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Variability in modern pollen rain from moist and wet tropical forest plots in Ghana, West Africa

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Abstract
How pollen moves within and between ecosystems affects factors such as the genetic structure of populations, how resilient they are to environmental change, and the amount and nature of pollen preserved in the sedimentary record. We set artificial pollen traps in two 100 m by 100 m vegetation plots, one in a wet evergreen forest, and one in a moist semi-deciduous forest in Ghana, West Africa. Five traps from each plot were counted annually from 2011 to 2014, to examine spatial and temporal variation in the pollen rain of the most abundant taxa shared between pollen and vegetation assemblages. Samples from the wet evergreen plot exhibited high variability within years, with the dominant pollen types changing between samples, and many pollen taxa being over-represented relative to their parent plant abundance in some traps whilst being entirely absent from others. The most abundant plant taxa of the wet evergreen plot (*Drypetes* and *Cynometra*) do, however, constitute major components of the pollen rain. There is less variation between samples from the moist semi-deciduous plot spatially, as it is dominated by *Celtis*, which typically comprises >70% of the pollen assemblages. We conclude that pollen rain in these tropical ecosystems is highly heterogeneous, and suggest that pollen assemblages obtained by trapping are susceptible to small-scale variations in forest structure. Conversely, this may mean that current recommendations of more than three years of trapping in tropical systems may be too high, and that space could substitute for time in modern tropical pollen trapping.

Keywords: *palynology, pollen, dispersal, Tropics, Ghana*

Pollen production and dispersal are crucial to the maintenance of plant populations, their genetic diversity, and their ability to adapt and evolve in response to changing conditions (Ellstrand & Elam 1993). Pollen dispersal in the tropics has, until recently, been largely under-studied compared to temperate regions (Giesecke et al. 2010), although molecular work has been carried out which allows parentage of individuals to be inferred, thereby indicating how far their parental pollen travelled (Dick et al. 2003; Gonzales et al. 2006). How pollen moves within and between ecosystems is of particular interest to palaeoecologists, who use pollen from sedimentary records to reconstruct past vegetation and therefore need to know how well past vegetation is represented in the fossil pollen

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record (Overpeck et al. 1985; Fægri et al. 1989). Pollen production has been shown to reflect physical variables such as temperature, precipitation (Nielsen et al. 2010) and solar irradiance (Haselhorst et al. 2017), as well as pollination syndrome (Bush 1995).

The movement and dispersal of pollen has been studied using molecular markers to identify offspring of individuals (Ellstrand 1992; Austerlitz et al. 2004; Smouse & Sork 2004; Ward et al. 2005; Gonzales et al. 2006; Dick et al. 2007, 2008). In the tropics, high levels of out-crossing and pollen dispersal over long distances (up to tens of kilometres) are observed despite the majority of tree taxa being entomophilous and therefore presumed to have relatively limited pollen dispersal capabilities (Ward et al. 2005). Genetic studies measure successful pollination events and subsequent population structure, but do not show how the bulk of pollen produced by plants moves within ecosystems, whether driven by air currents, rain, or gravity (DiLeo et al. 2014). The pollen distribution curve (the amount of pollen deposited against distance from source) has been shown to be a negative-exponential (strongly leptokurtic), meaning that a large proportion of all pollen produced is deposited very close to the plant (Miller 2016). Modern pollen studies in tropical forest also show high levels of local (within tens of metres of samples) pollen in traps (Bush & Rivera 1998; Gosling et al. 2005).

The interpretation of the fossil pollen record relies upon an understanding of how plants in modern ecosystems produce pollen (Davis 1963; Jackson & Lyford 1999; Farrell et al. 2016). In temperate regions, this issue has received much attention, with modern pollen rain studies having been carried out extensively for the past century, and the Pollen Monitoring Programme (Hicks et al. 2001) being established to standardise collection techniques (for a thorough review of the history of pollen trapping in Europe, see Giesecke et al. (2010), and for a meta-analysis of North American assemblages see Goring et al. 2013). Pollen assemblages recovered from artificial traps represent local vegetation (Haselhorst et al. 2013), and consequently they are not directly comparable to those recovered from large lakes. The larger the lake, the higher the proportion of regional and anemophilous, taxa it is likely to contain (Janssen 1966; Jacobson & Bradshaw 1981), whereas pollen traps tend to record local signals, meaning that entomophilous and locally abundant taxa can be relatively over-represented. Modern pollen studies can be useful in identifying taxa that, when identified at lower abundances in the fossil record, might be indicative of certain ecosystems (e.g. the Fabaceae [Watrin et al. 2007]), and may also allow the identification of taxa that are not useful in differentiating between ecosystems, or those that must be treated with caution, such as the Poaceae (Bush 2002).

In the tropics, and particularly in Africa, less work has been carried out on modern pollen–vegetation relationships than in temperate regions; Lézine et al. (2009) synthesised modern pollen studies in sub-Saharan Africa and returned 452 modern samples from the whole region. There have, however, been

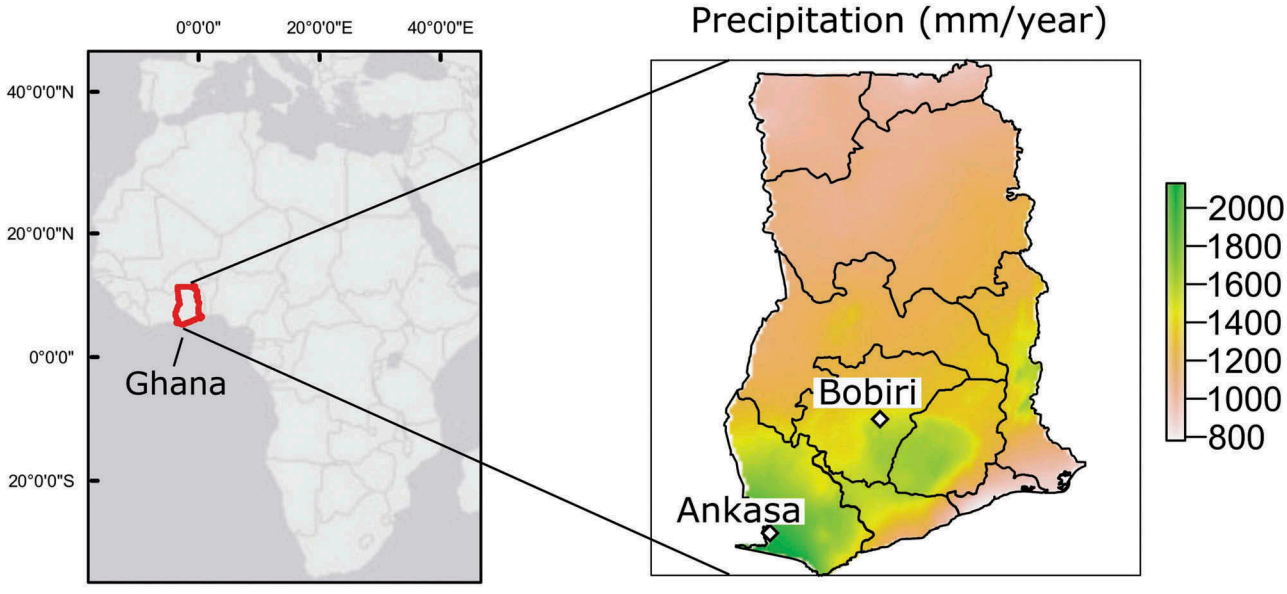


Figure 1. Map showing Ghana in wider context of Africa (left) and precipitation map of Ghana showing the position of the two field sites (right) (rainfall data from WorldClim).

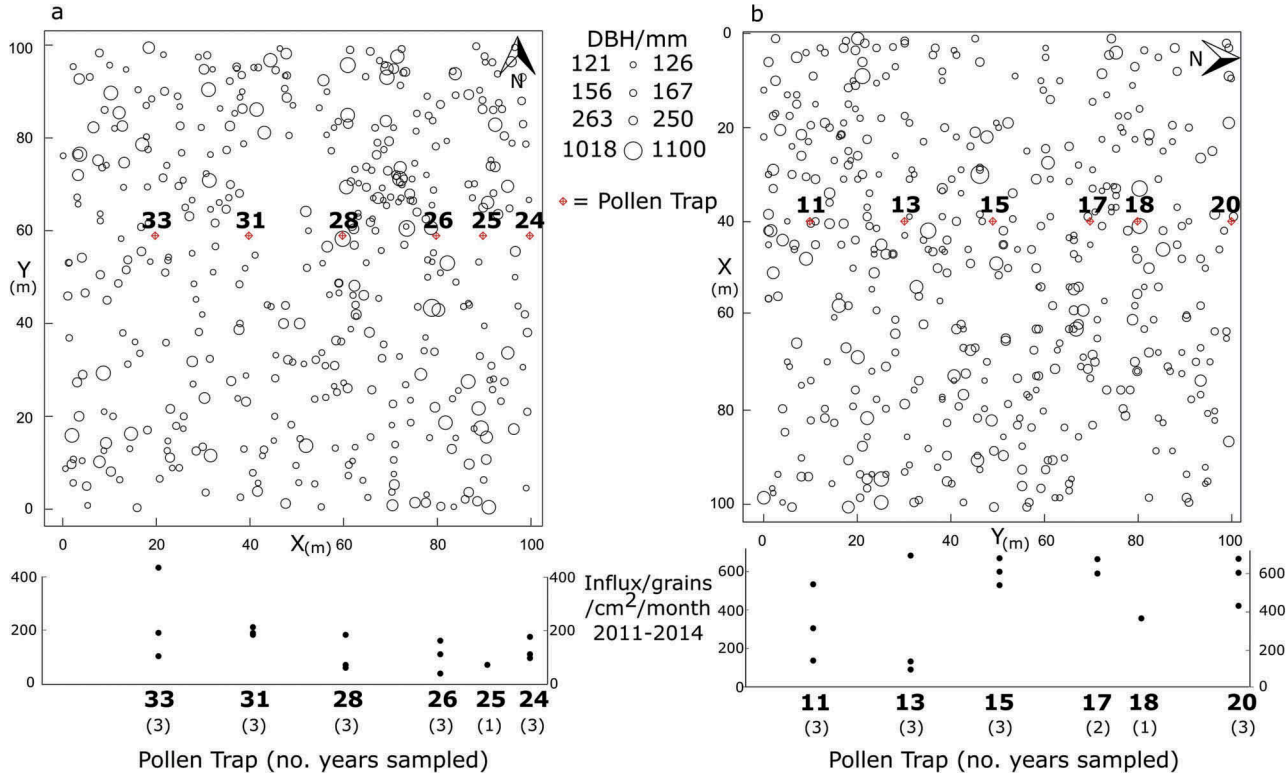


Figure 2. Maps of all trees in the plots (100 m × 100 m), scaled by the square root/10 of their diameter at breast height (DBH). **A.** Ankasa. **B.** Bobiri. Red symbols indicate trap positions and bold numbers trap numbers. Pollen influx is shown below for all samples from each trap. Bobiri plot is rotated by 90° in this plot, in order to display influx values below map.

some wide-ranging African studies that have shown that modern pollen assemblages, drawn mainly from surface samples, represent their parent vegetation types well (Gajewski et al. 2002; Watrin et al. 2007; Lebamba et al. 2009). Consequently, reconstructing vegetation, with a view to informing interpretations of the fossil record and predictions of the effects of future climate change is a possibility (Hély et al. 2006; Blois et al. 2013). Neotropical pollen studies also show that there are clear changes in pollen assemblages along savannah to forest transitions, with shifts from herbaceous and grass dominated assemblages to arboreal dominated forest assemblages (Gosling et al. 2009; Alejandra et al. 2013).

No modern pollen–vegetation relationship studies have been conducted in forested regions of Ghana and just one from the savannah–forest transitional zone (Julier et al. 2018). This study will therefore provide useful insights into pollen deposition in Ghana, and West Africa more widely. We present modern pollen assemblages collected in artificial pollen traps deployed in two forest settings in Ghana; one wet evergreen rainforest (Ankasa) and one moist semi-deciduous forest (Bobiri). These sites have been chosen due to their proximity to Lake Bosumtwi, a meteor-impact crater lake in Ghana, which has given rise to the longest terrestrial pollen record in West Africa (540 000 years) (Shanahan et al. 2006, 2012; Miller & Gosling 2014; Miller et al. 2016). We address the following aims:

1. Characterisation of assemblages from a wet evergreen ecosystem and a moist semi-deciduous forest ecosystem in terms of their most abundant and consistently occurring pollen taxa.
2. Exploration of drivers of variation in representation in each of the most abundant taxa.
3. Consideration of the implications of this work for models of pollen distribution and pollen trapping studies.

Site descriptions

The two forest sites in this study, Ankasa and Bobiri, are located in tropical West Africa, within the Guineo-Congolian centre of endemism (White et al. 1983; Gautier & Spichiger 2004). Guineo-Congolian forest accounts for much of the forest cover across tropical West Africa, from Senegal to Togo, and encompasses many endemic species and

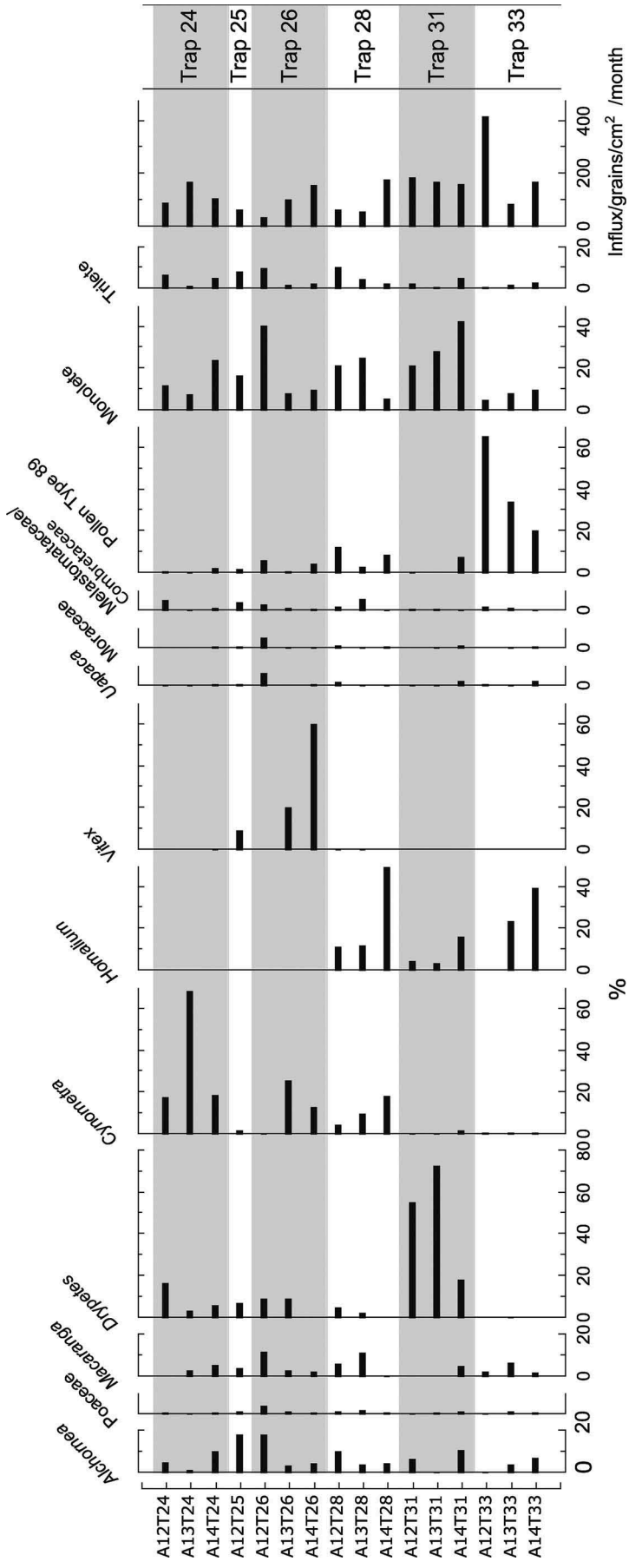


Figure 3. Pollen diagram (%) showing most abundant taxa from Ankasa. Zones are indicative of traps, with each bar within each zone indicating one year of sampling. 'A12T24 = Ankasa 2012, Trap 24'.

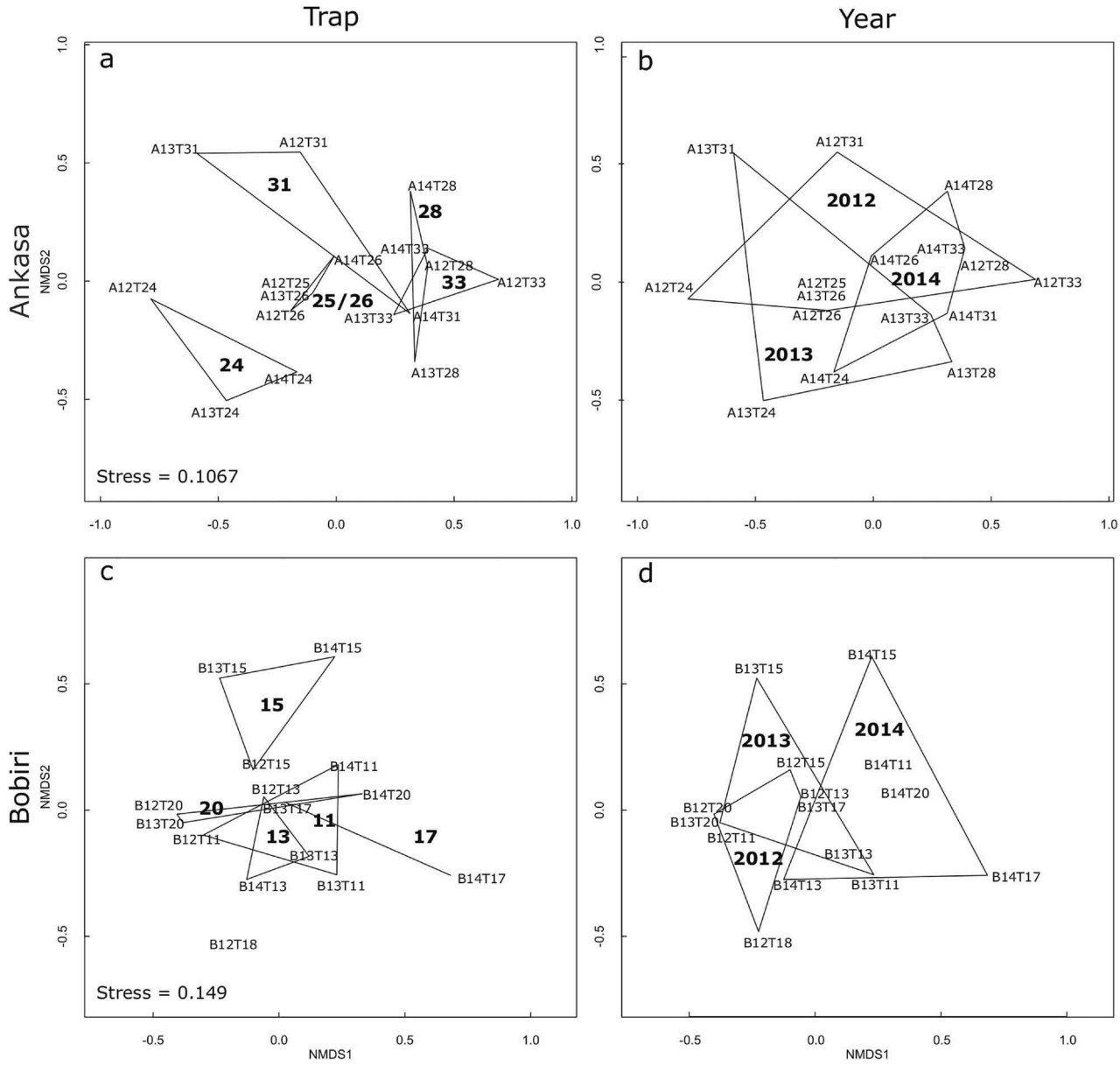
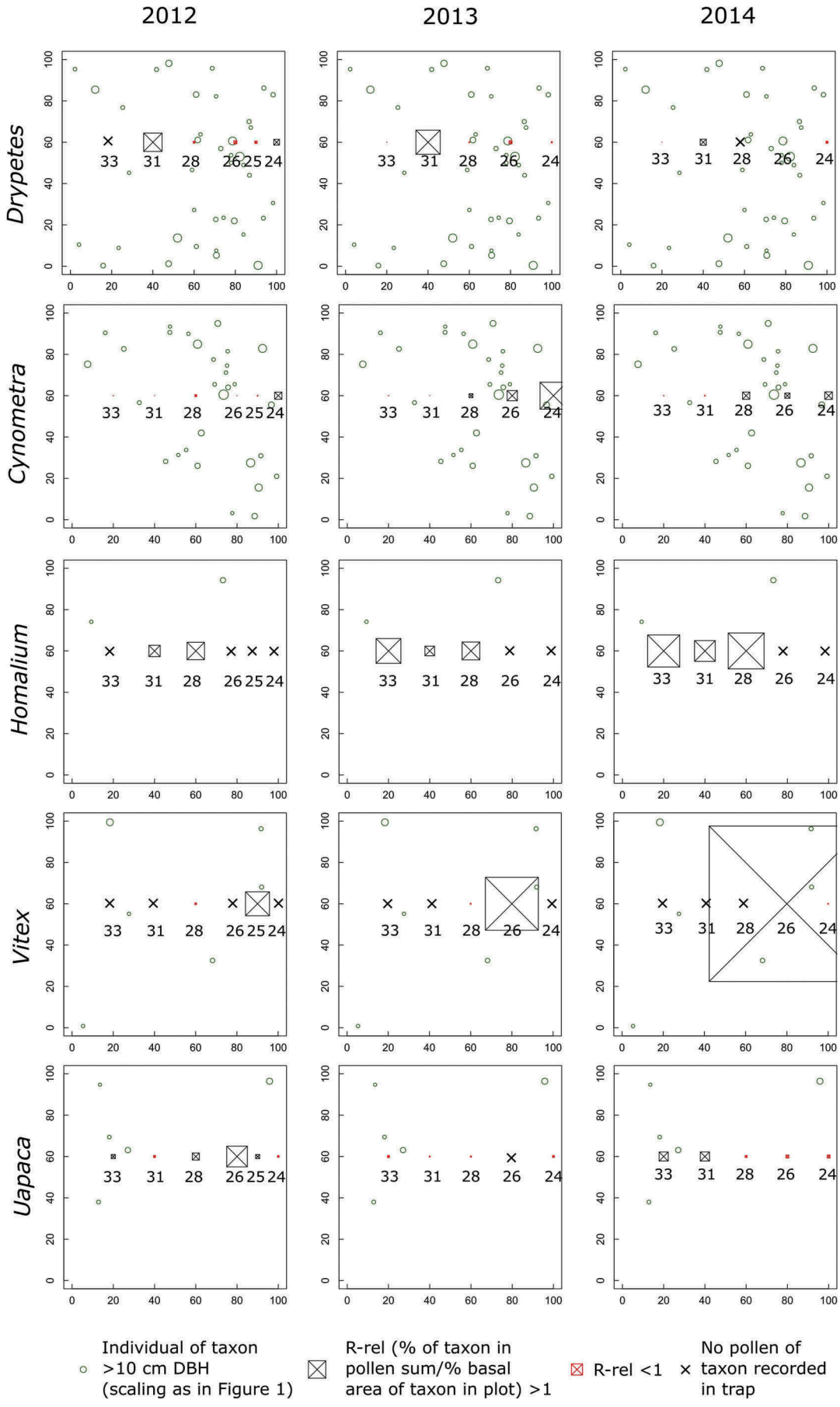


Figure 4. Non-Metric Multidimensional Scaling (NMDS) plots showing Ankasa (**A** and **B**) and Bobiri (**C** and **D**), with hulls overlain by trap (**A** and **C**) and by year (**B** and **D**). Bold numbers refer to traps, with non-bold labels referring to year and trap, i.e. A12T24 = Ankasa 2012, Trap 24.

different vegetation types (Bongers et al. 2004). The region is characterised by very high rainfall (up to 4000 mm/year) with the amount of rainfall being a determining factor in the vegetation type. According to the updated Köppen climate classification system, Ankasa is classified as wet evergreen rainforest, within the Aw Monsoon climate zone, and Bobiri as moist semi-deciduous forest, within the Aw Tropical savannah climate zone (Peel et al. 2007). During this study, rainfall varied from 1200 mm/year at Bobiri to over 2000 mm/year at Ankasa, and the rainy season was unusually dry in 2013 (OCHA 2013).

Ankasa (ANK02). — The first site, Ankasa is located in the Ankasa Conservation Area in south-west Ghana, and the plot is located at 5° 16′ 06″ N, 2° 41′ 38″ W. The plot was established in 2011 and a vegetation survey of all trees > 10 cm diameter at breast height (DBH) was conducted. Plot


2012
2013
2014
Drypetes
Cynometra
Homalium
Vitex
Uapaca
33 31 28 26 25 24
Individual of taxon >10 cm DBH (scaling as in Figure 1)
R-rel (% of taxon in pollen sum/% basal area of taxon in plot) >1
R-rel <1
No pollen of taxon recorded in trap

data is available from forestplots.net (Lopez-Gonzalez et al. 2011). The vegetation type of the Ankasa plot is wet evergreen rainforest, and is the most biodiverse area of Ghana, with multiple species of very high conservation priority (Hawthorne et al. 1998). The most abundant taxa in this plot, by percentage of stems, are *Drypetes aylmeri* Hutch. et Dalziel (8.9%), and *Cynometra ananta* Hutch. et Dalziel (7.1%). Herbaceous plants were not surveyed, but include taxa such as *Psychotria*, and members of the Zingiberaceae, Orchidaceae and Commelinaceae, along with various fern species (Hawthorne et al. 1998). The diversity of the surveyed vegetation in the Ankasa plot is 4.0 (Shannon Index) and there were 449 individual trees recorded (Figure 1A), of 100 different taxa.

The heights of the trees (> 10 cm DBH) in the Ankasa plot range from 4.1 to 41.6 m, with an average of 18.9 m. The soil is a Forest Oxysol, with a pH 3.5–4, which is prone to leaching and very infertile (Wildlife Division [Forestry Commission] 2000). Ankasa experiences some of the highest rainfall in Ghana; in 2011–2012, the total rainfall this plot experienced was 1902 mm, in 2012–2013 it was 1788 mm, and in 2013–2014 it was 2089 mm.

Bobiri (Bobiri Strict Nature Reserve; BOB01). — Bobiri is located at 6° 42′ 15″ N, 1° 19′ 06″ W, in the Bobiri Forest Reserve. The plot is designated as a 'Strict Nature Reserve' in which no logging was allowed. This forest plot was established in 2011 and a vegetation survey of all trees > 10 cm DBH was conducted. Plot data is available from forestplots.net (Lopez-Gonzalez et al. 2011). The vegetation type of this plot is moist semi-deciduous rainforest (Hall & Swaine 1981), and fits into the category of 'Drier peripheral semi-evergreen Guineo-Congolian rain forest' (White 1983). The most abundant taxa in this plot, by percentage of stems, are *Celtis mildbraedii* Engl. (14.7%) and *Funtumia elastica* (Preuss) Stapf (5.0%). Herbaceous taxa were not surveyed, although may comprise families such as the Marantaceae and Verbenaceae (White 1983). The diversity of the Bobiri plot (Shannon Index) is 3.8, and there were 483 individual trees recorded (Figure 1B), of 87 different taxa.

The height of trees (> 10 cm DBH) in Bobiri is around 37 m, with some emergents of up to 60 m (Hall & Swaine 1981). The soil is a Forest Ochrosol, which is red, well-drained, and relatively high in organic content near the surface but leached further down in the profile. The mean annual rainfall at this site over the years we sampled was 1443 mm. Rainfall was measured at the Forestry Research Institute of Ghana (FORIG), which is around 30 km away from the site, and there were some missing measurements, meaning that accurate yearly averages were not available.

Material and methods

Field methods

Pollen traps were deployed in 100 m × 100 m vegetation plots (Figure 2) in the Ankasa Nature Reserve and the Bobiri Strict Nature Reserve in October of 2011, 2012 and 2013, and were collected yearly. Sample dates are referred to by their year of collection e.g. '2012' is equivalent to October 2011–October 2012. The traps were placed at 10 m intervals along the 60 m east–west (E–W) line in Ankasa, and the 40 m south–north (S–N) line at Bobiri (Figure 1). Pollen traps were made following Gosling et al. (2003). Vegetation surveys were conducted by researchers from FORIG and the University of Oxford, and measured all plants with > 10 cm DBH. Vegetation data for these sites is available from www.forestplots.net.

Laboratory methods

Traps for processing were selected to give a relatively even spatial coverage of the plot across years, with at least five traps per year being processed and counted. The pollen was extracted from the traps for analysis following the method of Gosling et al. (2003). *Lycopodium* tablets (University of Lund, batch #12 4961, containing 12 542 ± 931 spores per tablet) were added to enable calculations of pollen concentration (Stockmarr 1971). Samples were counted at ×400 magnification using a Nikon Eclipse 50i microscope. Pollen counts were recorded digitally and were counted to a statistically representative number (Keen et al. 2014). Pollen taxa were identified using literature on tropical

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Figure 5. R-rel plots Ankasa. 100 m × 100 m vegetation plot maps of Ankasa, for the five most abundant vegetation taxa also represented in the pollen assemblages, over the three years of sampling. Numbers underneath or to the left of traps indicate pollen trap number. *Homalium* symbols are square rooted, as this taxon's R-rel values were too large to fit on the plots.

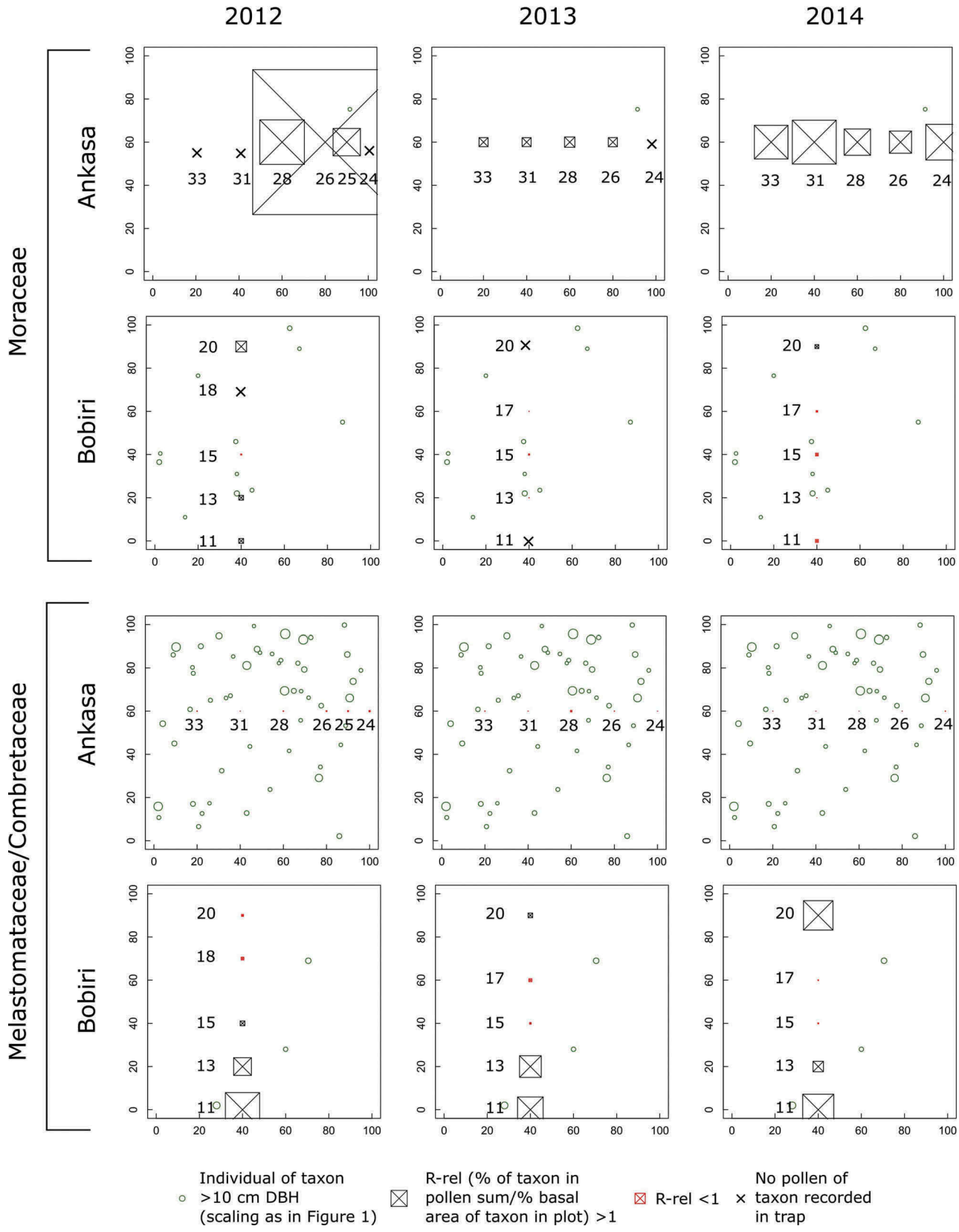

Figure 6. R-rel plots shared taxa 100 m × 100 m vegetation plot map of Ankasa and Bobiri, for the shared taxa Melastomataceae/Combretaceae and Moraceae, over the three years of sampling. Numbers underneath or to the left of traps indicate pollen trap number.

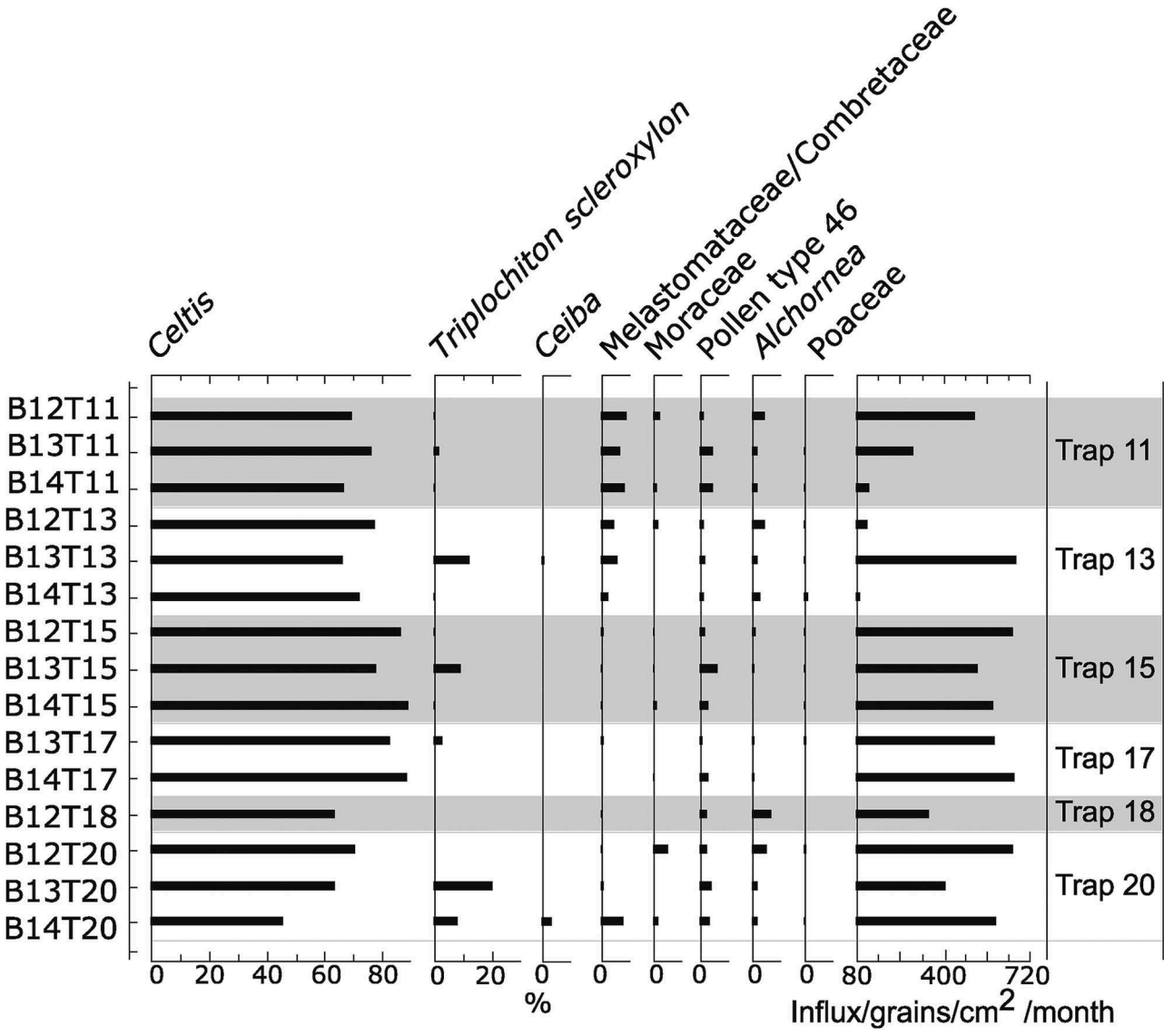

Figure 7. Pollen diagram (%) from Bobiri, showing most abundant taxa. Zones are indicative of traps, with each bar within each zone indicating one year of sampling. 'B12T11 = Bobiri 2012, Trap 11'.

West Africa (Van Campo 1974; Ybert 1979; Riollet & Bonnefille 1980; Gosling et al. 2013), the African Pollen Database (Vincens et al. 2007) and the reference collection at the University of Amsterdam, the Netherlands.

Statistical methods

Pollen to vegetation ratios, or R-rel values, were calculated by dividing the percentage of a pollen taxon in one sample by the basal area of the plot occupied by its parent taxon in the vegetation (Davis 1963). Non-Metric Multidimensional Scaling (NMDS) analysis was also undertaken in Vegan, excluding singletons (taxa which occur in only one sample) and using double Wisconsin standardisation (which corrects for sample size and effects of very rare or abundant taxa by diving each taxon by its column maximum, and then by its row total) with dimensions = 3 (Bray & Curtis 1957). Results were plotted in two-dimensions, as this captured the dominant patterns observed in three dimensions but in a simpler graphical presentation. 'Sample' is used to mean the pollen from one trap in one year, whereas 'Trap' refers to multiple samples from the same position within the plot over three years. Pollen assemblages were visualised in C2 (Juggins 2007). Statistical analyses were carried out in R statistical software (R Core Team 2016) with R studio version 1.0.136.

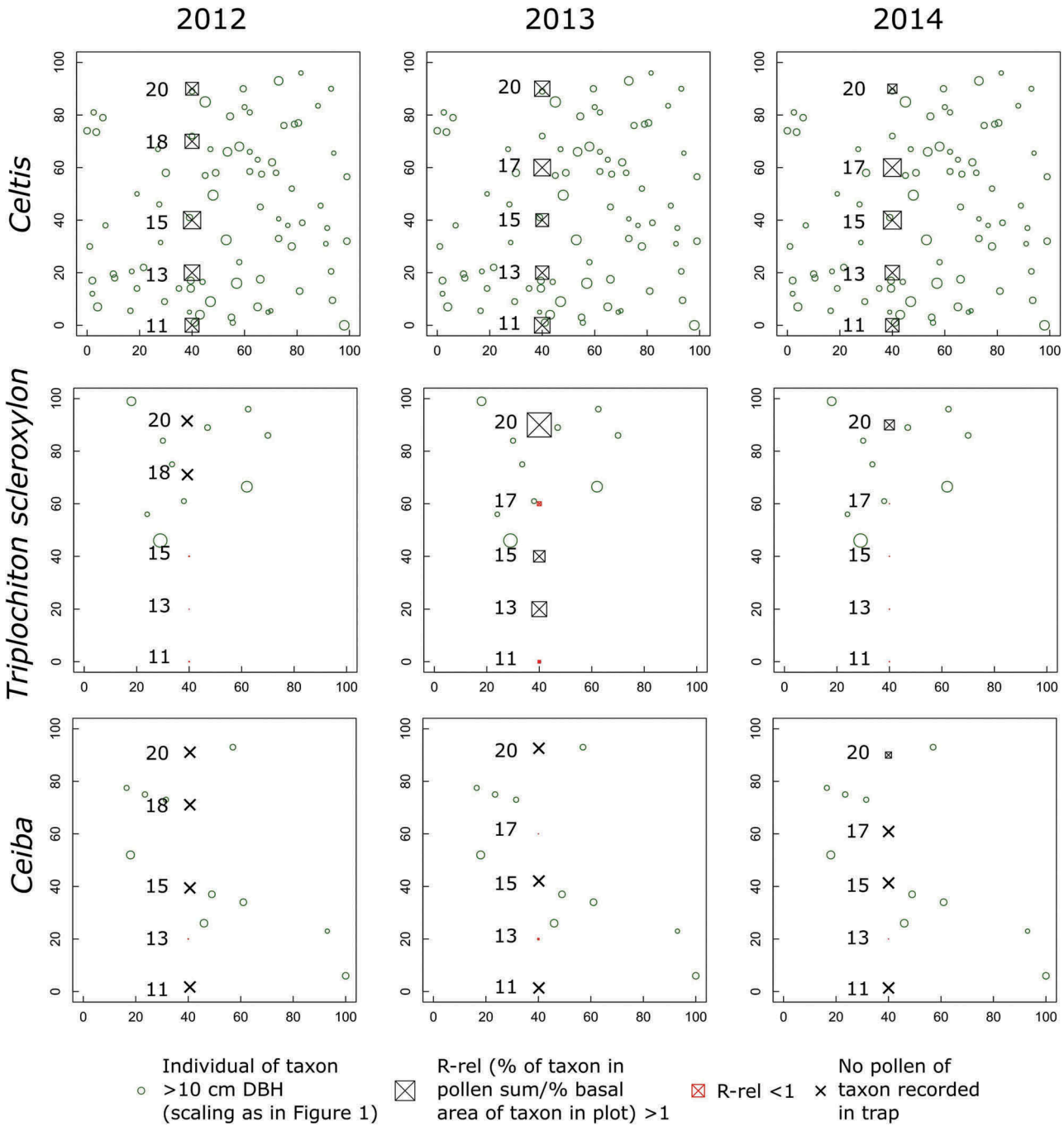

Figure 8. R-rel plots Bobiri 100 m × 100 m vegetation plot maps of Bobiri, for the three most abundant vegetation taxa also represented in pollen assemblages, over the three years of sampling. Numbers to the left of traps indicate pollen trap number.

Results

Ankasa

Pollen assemblages from Ankasa were variable, both between years and traps (Figure 3, 4). Taxa that occurred in all samples over all three years are *Cynometra* (0.3–68.8%), *Alchornea* (0.7–18.7%), Type 12 (0.3–6.6%), and Poaceae (0.3–4.2%). Monolete and Trilete spores are also present in all samples (but with percentages calculated outside of the pollen sum), with abundances ranging 5.2–43.0% and 1.0–10.7% of the pollen sum, respectively. The pollen influx varied from 36 to 422 grains/cm^2/month, with an average of 141 grains/cm^2/month. A total of

144 pollen taxa were recorded, of which 49 were assigned botanical affinities. Count totals for samples from Ankasa ranged from 183 to 743 grains, with an overall count of 5670 grains.

Major taxa. — Major taxa for Ankasa are presented in Figures 3, 5 and 6. *Drypetes* was over-represented in four samples, under-represented in ten samples, and absent from two samples. The R-rel values of this taxon ranged from 0.01 (Trap 26, 2014) to 7.64 (Trap 31, 2013), with a sample average of 1.37. In 2012, the average R-rel was 1.65, in 2013, 1.87 and in 2014, 0.52. The trap with the lowest average R-rel value was Trap 33 (0.03) and the highest was in Trap 31 (5.12). *Cynometra* was over-represented in seven samples, under-represented in nine samples and absent from none. The R-rel values of this taxon varied between 0.04 (Trap 31, 2013) and 8.48 (Trap 24, 2013), with a sample average of 1.44. In 2012 the average R-rel was 0.55, in 2013 it was 2.62 and in 2014 it was 1.33. Its lowest average R-rel was in Trap 31 (0.11) and the highest was in Trap 24 (4.36).

Homalium was over-represented in eight samples, and absent from the remaining eight samples. The R-rel values of *Homalium* ranged from 9.20 (Trap 31, 2013) to 127.92 (Trap 28, 2014), with a sample average of 26.05. In 2012, the average R-rel was 7.11, in 2013, 20.31 and in 2014, 54.52. The trap with the lowest average R-rel value was Trap 31 (21.5), and the highest was Trap 28 (63.09). *Vitex* was over-represented in three samples, under-represented in three, and not present in ten. It had R-rel values from 0.26 (Trap 24, 2014) to 49.01 (Trap 26, 2014). Its average R-rel in 2012 was 1.35, in 2013 it was 3.40, and in 2014, 9.85. The trap with the lowest average R-rel value was Trap 24 (0.09) and the highest was in Trap 26 (21.90). *Uapaca* was over-represented in six traps, under-represented in nine, and absent from one trap. Its R-rel values ranged from 0.32 (Trap 31, 2013) to 6.51 (Trap 26, 2012). Its average R-rel in 2012 was 2.08, in 2013 it was 0.38 and in 2014 it was 2.89. The trap with the lowest average R-rel was Trap 24 (0.69) and the trap with the highest R-rel value was Trap 26 (2.48).

Melastomataceae/Combretaceae was present, but under-represented in all samples. Its R-rel values ranged from 0.02 (Trap 28, 2014) to 0.45 (Trap 28, 2012). Its average R-rel in 2012 was 0.23, in 2013 it was 0.16, and in 2014, 0.07. The trap with the lowest average R-rel was Trap 31 (0.07) and the highest average R-rel was 0.22 (Trap 28). Moraceae-type pollen was over-represented in 12 samples and absent from four. Its R-rel values ranged from 2.70 (Trap 31, 2012) to 43.72 (Trap 26, 2012). In 2012, its average R-rel value was 10.90, in 2013 it was 2.26 and in 2014 it was 9.75. The trap with the lowest average R-rel was Trap 24 (3.58), and the trap with the highest average R-rel was Trap 26 (17.71).

Spatial and temporal separation of samples. — Ordination of the samples from Ankasa illustrates that samples cluster by trap (the same trap in different years e.g. Trap 24 in 2012, 2013 and 2014) rather than by year (e.g. Traps 24, 26 and 28 in 2012), this is illustrated by Figure 4, in which the hulls in: (a) demonstrate samples of the same trap over all three years, whereas (b) shows the traps linked by year of sampling.

Bobiri

Pollen assemblages from Bobiri were heavily dominated by one genus (*Celtis*), which was found in every sample and accounted for between 46.1% and 89.4% of the pollen sum. In addition to *Celtis*, taxa that were found in every trap were Pollen Type 46 (0.97–4.8%), Poaceae (0.1–1.5%), and Melastomataceae/Combretaceae (0.2–9.0%). Monolete and Trilete spores were present in abundances from 0.0% to 2.5% and 1.6% of the pollen sum, respectively. The pollen influx varied from 97 to 675 grains/cm^2/month, with an average of 462 grains/cm^2/month. A total of 104 pollen taxa were recorded, of which 43 were assigned botanical affinities. Count sizes for Bobiri ranged from 377 to 798 grains, with an overall count of 8295.

Major taxa. — Major taxa for Bobiri are presented in Figures 6, 7 and 8.

Celtis was over-represented in all samples. Its R-rel values ranged from 2.28 (Trap 20, 2014) to 4.41 (Trap 15, 2014). Its average R-rel in 2012 was 3.65, in 2013 it was also 3.65, and in 2014 it was 3.59. The trap with the lowest average R-rel value was Trap 15 (2.98) and the highest average R-rel was recorded in Trap 17 (4.25). *Triplochiton scleroxylon* K.Schum. was over-represented in four samples, under-represented in ten, and absent from two. Its R-rel values ranged from 0.04 (Trap 13, 2013) to 5.95 (Trap 20, 2013). The average R-rel of this taxon in 2012 was 0.07, in 2013 it was 2.83, and in 2014 it was 0.56. The trap with the lowest average R-rel value was Trap 18 (0.00), and the trap with the highest average R-rel value was Trap 20 (9.56).

Melastomataceae/Combretaceae pollen was over-represented in nine samples and under-represented in six. The R-rel values of Melastomataceae/Combretaceae in the plot ranged from 0.22 (Trap 17, 2014) to 10.31 (Trap 11, 2012). Its average R-rel in 2012 was 3.70, in 2013 it was 3.41 and in 2014, 4.37. The trap with the lowest average R-rel value was Trap 17 (0.57) and the trap with the highest average R-rel was Trap 11 (9.12). Moraceae pollen was over-represented in four samples, under-represented in eight, and absent from three. The R-rel values of this taxon ranged from 0.09 (Trap 13, 2014) to 1.45 (Trap 11, 2012). The average R-rel value of this taxon in 2012 was 1.29, in 2013 it was 0.12, and in 2014 it was 0.69. The lowest average R-rel per trap was 0.29 (Trap 17) and the highest was 1.47 (Trap 20). *Ceiba* was over-represented in one sample, under-represented in four, and absent from ten samples. Its R-rel values ranged from 0.06 (Trap 13, 2014) to 1.50 (Trap 20, 2014). The average R-rel value of this taxon in 2012 was 0.02, in 2013 it was 0.09, and in 2014 it was 0.31. The lowest average R-rel value per trap was 0.03 (Trap 17) and the highest was 0.5 (Trap 20).

Spatial and temporal separation of samples. — Ordinations of the samples from Bobiri illustrate that there is clustering by both trap and year (Fig-Figure 4). When hulls outlining the same trap in different years are overlain on the NMDS (Figure 4C), there is some overlap between traps.

When year hulls are overlain (Figure 4D), there is overlap in the ordination space occupied by the three years of sampling. Samples from 2013 fell among those from 2012 and 2014, indicating a temporal gradient along NMDS axis 1.

Discussion

Drivers of heterogeneity of pollen assemblages and characteristic taxa

Pollen assemblages from both plots, Ankasa and Bobiri, exhibit variation temporally and spatially. In some taxa, vegetation structure is likely to be the driving force in the depositional pattern observed, whereas for others, temporal factors, reproductive strategy or pollination syndrome are identified as potential drivers, although in reality, a complex interaction of all of these factors will have resulted in the results observed. Preservation is not, in this instance, likely to have affected the pollen assemblages recovered from traps, because pollen is highly resistant to degradation over long time scales (Fraser et al. 2012) and traps were deployed for intervals of one year only in this study.

There are many pollen types that do not have parent plants recorded in the vegetation surveys. This is partly due to limitations of the surveys themselves, as they do not encompass plants of < 10 cm DBH, or herbaceous taxa. Pollen from outside the boundaries of the plots may also contribute to pollen signals within the plots, but it is not possible to determine which taxa these are without more extensive vegetation surveys, and taking into account smaller plants and herbaceous taxa.

Ankasa. — *Drypetes* exhibits some spatial and temporal heterogeneity in R-rel values. *Drypetes aylmeri*, the only species of *Drypetes* in this plot, accounts for 9.6% of the basal area, and has an average height of 18.3 m. Trap 31 shows larger R-rel values than the other traps in the plot, despite there being a higher density of *Drypetes* trees in the proximity of Traps 24–28. There is a lower density of all trees in the vicinity of Trap 31 (Figure 2A), because a very large canopy tree died and left a gap in the canopy. The overall influx of pollen into Trap 31 is not higher than for the other traps, but the proportion of *Drypetes* pollen is higher. *Drypetes* is an entomophilous genus, but it is also dioecious, which may contribute to its pollen being dispersed by wind as well as by insects (ambophily), as described for other dioecious taxa (Bush & Rivera 1998).

Cynometra is a chiropterophilous taxon, in which flowers are borne on the trunk in the dry season. This may explain the taxon's abundance, as its pollen is released not into the canopy, but the understorey, making it more likely to be deposited in traps placed near the forest floor. This taxon is both under- and over-represented in traps within the plot, indicating that pollen deposition is very local and originates from trees close to traps.

Homalium exhibits the highest R-rel values of any taxon in this study, and is also highly spatially heterogeneous, being either consistently over-represented or consistently absent in the same trap over all years (apart from Trap 33, from which it is absent in 2012 but over-represented in 2013 and 2014). *Homalium deweverei* De Wild. et T. Durand, the only *Homalium* species in this plot, is bisexual but has open flowers, and produces flowers in large inflorescences, potentially accounting for the high levels of over-representation observed here. There is not a clear link between proximity to individuals and amount of pollen present. For instance, Trap 33 is nearest to one of the *Homalium* trees, but is not the Trap in which *Homalium* pollen is most abun-

dant. This discrepancy could be due to smaller (under 10 cm DBH) *Homalium* plants producing pollen at a local scale within the plot.

Vitex shows a localised signal, being over-represented in Trap 25 and 26, but almost absent from the other traps in the plot. Members of the genus *Vitex* do not account for a large part of the vegetation (1.2% of the basal area). The degree of over-representation varied between years, being most over-represented in 2014. *Vitex micrantha* Gürke, the most abundant species of *Vitex* in the Ankasa plot, is generally a small tree, whose average height in the plot is 20 m. The height of the individual closest to Traps 25 and 26 is 15 m, meaning that pollen produced by this individual would be unlikely to travel far, due to a lack of air currents in the understory of the forest (Kuparinen et al. 2007).

Uapaca corbisieri De Wild., the only species of *Uapaca* in this plot, is dioecious and is most over-represented in 2012 but consistently under-represented in 2013. The majority of trees of this taxon are near Traps 33 and 31, but its pollen does not show a clear spatial pattern of representation, with Trap 26 showing the most over-representation in 2012, but Traps 33 and 31 in 2014. The sexes of the plants of *U. corbisieri* in this plot are not known, a factor that may contribute to the spatial discrepancy observed in its pollen signal.

Bobiri. — *Celtis* exhibits a relatively uniform distribution of R-rel values over both years and traps, and is consistently over-represented. It is an anemophilous taxon, meaning that over-production and wide dispersal of pollen is expected. This taxon is also the most abundant in the vegetation, accounting for 14.7% of the stems in the plot. This taxon is one of the most evenly distributed, although the proportion of its pollen that originates from outside the plot is not discernible.

Triplochiton scleroxylon is most noticeably variable by year, being most abundant in 2013. Ghana experienced a rainfall deficit in summer 2013 (OCHA 2013) and, therefore, this pattern of pollen dispersal is consistent with observations that this species tends to flower primarily during years in which the July–August rainfall is below average (Jones 1974). That pollen is observed in 2012 and 2014 as well as 2013 implies that *T. scleroxylon* may flower more frequently than herbarium records suggest (albeit with a lower frequency of individuals flowering, or trees producing fewer flowers). The nature of botanical collection is such that observing flowers in the canopy is often very difficult, and therefore, collection of specimens is most likely to occur when flowers are abundantly apparent. It is possible, therefore, that when few flowers are produced, they are less likely to be sampled for herbarium specimens (an effect that has been noted for other taxa e.g. Asteraceae [Schmidt-Lebuhn et al. 2013]). This highlights a potential use for pollen traps in assessing phenology of tropical trees, as direct observations of these taxa is often impractical or impossible.

Ceiba is a pan-tropical genus that has been identified, in very low abundances (< 1.0% of pollen rain), in the Lake Bosumtwi record (Maley & Livingstone 1983), although it was not found in more recent studies of the Bosumtwi record (Miller & Gosling 2014). *Ceiba* is chiropterophilous, with pollen being distributed long distances by bats (20 km) (Dick et al. 2007). This may explain its scarcity in the fossil record, as pollen from bat pollinated flowers tends to be larger and therefore may be less likely to be borne on air currents and deposited in sediments (Stroo 2000). Here, there is a consistent presence of *Ceiba* pollen in all years in one trap, Trap 13, which is close to an individual of *Ceiba pentandra* (L.) Gaertn. Trap 20 in 2014 exhibits an over-representation of *Ceiba* pollen relative to the vegetation of the plot, although this may result from extra-plot pollen rain, as Trap 20 is relatively close to the edge. The presence of *Ceiba* indicates that small amounts of its pollen are transported on air currents, potentially also accounting for its presence in the fossil record.

Monolete and trilete spores are abundant in Ankasa assemblages, likely due to ferns growing (although not captured in the vegetation surveys) in the ecosystem. Ferns are abundant in moist environments due to their need for water to reproduce, and their lack of tolerance of fluctuating water availability (Page 2002).

Shared taxa. — Melastomataceae/Combretaceae pollen was present in both plots, although tended to be over-represented in Bobiri and under-represented in Ankasa. This taxon accounted for under 10% of the pollen sum in all samples at both plots, but accounted for a much larger proportion of the number of trees (52 stems) and basal area of Ankasa (13.2%) than in Bobiri (three stems and 0.9%).

Moraceae pollen was found in both plots at relatively low abundances (not above 5.5% in any sample), in Ankasa being heavily over-represented, whilst in Bobiri being under-represented. This is due to the differing number Moraceae individuals in each plot (one in Ankasa, and 11 in Bobiri, accounting for 0.12% and 1.64% of the vegetation, respectively), but could also be accounted for by pollen from outside of the plot contributing to the

signal in Ankasa. This finding differs from that in the Neotropics (Gosling et al. 2009) in which Moraceae pollen is found to be over-produced in a variety of ecosystems.

Melastomataceae/Combretaceae and Moraceae have been shown to over-produce pollen relative to their vegetative abundance in other modern pollen studies (Bhattacharya et al. 2011; Urrego et al. 2011). Here, however, we show that there is disparity in the representation of these taxa at a local level, and that pollen production by these taxa does not consistently over- or under-represent their vegetative abundance. At a sub-plot level, the more even distribution of the pollen of Melastomataceae/Combretaceae and Moraceae could indicate that these taxa disperse pollen higher up in the canopy, so that it is dispersed further and is rained into traps in a relatively more even manner, potentially giving a regional vegetation signal, but one that is not necessarily representative of the local vegetation.

The Melastomataceae and Combretaceae families together contain more than 4000 species, of which many are herbaceous and constitute elements of the under-storey. This may contribute to the seeming lack of correlation between large trees of these families and their pollen signal. The Moraceae is also a large and diverse family (> 1000 species), meaning that shrubby taxa of < 10 cm DBH may also be contributing to the pollen rain, confounding the wider signal.

Poaceae is present in low abundances in all samples from Ankasa and Bobiri, and *Alchornea* is present in all samples but one (Bobiri Trap 15, 2014). *Alchornea* has been recorded in the wider Ankasa Conservation Area, and the genus contains several shrubby species that are widespread in West Africa. Due to the fact that it is a small shrub whose recorded measurements are mostly < 10 cm DBH (Hawthorne et al. 1998; Hawthorne & Jongkind 2006), it is not recorded in the vegetation surveys of our plots, even if present. *Alchornea* is wind pollinated and so is likely to produce abundant pollen, meaning that its presence in all samples may also be due to transport from outside of the plots.

The presence of Poaceae in low abundances likely represents longer-distance transportation (the nearest open areas in which grasses could feasibly grow are not within 100 m of the plots). The likely presence of long distance transported pollen demonstrates that although the pollen assemblages within these plots are highly dominated by heterogeneous local pollen signals, a regional element may still be present, most notably evidenced by Poaceae grains, but potentially also by other pollen types without botanical parents within the plot. The reason for the low abundance of these grains is likely due to the closed-canopy nature of the ecosystems in which traps are placed, and the small size of the pollen traps resulting in a predominantly local signal being record (Jacobson & Bradshaw 1981). Identifying grass pollen to genus level would help to determine the local and regional components of the grass pollen signal; this is not generally possibly using light microscopy, but it has been shown that there is potential to identify grass pollen taxa based on their wall chemistry (Julier et al. 2016).

Comments on movement of pollen

Implications for models of pollen dispersal. — The movement of pollen within ecosystems has long been recognised as a complex phenomenon (Davis 1963; Tauber 1965). Factors such as wind speed and direction, canopy structure, and pollen weight and morphology can all influence how pollen grains move (Prentice 1985). Here, we have demonstrated that both spatial and temporal factors influence how pollen generated by plants in tropical West African forests moves and is deposited in ecosystems, and that pollen does not appear to be produced by plants in these plots in a consistent manner.

Some models assume an isotropic pollen dispersal curve (Sugita 1994), that is, that pollen is equally likely to be distributed all around the source. In our data, however, there are many instances where a taxon is over-represented in one trap, and under-represented or absent from one of the traps adjacent to it. This is likely due to the structure of the forest impeding pollen movement, so although in theory pollen distribution may be isotropic, in this example, it appears to be strongly anisotropic. Langrangian stochastic dispersal models of pollen dispersal (Kuparinen et al. 2007; Theuerkauf et al. 2013), which have now been integrated into the REVEALS model of quantitative vegetation reconstruction (Theuerkauf et al. 2016) may help to account for this discrepancy by modelling the movement of individual grains, although these models have yet to be applied to complex tropical systems.

Pollen sources of the same taxon in models of pollen distribution are often assumed to produce the same amounts of pollen, with pollen productivity values being generated for taxa using empirical data (Theuerkauf et al. 2016). Our data show that this does not appear to be the case: not only does the amount of pollen arriving in traps vary between traps within the same plot, even when there is a relatively uniform distribution of the

parent vegetation within the plot (e.g. *Drypetes*) but it also varies between years (e.g. *Triplochiton* and *Vitex*), indicating that pollen production from the same ecosystem may vary between years and sampling locations. Local variation in pollen deposition could be affected by small-scale variations in canopy openness and air movements within the forest (Kuparinen et al. 2007; Pan et al. 2014), whereas year-on-year variation could be due to small variations in temperature affecting phenology (Pau et al. 2013). Rainfall may also affect the amount of pollen reaching traps, either through being washed into them from the air or off leaves and flowers over-hanging the traps. Therefore, the amount of rainfall received at each site may affect the pollen assemblages at that site, depending on which taxa were flowering during rainfall (although the majority of taxa flower in the dry season). Melastomataceae/Combretaceae and Moraceae R-rel values (Figure 6) demonstrate that in different ecosystems, estimates of pollen productivity for the same taxon can be very different, and therefore that generating reliable pollen productivity estimates for tropical taxa could be problematic.

It is notable that the majority of the tree taxa in both plots are entomophilous, but only a relatively small proportion are represented in pollen traps. This indicates that there is significant variation in the amount of pollen produced and released into the environment by entomophilous taxa, and that despite the lack of anemophily, there was still considerable air-borne pollen deposition occurring in the plots.

Implications for artificial pollen trapping studies. — At Ankasa, we observed a high level of spatial consistency of pollen rain between years, likely due to low wind speeds under the canopy of the systems studied (Kuparinen et al. 2007). This leads to very different relationships between pollen and vegetation being observed within very small spatial scales. For instance, if Trap 33 alone had been sampled across the three years of the study, *Drypetes*, *Cynometra* (two of the most abundant tree species in the plot) and *Vitex*, would have been severely under-represented or entirely absent from the resultant pollen assemblages, whilst a mere 20 m away, Trap 31 exhibits very high levels of *Drypetes*. Based on the levels of heterogeneity observed, it is likely the case that, had more pollen traps been counted, a higher level of spatial heterogeneity would have been revealed.

At Bobiri, although there was separation of traps and years, a temporal change was clearer than at Ankasa. The three years over which pollen was collected in this study were not highly heterogenous, climatologically; 2013 was relatively dryer than 2012 and 2014, but this signal was only reflected noticeably in one taxon, *Triplochiton scleroxylon*. As only three years of data collection was possible, it is possible that a stronger temporal signal would be observed had more years of sampling been undertaken.

The disparity between artificial pollen trap samples from within single vegetation plots has implications for the design of future pollen-trapping studies, because high spatial resolution sampling is not the norm in such studies. It is also possible that estimates of the number of years needed for pollen trapping studies in the tropics of at least three (Bush & Rivera 1998) or at least ten (Haselhorst et al. 2013) in order to obtain representative samples may be unnecessarily high, and a good level of representation may be possible by increasing the spatial resolution of sampling within years, particularly in rainforest settings.

Although the most abundant trees and pollen taxa are the same for both plots, some of the most abundant pollen taxa (such as *Alchornea* and *Macaranga*) are not recorded in the vegetation. This is, largely, a vegetation survey design problem, however, and we would therefore recommend that vegetation surveys for palynological purposes include samples of shrubby and herbaceous taxa of < 10 cm DBH so that R-rel values can be obtained for taxa such as these.

Conclusion

In pollen assemblages recovered from Ankasa, the two most abundant vegetation taxa (*Cynometra* and *Drypetes*) are also the most abundant taxa in the pollen assemblages. In Bobiri, *Celtis* is the most abundant vegetation and pollen taxon. There are, however, many vegetation taxa in both plots that are not represented in the pollen assemblages, which is likely due to the dominance of entomophilous vegetation taxa.

Pollen production and dispersal are not homogenous in the plots studied, and there is considerable heterogeneity between pollen assemblages recovered from artificial pollen traps placed within the same plot. This is likely due to the structure of the vegetation and the phenology and pollen dispersal mechanisms of the vegetation taxa within our plots.

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