enough pollen grains (minimum of nine grains in smallest count of 300) 263 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 taxa
counts to their taxon maxima and sample counts to their sample size, was used to minimise

| 267 | the effect of rare and very abundant taxa, and to reduce the effect of sample size. Singletons |
|---|--|
| 268 | (taxa that only occur in one sample and as such provide no useful grouping information) were |
| 269 | removed. NMDS is considered an appropriate ordination technique for count data as it is non- |
| 270 | parametric (Oksanen et al. 2015) and has previously been used to analyse fossil and modern |
| 271 | pollen assemblages (Jardine & Harrington 2008; Schüler et al. 2014). The Shannon index was |
| 272 | used to calculate diversity, as this metric has been shown to give equal weight to rare and |
| 273 | abundant taxa (Morris et al. 2014). All statistical analyses were conducted using R statistical |
| 274 | software (R Core Team 2016) with R Studio (RStudio 2012) and with the package Vegan |
| 275 | (Oksanen et al. 2015). Code for all analyses run in this section may be found in |
| 276 | Supplementary Materials. |
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| 278 | 5 Results |
| 279 | 5.1 Modern pollen rain |
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| 200 | Of the 20 trans deployed in Kagyan, 20 years recovered and every other tran (add |
| 280 | Of the 30 traps deployed in Kogyae, 30 were recovered and every other trap (odd |
| 280 281 | Of the 30 traps deployed in Kogyae, 30 were recovered and every other trap (odd numbers) was processed and counted, to give five traps from each plot and an even coverage |
| 280 281 282 | Of the 30 traps deployed in Kogyae, 30 were recovered and every other trap (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 |
| 280281282283 | Of the 30 traps deployed in Kogyae, 30 were recovered and every other trap (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 |
| 280 281 282 283 284 | Of the 30 traps deployed in Kogyae, 30 were recovered and every other trap (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: <i>Celtis</i> , |
| 280 281 282 283 284 285 | Of the 30 traps deployed in Kogyae, 30 were recovered and every other trap (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: <i>Celtis</i> , <i>Alchornea</i> , Poaceae and Melastomataceae/Combretaceae (Figure 5). In total, 121 pollen taxa |
| 280 281 282 283 284 285 286 | Of the 30 traps deployed in Kogyae, 30 were recovered and every other trap (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: <i>Celtis</i> , <i>Alchornea</i> , Poaceae and Melastomataceae/Combretaceae (Figure 5). In total, 121 pollen taxa were defined in Kogyae, of which 37 were assigned botanical affinities. |

289 The Forest traps displayed broadly similar pollen assemblages, with Poaceae 290 accounting for 19.0 - 25.0% of grains, and with a consistent presence of Alchornea (7.4-291 12.6%) and *Erythrophleum* (1.0-38.0%). Melastomataceae/Combretaceae was present in all traps, but varied in abundance from 3.6-23.0%. Celtis, although present in all of the traps, 292 293 varied from 0.5-4.0% 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%). 294 295 Milicia was present in three of the traps, from 0.3-7.0%. Nine taxa were identified in both the 296 pollen and vegetation assemblages, these were Afzelia africana (R-rel = 0.02), Bombax (R-rel 297 = 0.02), Celtis (R-rel = 1.44), Erythrophleum suaveolens, (R-rel = 3.64), Ficus (R-rel = 0.24), 298 Lannea (R-rel = 0.05), Manilkara obovata (R-rel = 0.61), Melastomataceae/Combretaceae 299 (R-rel = 6.37), and *Milicia* (R-rel = 0.89) (Table 1, Figures 6 and 7). Within the Forest plot, 300 37 vegetation and 86 pollen taxa were identified, with nine taxa identified in both. The influx rates in this plot varied between 85 grains/cm²/month and 258 grains/cm²/month, with an 301 302 average of 154 grains/cm²/month and the diversity of the samples ranged from 2.0-2.9, with 303 a mean of 2.5 (Figure 8).

304

305 5.1.2 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%.

308 *Erythrophleum* was present in three traps in abundances of <5%. The

309 Melastomataceae/Combretaceae signal ranged from 0.9% to 31.5% between the five traps.

310 The two Asteraceae types accounted for up to 5.0% each of the pollen sum, but with variable

| 311 | percentage abundances (| 1.2-10.0%), and with | n neither being presen | t in all five traps. |
|-----|-------------------------|----------------------|------------------------|----------------------|
| - | | | | |

- 312 Manilkara obovata accounted for between 2.3% and 4.5% of the pollen sum in four traps, but
- 313 16.9% in the fifth. 'Pollen type 135a' was only present in Trap 69, at 15.5%. Seven taxa that
- 314 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),
- 316 *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
- 318 Transition plot, 34 vegetation and 71 pollen taxa were identified, with eight taxa identified in
- both. Influx rates in this plot varied from 92-204 grains/cm²/month, with an average of 146
- 320 grains/cm²/month and diversity of the traps ranged from 1.8-2.5, with an average of 2.3
- 321 (Figure 8).
- 322

323 5.1.3 Savannah

324 The traps exhibited largely similar pollen assemblages, with Poaceae and Melastomataceae/Combretaceae contributing more grains than any other taxa. Poaceae 325 326 percentages were between 17.0-42.4%, and Melastomataceae/Combretaceae grains contribute 327 12.5-68.1%. Alchornea was present in all traps, but at <3.0% in four. Asteraceae 2 was 328 present in three traps at percentages of >3.0%, but not in the other two. *Celtis* was present in 329 four out of the five traps, but at abundances of <3.0%. *Pterocarpus* pollen was found at 4.3% 330 and 14.9% in two traps. Uapaca was present in the same two traps (57 and 59) as 331 Pterocarpus, at 0.9% and 6.5% respectively. Terminalia was present in all of the Savannah 332 traps, from 4.6-27.1%. Five taxa were present in both the vegetation and pollen assemblages: 333 *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, Figure 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 61-478 grains/cm²/month (Trap 55 has an
unusually low influx rate compared to the other traps) with an average of 322
grains/cm²/month and the diversity of the traps ranged from 1.2-2.6, with an average of 2.1
(Figure 8).

340

341 5.2 Multivariate analysis

342 The NMDS plot (Figure 9) shows the distribution of the samples (indicated by black, capital letter e.g. 'FT71' = Forest, Trap 71) in ordination space. The Forest and Savannah 343 344 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 345 346 ordination space occupied by Savannah samples. Abundant pollen taxa from the plots fall out 347 with their parent vegetation types, such as *Erythrophleum suaveolens* with the Forest traps, 348 Manilkara obovata with the Transition traps and Uapaca with the Savannah traps. Poaceae is 349 positioned roughly centrally to the distribution of all of the samples.

350

351 6 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).

361

362 6.1 Characterisation of vegetation plots by their modern pollen rain

363 6.1.1 Forest

364 The Forest traps are relatively homogenous in terms of pollen assemblage, influx 365 values, and diversity (Figure 5 and Figure 8). The characteristic pollen taxa in the Forest plot 366 were Poaceae, Alchornea, Erythrophleum suaveolens and Melastomataceae/Combretaceae (Figure 5). Of these characteristic taxa, Erythrophleum suaveolens (1.0-38.0% of the pollen 367 368 sum) and Melastomataceae/Combretaceae (3.6-23.2% of the pollen sum) exhibited the most 369 variation between traps. The other characteristic taxa had less variable signals, with Poaceae 370 accounting for between 19.1-26.0% and Alchornea between 7.4-12.6% of the pollen sum. 371 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*.

373 *Erythrophleum suaveolens* is widespread across tropical Africa (Hawthorne & Jongkind

374 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

376 strongly over-represented in this plot, with a R-rel ratio of 3.64.

377 Melastomataceae/Combretaceae was a characteristic pollen taxon (up to 38.0% of the 378 pollen sum). It did not, however, account for a large component of the vegetation inventory, 379 comprising just 1.6% of the basal area of the plot. Consequently, the R-rel value for this 380 group was 6.37. This large R-rel value could be due to the over-production of pollen by 381 Combretaceae, in which andromonoecious inflorescences are known to occur (Watson & 382 Dallwitz 1992). There are no woody Melastomataceae recorded in the Forest plot, but there 383 may be understorey plants which contribute to the pollen signal. Any herbaceous 384 Melastomataceae would likely, however, contribute only a small amount of pollen, as many 385 Melastomataceae are buzz-pollinated, meaning that their pollen is not freely released into the 386 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 herbaceaous 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).

393 One of the characteristic pollen taxa of the Forest plot is Alchornea, which occurs in 394 all traps at percentages of up to 12.6%. This taxon is not, however, present in the vegetation 395 survey for the plot. This could be due to one of several factors: i) that Alchornea is genuinely 396 not present in the vegetation plot, but is present in the surrounding vegetation; ii) that the 397 pollen grain identified as Alchornea is a misidentification and originates from a different 398 plant, or iii) that the Alchornea plants contributing to the signal possess stems that are too 399 small to be included in the vegetation surveys, which only records plants of >10 cm DBH. It 400 is likely that the latter is true of Alchornea cordifolia (Schumach. & Thonn.) Müll.Arg, which

401 is a commonly recorded species in Guineo-Congolian Transition woodland and exhibits a
402 scandent habit, making it likely that it could have been excluded from surveys and therefore
403 account for the apparently orphan *Alchornea* pollen.

404 Taxa that occurred at >3% but in less than four traps included *Milicia* and *Celtis*. 405 *Milicia* accounted for >3% of the pollen sum in two traps, although it was present in three, 406 and *Celtis* only occurred at >3% in two traps, although was present in four. The low 407 abundances of Milicia and Celtis mirror their abundance in the vegetation, which is 408 surprising, as both the Moraceae (the family to which Milicia belongs) and Celtis have 409 previously been found to be over-represented in pollen rain (Gosling et al. 2005; Bush et al. 410 2011). Possible reasons for their relative low representation compared to similar studies could 411 relate to over-production by Melastomataceae/Combretaceae and Poaceae swamping the 412 traps. It is also possible that due to only one year of data being available, the climatic 413 conditions may not have favoured flowering that year, or a biological factor such as a fungal 414 infection or pest could have prevented the Celtis individuals from producing as much pollen 415 as usual.

416 There were 27 vegetation taxa whose pollen was not identified in the pollen 417 assemblages, including all but two of the most abundant species recorded in the vegetation 418 surveys (Erythrophleum suaveolens and Afzelia africana). This abundance of palynologically 419 silent taxa could be due to their entomophilous pollination syndromes (Supp. Mat.), climatic 420 conditions not favouring flowering in the year 2013-2014, or the individuals of those taxa 421 being located in the plot in such a way as to make pollen deposition unlikely. Although the 422 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 423 424 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 pollenrain (Bush & Rivera 2001; Gosling et al. 2005).

427

428 6.1.2 Transition

429 Characteristic taxa for the Transition plot were Poaceae, *Alchornea*,
430 Melastomataceae/Combretaceae and *Manilkara obovata*. The percentage abundances of
431 Poaceae (19.1-61.1%), Melastomataceae/Combretaceae (1.0-31.5%) and *Manilkara obovata*432 (2.3-16.9%) vary considerably between traps. *Alchornea* (2.7-6.8%) does not exhibit such
433 variability.

434 Melastomatacee/Combretaceae were over-represented (R-rel = 5.18), likely due to 435 over-production by Combretaceae. All other taxa identified in both pollen and vegetation in 436 this plot, besides Poaceae, were under-represented. Manilkara obovata exhibits the closest to 437 1:1 ratio in this plot, of 0.8 (Figure 6). Although Manilkara obovata is primarily a forest 438 species (White et al. 1983), it is characteristic of this particular plot's pollen assemblage. It 439 has entomophilous, hermaphroditic flowers whose anthers protrude from the perianth, 440 potentially allowing pollen to be released more freely than from a closed flower and resulting 441 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).

446 The Moraceae in the Transition plot were under-represented (R-rel = 0.15), as were 447 Ceiba (R-rel = 0.08), Afzelia africana (R-rel = 0.06) and Lannea (R-rel = 0.05). Of these, the 448 Moraceae, Ceiba, and Afzelia africana were all only represented by a small number of 449 individuals (two, two and three individuals respectively), meaning that pollen production may 450 have been genuinely low for these taxa. Lannea is represented by 10 individuals, however, 451 and has the lowest R-rel ratio (0.05), indicating that it is most under-represented. These taxa 452 are all monoecious or hermaphroditic, and insect pollinated, leading to no clear explanation 453 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 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.

458

459 6.1.3 Savannah

The characteristic pollen taxa of the Savannah plot were Poaceae (14.1- 42.4%), Melastomataceae/Combretaceae (12.5-68.1%), and *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* (Rrel = 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 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 (62 473 grains/cm²/month) in comparison to the other Savannah plot traps, which exhibited 474 475 concentration of between 187 and 475 grains/cm²/month. Despite its low pollen accumulation 476 rate, Trap 55 did not contain an anomalous pollen assemblage, with similar percentages of 477 abundant taxa to the other traps, and a high diversity. It is possible that it was covered by a 478 leaf or other debris for part of the year, leading to less pollen accumulating in this trap than 479 the other traps. We decided however to include Trap 55 in the analysis despite its 480 anomalously low pollen accumulation rate, as we consider that it represents the pollen 481 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, therefore possibly representing transport from outside the plot.

486

487 6.2 Differentiation of vegetation plots within a forest-savannah mosaic

488 Despite their close geographical proximity within the forest-savannah mosaic, the 489 plots give rise to different palynological assemblages, in both the relative abundances of 490 common taxa and the presence or absence of rarer taxa. The pollen assemblages differ in 491 abundance of dominant, over-producing taxa, such as Poaceae and 492 Melastomataceae/Combretaceae, but there are also differences in the less abundant

493 components of the assemblages such as *Erythrophleum suaveolens* in the Forest plot,

494 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

496 R-rel values for taxa are often not consistent across plots; although

497 Melastomataceae/Combretaceae is consistently over-represented in the pollen sum, the

498 degree of over-representation varies widely (Figure 6 and Figure 7).

499 *Erythrophleum suaveolens*, whilst over-represented in the Forest plot (R-rel = 3.64), 500 is under-represented in the Transition plot (R-rel = 0.39). As there are relatively few 501 individuals in each plot (nine in the Forest and six in the Transition), this discrepancy in 502 representation may be due to factors such as tree location in the plot, wind direction, tree 503 height or openness. Although there are fewer individuals of *E. suaveolens* in the Transition 504 plot, they account for a similar total percentage of the basal area as in the Forest plot, 505 indicating that the Transition plot individuals may be larger; a factor which does not appear 506 to have influenced their representation in the pollen rain.

507*Terminalia* is under-represented in both the Transition and Savannah pollen508assemblages, but has a lower R-rel value in the Transition plot (R-rel = 0.34) than in the509Savannah plot (R-rel = 0.66). This is despite it being more vegetatively abundant in the510Transition plot than it is in the Savannah plot (24 stems in Transition, 23 in Savannah).511*Terminalia* does account for a greater percentage of total stems and has a larger basal area512percentage coverage in the Savannah plot than in the Transition, however, suggesting that513*Terminalia* trees in the Savannah plot may be larger than those of the Transition.

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

519 Poaceae, one of the most abundant taxa in all three plots, does not display an increase 520 in percentage abundance from Forest to Savannah (Figure 5). Its influx values, however, 521 increase along the gradient with the Forest having an average of 36 grains/cm²/month, the 522 Transition traps 51 grains/cm²/month and the Savannah traps 79 grains/cm²/month. 523 Melastomataceae/Combretaceae pollen shows an increase in percentage abundance along the 524 Forest-Transition-Savannah gradient, but also displays very high influx values in the 525 Savannah plot (an average of 54 grains/cm²/month) compared to the other two plots (an 526 average of 8 grains/cm²/month in the Forest plot, and 9 grains/cm²/month in the Transition). 527 This very high Melastomataceae/Combretaceae influx effectively masks the Poaceae signal in 528 the Savannah plot and accounts for its similarity to the Transition and Forest plots in the 529 percentage data. The absence of a clear differentiating signal from Poaceae percentage 530 abundance in this study is illustrated both by its lack of clear increase from forest to savannah 531 (Figure 5), and by its position in the ordination roughly centrally to all three plots (Figure 9). 532 The absence of variation in the Poaceae signal differs from the findings of Vincens (Vincens 533 et al. 2000) and Ybert (Ybert 1975), who both observed a strong increase in the percentage 534 abundance of Poaceae pollen along the forest-savannah gradient in Cameroon and Côte 535 d'Ivoire respectively. The discrepancy between this study and previous studies could be due 536 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 537

Ybert (1975) encompass wider vegetational gradients than the plots used in this study, with samples 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 (Supp. Mat.).

545 There are 67 pollen taxa in this dataset whose abundance is low enough (<3% in any 546 trap) that it would not be informative or practical to include them in a pollen diagram, but 547 whose presence may nevertheless contribute to the separation of the plots palynologically. 548 The differences between the pollen assemblages of the plots are highlighted by the fact that 549 the Forest and Savannah samples form two clearly separate groups in ordination space, with 550 Transition traps overlapping with the Savannah (Figure 9). There were, however, a variety of 551 pollen taxa which contributed to the spread of the data but which are not recorded in the 552 vegetation plots including Borassus, Schefflera, Sloanea, Diodia, Trema, Nesogordonia, and 553 *Pycnanthus*, as well as multiple distinctive pollen morphotypes. These taxa may represent 554 extra-plot pollen, or may have been present in the plot, but not recorded due to being too 555 small (< 10 cm DBH).

556

557

7 6.3 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 561 trend of increasing pollen diversity with increasing vegetation diversity (Figure 8), with the 562 Forest traps showing less variation than the Transition traps, which in turn showed less than 563 the Savannah traps. The large variability in the diversity of the Savannah plot pollen traps 564 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 565 566 small number of vegetation diversity measures (three) available. The positive relationship 567 between vegetation and pollen diversity has been demonstrated in modern pollen traps (Jantz 568 et al. 2014), and in lake sediments (dependent on the situation of the lake in question) (Felde 569 et al. 2016), although there are difficulties involved with using these data to interpret fossil 570 pollen assemblages due to features of depositional environments that may affect the 571 relationship between pollen and parent vegetation in the fossil record (Odgaard 1999).

572

573 6.4 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 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).

588 Even with the strong bias towards anemophilous taxa displayed in the fossil record, 589 the forest stages identified in the Lake Bosumtwi record have higher Moraceae abundances 590 than the traps in this study, indicating that the inference of some form of wooded 591 environment is well-justified. However, in the forest zones of the Lake Bosumtwi record, 592 taxa used to indicate a moist, broadleaf forest vegetation type include Uapaca, Alchornea and 593 *Celtis. Uapaca*, in the samples analysed here, is only present in the Savannah plot (although it 594 is not a characteristic taxon of this plot). Alchornea and Celtis are present in the pollen rain of 595 the majority of trap samples from all three plots, at similar abundances as those observed in 596 the Bosumtwi record. Melastomataceae/Combretaceae, along with Poaceae percentages of up 597 to 40%, are used to indicate a moist, rainforest environment in the Bosumtwi record, but here 598 are indicative of the Savannah plot. It is possible, therefore, that the ecosystems characterised 599 in the Bosumtwi record as 'moist broadleaf forest' may represent drier vegetation types (the 600 inferred rainfall of the Bosumtwi forest zones were 1000-3300 mm/year, whereas the rainfall 601 at Kogyae, and within the transitional zone in general is 900-1200 mm/year) (Miller & 602 Gosling 2014). The forest zone may include the transitional mosaic explored here, an 603 observation that could have implications in 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 pollen regional) (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 are, therefore, able to be considered as capturing 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.

614

615 The observation that the Poaceae percentages in this study differ from those of the 616 fossil record is not, alone, an indication that the interpretation of the fossil record needs to be 617 re-examined. Poaceae is wind dispersed, highly productive, and therefore more likely to 618 appear in high percentages in the sediment record as opposed to traps under the canopy, in 619 relation to other, entomophilous or zoophilous taxa. When treated alone, Poaceae is an 620 unreliable indictor taxon (Bush 2002). It is, therefore, sensible to use other taxa along with 621 Poaceae to distinguish between vegetation types; the taxa outlined here may help to provide 622 better constraints on the interpretation of transitional zones within pollen records.

623

624 **7** 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 straight forward 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

631 Savannah vegetation type. These taxa, and many other rarer taxa, contribute to the plots 632 producing pollen assemblages that can be separated using multivariate methods, and to the 633 biodiversity of the pollen assemblages reflecting that of the vegetation. The plots also differ 634 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 635 636 interpretation of the fossil record. Based on the insights gained from the modern pollen data, 637 a re-examination of the fossil pollen record from Lake Bosumtwi may benefit from a lower 638 threshold of Poaceae pollen to categorise an assemblage as being from a savannah or 639 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 640 641 transition between forest and savannah may benefit from the results outlined in this study, 642 thereby improving knowledge of how vegetation responds to climate fluctuations in the past 643 and helping to shape predictions of how ecosystems might respond to climate change in the 644 future.

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- many researchers to apply a range of techniques to gain a comprehensive picture of how environments
- have changed in the past.
- 725

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- 988 Figure 1: Location of the field study site in Ghana as a whole, relative to vegetation types
- 989 (left) and location of vegetation plots relative to one another (right).



- Figure 2: Photographs of the vegetation in the three plots; a) Forest (KOG02) 7°15'41.9"N,
- 992 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,
- 993 and c) Savannah (KOG05) 7°18'04.1"N, 1°09'53.8"W and 186 m asl.



Figure 3: Bar chart showing the vegetation types as outlined by White 1983 to whichthe species in the three plots belong.



Figure 4: Diagram showing layout of pollen traps (represented by triangle symbols)
within vegetation survey plots. Circled traps indicated 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.



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'.



1009 Figure 6: Bar chart showing R-rel values of taxa represented in both pollen and

1010 vegetation, where p = average % abundance of a taxon and v = total basal area of taxon in the

1011 vegetation. The asterisks indicate that the R-rel values were too high to show on the figure;

1012 the Forest Melastomataceae/Combretaceae R-rel = 6.37 and *Erythrophleum suaveolens* =

1013 3.64. The Transition Melastomataceae/Combretaceae R-rel = 5.18, and the Savannah

1014 Melastomataceae/Combretaceae = 3.53



Figure 7: Scatter plot of Vegetation Basal Area % against Pollen Abundance %. Taxa names are as in manuscript, except Melastomataceae/Combretaceae, which is abbreviated to 'MelCom'. 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.

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Figure 9: NMDS plot of pollen trap assemblages. Forest traps begin 'FT' Transition traps 'TT' and Savannah Traps 'ST'. Polygons encompass all traps of the each plot. Named taxa are included in grey. Un-identified pollen taxa were used in the analysis but are not shown on the figure.



1040 Plate 1: Plate showing characteristic taxa from all plots. 1 = *Erythrophleum suaveolens*, 2 =

- *Manilkara obovata*, 3 = *Alchornea*, 4 = Melastomataceae/Combretaceae 5 = *Terminalia* sp. 6
- 1042 = Poaceae sp. 'a' and 'b' denote polar and equatorial views of the same grain.

1044 Tables

1045 Table 1: Taxa that occur in both pollen assemblages and vegetation survey for the Forest plot,

1046 their abundances in the data set and their R-rel (Average pollen abundance in samples/%

1047 basal area of plot covered by vegetation taxon) values.

| Taxon | No. stems > = 10 cm DBH | Stems in vegetation (%) | Basal area (% of plot area) | Average pollen abundance (%) | R-rel (Average pollen abundance/Basa l 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 |
| Melastomatacea e/Combretaceae | 2 | 1.1 | 1.67 | 10.64 | 6.37 |
| Milica | 2 | 1.0 | 2.62 | 2.33 | 0.89 |

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- 1050 Table 2: Taxa that occur in both pollen assemblages and vegetation survey for the Transition
- 1051 plot, their abundances in the data set and their R-rel (Average pollen abundance in samples/%

| 1052 | basal area of plot covered by vegetation taxon) values. |
|------|---|
|------|---|

| 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 suaveolens | 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 |

1054 Table 3: Taxa that occur in both pollen assemblages and vegetation survey for the

1055 Savannah plot, their abundances in the data set and their R-rel (Average pollen abundance in

| 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 |

1056 samples/% basal area of plot covered by vegetation taxon) values.