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Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record

William D. Gosling¹*, Francis E. Mayle², Nicholas J. Tate³ and Timothy J. Killeen⁴,⁵

1 = Department of Earth and Environmental Sciences, CEPSAR, The Open University, Walton Hall, Milton Keynes, MK7 6AA, UK.
2 = School of Geosciences, University of Edinburgh, Drummond Street, Edinburgh, EH8 9XP, UK.
3 = Department of Geography, University of Leicester, Leicester, LE1 7RH, UK.
4 = Centre for Applied Biodiversity Science, Conservation International, 2501 M Street, NW, Suite 200, Washington, DC 20037, USA.
5 = Museo de Historia Natural “Noel Kempff Mercado”, Avenida Irala 565, Casilla 2489, Santa Cruz de la Sierra, Santa Cruz, Bolivia.

* Corresponding author:
tel.: +44 (0)1908 655147
fax.: +44 (0)1908 655151
e-mail: W.D.Gosling@open.ac.uk
Abstract

Accurate differentiation between tropical forest and savannah ecosystems in the fossil pollen record is hampered by the combination of: i) poor taxonomic resolution in pollen identification, and ii) the high species diversity of many lowland tropical families, i.e. with many different growth forms living in numerous environmental settings. These barriers to interpreting the fossil record hinder our understanding of the past distributions of different Neotropical ecosystems and consequently cloud our knowledge of past climatic, biodiversity and carbon storage patterns. Modern pollen studies facilitate an improved understanding of how ecosystems are represented by the pollen their plants produce and therefore aid interpretation of fossil pollen records. To understand how to differentiate ecosystems palynologically, it is essential that a consistent sampling method is used across ecosystems. However, to date, modern pollen studies from tropical South America have employed a variety of methodologies (e.g. pollen traps, moss polsters, soil samples). In this paper, we present the first modern pollen study from the Neotropics to examine the modern pollen rain from moist evergreen tropical forest (METF), semi-deciduous dry tropical forest (SDTF) and wooded savannah (cerradão) using a consistent sampling methodology (pollen traps). Pollen rain was sampled annually in September for the years 1999-2001 from within permanent vegetation study plots in, or near, the Noel Kempff Mercado National Park (NKMNP), Bolivia. Comparison of the modern pollen rain within these plots with detailed floristic inventories allowed estimates of the relative pollen productivity and dispersal for individual taxa to be made (% pollen / % vegetation or ‘p/v’). The applicability of these data to interpreting fossil records from lake sediments was then explored by comparison with pollen assemblages obtained from five lake surface samples.
Pollen productivity is demonstrated to vary inter-annually and conforms to a consistent hierarchy for any given year: METF > SDTF > cerradão. This suggests an association between pollen productivity and basic structural characteristics of the ecosystem, i.e. closed canopy vs. open canopy vs. savannah. Comparison of modern pollen and vegetation revealed that some important floristic elements were completely absent from the pollen: Qualea and Erisma (METF), Bauhinia, Simira and Guazuma (SDTF), and Pouteria and Caryocar (cerradão). Anadenanthera was found to be abundant in both the pollen and flora of SDTF (p/v = 3.6), while Poaceae was relatively poorly represented in cerradão (0.2). Moraceae, Cecropia and Schefflera were found to be over-represented palynologically in all ecosystems. Overall, the data demonstrated that no one taxon could be used as a definitive indicator of any of the ecosystems. Instead, associations of taxa were found to be important: METF = Moraceae (>40%), Cecropia, Hyeronima, Celtis; SDTF = Anadenanthera, Apuleia, Ferdinandusa and non-arboreal Asteraceae, Bromeliaceae, Piper and fern spores; cerradão = Poaceae, Myrtaceae, Borreria, Solanum plus Asteraceae and fern spores. Interpretation of Poaceae pollen was highlighted as problematic, with relatively low abundance in the cerradão (<20%) in comparison to high abundance in lake environments (c. 30-50%). Re-examination of fossil pollen records from NKMNP revealed that modern vegetation associations were only established in the last few thousand years.

Words: 499/500

Keywords (x6): Amazon, Bolivia, Pollen trap, rainforest, dry forest, savannah
1. Introduction

The Late Quaternary vegetation history of much of the Neotropics remains poorly understood due to an insufficient understanding of the palaeoecological significance of fossil pollen records from this region (Bush et al., 2007). Attempts to reconstruct past changes in the relative distributions of moist evergreen tropical forests (METF), seasonally dry semi-deciduous tropical forests (SDTF) and savannahs have been hampered by difficulties in distinguishing between these ecosystems in palynological studies. This is because the majority of families and genera occur in more than one of these ecosystems, and their pollen can only rarely be identified to the species level (Pennington et al., 2000; Mayle, 2004, 2006; Mayle et al., 2004). For example, because grass pollen cannot be identified below the family level, it is often unclear in the fossil pollen record whether peaks in this pollen type reflect upland open savannas, or instead, aquatic grasses (Bush, 2002). Given that METF, SDTF and savannah ecosystems have marked differences in climatic requirements (UNESCO, 1981), species richness (Gentry, 1988; ter Steege et al., 2000), and/or carbon storage values (Adams and Faure, 1998), evidence for significant past changes in their respective geographic cover would be expected to reflect marked changes in past environmental conditions, patterns of biodiversity, and carbon storage values for the Amazon and adjacent regions (Pennington et al., 2000; Mayle and Beerling, 2004; Beerling and Mayle, 2006).

The characterization of modern pollen rain assemblages from different tropical ecosystems is an essential pre-requisite for the reliable interpretation of fossil pollen records. Although the number of modern pollen rain studies of Neotropical METF (Bush, 1991; Behling et al., 1997; Behling and da Costa, 2000; Bush, 2000; Bush et al., 2001; Bush and Rivera, 2001; Weng et al., 2004; Gosling et al., 2005), SDTF (Grabandt, 1980; Rodgers III and Horn, 1996; Bush and Rivera, 1998, 2001; Bush,
and savannah (Salgado-Labouriau, 1973, 1978; Ferraz-Vicentini and Salgado-Labouriau, 1996; Salgado-Labouriau et al., 1997; Parizzi et al., 1998; Ledru, 2002; Bastos et al., 2003; Martins and Batalha, 2006), has grown significantly over the last few decades, most of these studies come from outside the Amazon lowlands and very few have explored pollen-vegetation relationships. Furthermore, different investigators have typically employed differing sampling methods and approaches, thereby rendering comparison of pollen rain data between these different studies problematic.

Here, we use a consistent methodology (artificial pollen traps) to sample the pollen rain of METF, SDTF, and wooded savannah (cerradão) ecosystems in southwestern Amazonia and compare these data with floristic inventories of the parent vegetation to determine pollen-vegetation relationships. Once we have determined the characteristic pollen rain signature of each of these ecosystems, we then examine whether they can be reliably differentiated from each other. Comparison between these artificial pollen trap data and surface sediment pollen spectra from five lakes (two in evergreen forest and three in semi-deciduous dry forest) provide insights into the applicability of our findings to lake systems. The spatial extent to which our findings can be applied is then tested through comparison with previously published modern and fossil pollen records from the lowland Neotropics.

2. Study area

Noel Kempff Mercado National Park (NKMNP), in north-east Bolivia, provides an ideal location for investigating a range of lowland Neotropical ecosystems for three reasons. Firstly, located toward the southern margin of Amazonia, this 15,230 km² ecotonal area contains a mix of apparently mature METF, SDTF and savannah ecosystems (Killeen, 1998). This high beta (ecosystem) diversity makes it possible to
sample modern pollen rain across a variety of distinct ecosystems within a relatively small area. Secondly, numerous permanent vegetation study plots have already been established and surveyed within and around the park (Killeen, 1998; Panfil, 2001). By studying the pollen rain within these vegetation study plots, we are able to draw detailed pollen-vegetation comparisons. Thirdly, fossil pollen data from two lakes within NKMNP, Laguna Bella Vista and Laguna Chaplin (Mayle et al., 2000; Burbridge et al., 2004), are available for reanalysis based upon the modern pollen data.

Each ecosystem within our study belongs to a floristically distinct ‘ecoregion’ (Figure 1; Olson et al., 2001): 1) Madeira-Tapajós — dominated by METF and receives 2000-4000 mm precipitation per year with temperatures ranging from 23-27°C (UNESCO, 1981). Common arboreal families are Arecaceae (ex. Palmae), Cecropiaceae, Fabaceae, Melastomataceae, Moraceae, Myristicaceae and Vochysiaceae (Boom, 1986; Killeen, 1998; Panfil, 2001). 2) Chiquitano dry forest (SDTF) – characterized by mean annual precipitation between 700 and 1600 mm and a prolonged dry season (Gentry, 1995). Fabaceae and Bignoniacae are by far the most dominant families, whilst the Anacardiaceae, Capparidaceae, Euphorbiaceae, Flacourtiaceae, Myrtaceae, Rubiaceae and Sapindaceae are also important (Gentry, 1993a, b; Killeen et al., 2006). 3) The Cerrado – covers c. 1,900,900 km², as mapped by Olson et al. (2001), and is a complex gradation of terra firme South American savannahs that equates with the cerrado (sensu lato), as defined by Eiten (1972). A wide range of climatic conditions exists across the Cerrado ecoregion: 1000-2000 mm precipitation per year with a pronounced dry season (April – September) and mean annual temperatures ranging from 16°C to 25°C (Eiten, 1972; UNESCO, 1981). Despite the diversity of form and structure at the formation level (Furley, 1999), characteristic species include *Caryocar brasiliense, Qualea grandiflora, Byrsonima coccobifolia* and *Tabebuia*
ochracea (Killeen, 1998; Killeen et al., 2003; Oliveira and Marquis, 2002). In this paper we focus on the most wooded end of this spectrum; i.e. cerradão ‘densely wooded savannah’, which has a closed or slightly open canopy as defined by Eiten (1972).

3. Study locations

Modern pollen rain was collected from within permanent vegetation study plots from each of the ecosystems (ecoregions); METF from ‘Los Fierros 1’ (LF-1), SDTF from ‘Acuario 2’ (AC-2) and densely woody savannah from ‘Los Fierros cerradão’ (FC-2). Establishment of pollen traps within these plots affords a key opportunity to determine pollen-vegetation relationships by comparison between the pollen rain data and the detailed vegetation inventories (Killeen et al., 2006; www.salvias.net). The modern pollen rain from LF-1 was examined in detail by Gosling et al. (2005), with particular attention focused on the within-plot patterns of: i) spatial and temporal variations, ii) pollen-vegetation relationships, and iii) characteristic taxa. The findings of Gosling et al. (2005) are summarised below (sections 3.1 and 5.2.1) and placed in a broader ecological context through comparison with new data from AC-2 and FC-2. In addition, surface sediment samples were analysed to ascertain the nature of modern pollen deposited in a lake setting. These were Lagunas Bella Vista (13°37’S, 61°33”W) and Chaplin (14°28”S, 61°04”W), located within the Madeira-Tapajós ecoregion (METF) (Mayle et al., 2000; Burbridge et al., 2004), and Lagunas Mandioré (18°05”S, 57°33”W), Socórros (16°08”S, 63°07”W) and La Gaiba (17°47”S, 57°43”W), located within the Chiquitano ecoregion (SDTF) (Figure 1).

3.1 Los Fierros 1 (METF)
The LF-1 study plot (14°34′50″S, 60°49′48″W, c. 250 metres above sea level [m a.s.l.]) is 500 x 20 m and contains closed-canopy tall *terra firme* METF located within NKMNP. The vegetation of this plot is apparently mature and every plant ≥10 cm diameter breast height (d.b.h.) has been recorded and the floristic composition shown to be similar to that of the sister plot, ‘Los Fierros 2’, 460 m away (Panfil, 2001; Killeen *et al.*, 2003; Peacock *et al.*, 2007). Selective logging of *Swietenia* (mahogany) that has occurred within the wider region is thought to have had little effect on forest composition and structure (Killeen, 1998; Panfil and Gullison, 1998).

The important tall evergreen tree species within the plot are *Erisma uncinatum*, *Qualea paraensis* (both Vochysiaceae) and *Pseudolmedia laevis* (Moraceae), while *Phenakospermum guianensis* (Strelitziaceae), an arboreal herbaceous plant, is most abundant. Other important floristic elements are the palms, *Euterpe precatoria* and *Socratea exorrhiza* (Panfil, 2001; Gosling *et al.*, 2005). These floristic characteristics support our assertion that the LF-1 plot can be seen as representative of the tall *terra firme* METF in NKMNP and part of the wider Madeira-Tapajós ecoregion.

### 3.2 Acuario 2 (SDTF)

The AC-2 study plot (15°14′58″S, 61°14′42″W; c. 250 m a.s.l.), is 500 x 20 m and contains closed-canopy *terra firme* SDTF, located toward the northern limit of the Chiquitano Dry Forest ecoregion (Figure 1a). All woody stems ≥10 cm d.b.h. within the plot have been tagged and identified (Killeen *et al.*, 2006).

The three most abundant species within the plot are *Caesalpinia floribunda*, *Tabebuia roseo-alba*, and *Anadenanthera colubrina*, which comprise a quarter of all stems ≥10 cm d.b.h. (Table 1). The vegetation in the neighbouring ‘Acuario 1’ plot (parallel to AC-2, 460 metres away) is similar to that of AC-2, as revealed by
Sorensen’s Index of 0.64, when based on presence/absence data, and 0.61 when based on abundance data (Killeen et al., 2003). A detailed quantitative floristic analysis using 110 permanent plots in Chiquitanía and adjacent regions has shown that Caesalpinia, *Tabebuia*, and *Anadenanthera* are important in geographically separated regions of the Chiquitano Dry Forest but become less common in both the Amazonian and Gran Chaco forests (Killeen et al., 2006). These floristic findings support our assertion that pollen rain data from our study site are likely to be representative of SDTF on a regional scale across eastern Bolivia.

### 3.3 Los Fierros cerradão (densely wooded savannah)

The FC-2 plot is a 500 m transect (permanent vegetation plot) of undisturbed cerradão (14°35′10″S 60°50′26″W; c. 200 m a.s.l.). A line-transect survey of stems provides detailed floristic data of vegetation cover within the plot for comparison with pollen rain data (Mostacedo and Killeen, 1997; Killeen, 1998; Panfil, 2001).

The understorey of the plot is dominated by grasses, of which there are 16 species, comprising 79% of the vegetation cover. *Trachypogon plumosus* is the most dominant species, accounting for 42% of cover (Table 2). The most abundant woody taxa (≥1% cover) are *Caraipa aff. densifolia* (34 occurrences), *Miconia albicans* (27 occurrences), *Tibouchina* sp. (21 occurrences) and *Ormosia* sp. (14 occurrences). In addition, this plot contains many floristic elements typical of the wider Cerrado ecoregion, e.g. *Myrica* (14 occurrences), *Ouratea* (14 occurrences), *Roupala* (13 occurrences), *Eriotheca* (5 occurrences), *Pouteria* (5 occurrences), *Hancornia* (4 occurrences), *Caryocar* (4 occurrences), *Bowdichia* (4 occurrences) and *Emmotum* (4 occurrences), alongside eleven genera of commonly found broadleaf shrubs and semi-shrubs (Eiten, 1972, p. 211-212).
The cerradão vegetation of FC-2 has some similarities with its sister plot ‘Los Fierros cerrado (sensu stricto)-1’ (FC-1, 14º36’16”S, 60º 51’05”W), 2.3 km south-west, as shown by Sorensen’s Indices of 0.26 (presence/absence) and 0.19 (abundance) (Mostacedo and Killeen, 1997). In addition, the cerrado (sensu stricto) vegetation within NKMNP contains woody species which are prevalent across the Cerrado ecoregion, e.g. Qualea grandiflora and Tabebuia ochracea (Killeen, 1998).

4. Methods

4.1 Field and laboratory

To sample the pollen rain from METF (LF-1), SDTF (AC-2) and cerradão (FC-2) ten artificial pollen traps were deployed in each plot, each year for three years, providing a total of 30 traps per plot by the end of the three year study. These were positioned along the centre of the plots at 50 m intervals. Each pollen trap consisted of a plastic funnel, 7 cm in diameter, the outflow of which was covered by a 2.7 µm filter paper (Whatman GF/D) sealed to the plastic using putty. Above the filter paper the rest of the space within the funnel was filled with viscose rayon staple which was held in place by a coarse plastic mesh fastened across the mouth of the funnel with wire. This design allowed all pollen-sized material to be retained and water to drain freely. Each trap was mounted on a stake 50 cm above the ground, sufficiently high to ensure it was not covered by leaf litter and was clearly visible to allow for relocation. See Gosling et al. (2003) for further details on the trap design. Samples were collected annually, each September, over a 3 year period and are referred to by the year of their collection, i.e. 1999, 2000 or 2001.

Once collected, samples were sealed in grip-lock plastic bags and transported to the laboratory where they were stored at c. 4°C until processing using standard
techniques outlined in Faegri and Iversen (1989), with modifications detailed in Gosling et al. (2003). Two or three Lycopodium tablets were added to each sample to allow the calculation of pollen accumulation rates (Stockmarr, 1972). Pollen identifications were based primarily upon the modern pollen reference collection of c. 1000 taxa held at the University of Leicester and University of Edinburgh, compiled from herbarium material collected from the Museo de Historia Natural “Noel Kempff Mercado” (Santa Cruz, Bolivia) and the Edinburgh Royal Botanic Gardens (UK). Reference was also made to two pollen atlases (Roubik and Moreno, 1991; Colinvaux et al., 1999). Nomenclature follows Killeen et al. (1993) with modifications for pollen taxa following Burbridge et al. (2004). It should be noted that although Moraceae pollen is often difficult to distinguish from Urticaceae pollen, commonly depicted in the literature as Moraceae/Urticaceae-type, we are confident in assigning 2-pore grains to Moraceae because Urticaceae in NKMNP (Urera and Pouzolzia) has 3-pore pollen grains (Burn and Mayle, 2008). Even where Moraceae/Urticaceae (3 pore) grains are encountered, these are highly likely to belong to Moraceae because Urticaceae is only rarely found in the region (Killeen, 1998; www.salvias.net).

A total of 30 trap samples (10 traps x 3 years) were collected from each plot, although it was subsequently determined that five traps per year could adequately capture the spatial variation in the pollen rain (Gosling, 2004; Gosling et al., 2005). The research reported here is primarily concerned with differentiating between the pollen rain of different ecosystems, rather than the pattern of spatial variability of the pollen signal within a particular ecosystem. We have therefore aggregated the ≥100-grain pollen counts of each of the 5-10 pollen traps in a given plot in a given year to provide a total annual pollen count for each plot of ≥500 grains per year to allow inter-annual variations to be examined (Figure 2a). In addition, we present a summary ‘plot’ bar of
the average (mean) total land pollen (TLP) for the three years to facilitate easier
comparison between pollen data from ecosystem pollen traps and lake surface sediment
samples (0-1 cm below the mud-water interface, \( \geq 300 \) grains TLP) from five lakes
(Figure 2).

4.2 Pollen-vegetation comparisons

Modern pollen-vegetation relationships were investigated in the vegetation study
plots (LF-1, AC-2, FC-2). This was achieved by comparing the pollen rain data with
ecological and floristic data collected previously by Mostacedo and Killeen (1997),
Panfil (2001), Killeen et al. (2003, 2006) and http://www.salvias.net, with particular
reference to percentage occurrence of stems \( \geq 10 \) cm d.b.h. in the forest plots (LF-1 and
AC-2). This analysis was conducted at the plot scale, i.e. using the mean TLP from each
plots three years pollen trap data.

Pollen-vegetation comparisons were made by calculating the \% plot TLP / \% vegetation (‘p/v’). In the forest plots (LF-1 and AC-2) the vegetation value was based
on number of stems (\( \geq 10 \) cm d.b.h.) and basal stem areas of taxa were also calculated to
determine pollen production in relation to tree form and biomass (where basal area is
\( \pi r^2 \) calculated from d.b.h.). The combination of pollen, stem, and biomass data can
potentially differentiate between pollen arising from a few large trees, or instead
numerous small trees, of a given taxon. In the cerradão (FC-2) plot, vegetation data was
calculated from the percentage cover estimates from the line transect survey. It should
be noted, though, that these different methods of vegetation measurement, i.e. three-
dimensional biomass (based on basal area) vs. two-dimensional \% cover, potentially
complicates comparison of forest vs. savannah vegetation data.
We stress that the p/v ratios presented here are not intended as statistically robust calculations for the purpose of reconstructing vegetation cover from fossil pollen records. This is principally because of a poor understanding of the pollen source area, which is likely to extend beyond the plots from which the ecological data is derived (20 m wide plots). Instead, these values are intended solely as a rough guide or first-order approximation of the relative pollen productivity and dispersal of different taxa within these ecosystems.

5. Results

5.1 Modern pollen assemblages

Modern pollen assemblages from artificial pollen traps from the three vegetation study plots and surface sediment samples from five lakes are presented in Figure 2. Photographs of the most abundant taxa in the pollen rain of each of these ecosystems are shown in Figures 3 to 6.

5.1.1 Artificial pollen trap data

The pollen rain from the METF plot is dominated by Moraceae (>50% in all years) with Melastomataceae/Combretaceae present in every year >3%. Other taxa present in the pollen rain of all three years (≥1%) were Schefflera (ex. Didymopanax), Euterpe, Cecropia and Celtis. These taxa, plus Alchornea, were identified by Gosling et al. (2005) as the major components of the pollen rain within this plot. No one taxon dominates the modern pollen rain from the SDTF plot; Anadenanthera is the largest component in 1999 and 2001, and Moraceae during 2000. Both these taxa are present in all three years, along with Schefflera, Attalea, Poaceae and Pteropsidia (trilete) undif. (≥1%). The only two pollen types consistently present at values >3% in the cerradão
pollen rain are Moraceae and Poaceae. Other taxa ever-present (≥1%) in the cerradão plot are Schefflera, Cecropia, Alchornea, Melastomataceae/Combretaceae and Myrtaceae. While Euterpe, Borreria and Solanum are abundant (>3%) in the cerradão plot in one or two years (Figure 2a).

Pollen Accumulation Rates (PARs) vary widely, both between plots and inter-annually (Figure 2b). The largest individual component of the pollen rain in all plots is Moraceae, except in AC-2-99 and -01. Total PARs, considered on a year-by-year basis, show a consistent trend: METF > SDTF > cerradão. The two forest types show a similar inter-annual pattern in PARs; both exhibit PARs for 2000 and 2001 which are more than treble those of 1999. The PARs within the cerradão plot are consistently low over the 3-year study (<3000 grains cm⁻² year⁻¹).

5.1.2 Lake surface-sediment data

Surface pollen samples from Lagunas Bella Vista (LBV) and Chaplin (LC), which are both within the Maderia-Tapajós moist evergreen forest ecoregion, are dominated by Moraceae (53.9% and 40.0%, respectively). Other important pollen taxa at these two sites are: Cecropia, Poaceae and Celtis (>3%) and Arecaceae undif., Cyperaceae, Alchornea, Melastomataceae/Combretaceae and Pteropsidia (monolete) undif. (consistently ≥1%). Poaceae is the major component of the modern pollen rain at Lagunas Mandioré (LM), Socórros (LS) and La Gaiba (LLG) (51.6%, 34.2% and 33.1%, respectively), all of which are within the Chiquitano semi-deciduous dry forest ecoregion, but are also adjacent to extensive grass-dominated, seasonally-flooded, savannah wetlands. Pollen of Anadenanthera, Moraceae and Cyperaceae is also present in all these SDTF lakes (≥1%).
5.1.3 Inter-ecosystem comparison of pollen assemblages

Seven taxa occur in traps from every year and every ecosystem (*Schefflera*, Arecaceae undif., *Cecropia, Alchornea*, Melastomataceae/Combretaceae, Moraceae and *Celtis*). As a proportion of the pollen (Figure 2a), Moraceae is of greater abundance in the METF (60.4% total plot, 53.9% LBV, 40.0% LC) compared with SDTF (21.3% total plot, 7.3% LM, 4.5% LS, 12.4% LLG) or *cerradão* (23.0% plot). Moraceae PAR from traps in METF is more than ten times that of the other ecosystems (Figure 2b). The other six taxa ever-present in the trap data all comprise similar proportions of the pollen assemblages in all ecosystems (Figure 2a) but all produce more pollen, i.e. have higher PARs, in the METF (Figure 2b).

Poaceae reaches its highest proportion of the pollen rain in *cerradão* pollen traps (12.3% total plot) (Figure 2a) but has highest PARs in SDTF (Figure 2b) and lowest PARs in METF traps. Lake surface sediments have consistently higher proportions of Poaceae than their trap ecosystem counterparts.

Nine taxa are found predominantly in traps from one ecosystem: METF = *Hyeronima*; SDTF = Bromeliaceae undif., *Acacia, Anadenanthera, Apuleia leiocarpa* and *Ferdinandusa eliptica; cerradão* = *Machaerium* type, *Borreria* and *Solanum* (Figure 2). The most abundant of these is *Anadenanthera* (25.3% total plot TLP), which is also present in all the SDTF lake surface sediments; 1.9% LM, 8.9% LS, 4.7% LLG (Figure 2a).

5.2 Modern pollen and vegetation

5.2.1 METF

Within the METF plot, Gosling *et al.* (2005) found nine floristically important woody taxa (together comprising 39.7% total stems ≥10 cm d.b.h. within the plot) to be
completely absent from the pollen rain (see Table 1 in Gosling et al., 2005). Particularly noteworthy are the absence of the large canopy emergents, *Qualea paraensis* and *Erisma uncinatum*.

However, five taxa within the plot pollen rain were found to be important within the plot vegetation (see Table 2 in Gosling et al., 2005). Principal among these is Moraceae (16.0% stems), which is over-represented in the pollen relative to the vegetation (pollen/vegetation, i.e. p/v = 4.0). Other floristically important taxa are relatively over- or under-represented in the plot pollen rain: *Hieronima* (p/v = 1.7), *Melastomataceae/Combretaceae* (0.6), *Euterpe* (0.6), *Sloanea* (0.1), *Aspidosperma* (0.1) and *Crepidospermum* (0.03). Three taxa, *Alchornea*, *Celtis* and *Trema*, were found to be important in the modern pollen rain, but absent from the vegetation of the METF plot (stems ≥10 cm d.b.h.).

**5.2.2. SDTF**

The SDTF plot contains eight species identified as floristically important (stems ≥10 cm d.b.h.) that are absent from the pollen rain (Table 1). The most floristically important of these ‘palynologically silent’ taxa, in descending order of abundance, are: *Bauhinia rufa* (3.3% stems), *Simira cordifolia* (2.9%), *Guazuma ulmifolia* (2.7%), *Aspidosperma cylindrocarpon* (2.3%) and *Cedrela fissilis* (1.8%). Twenty-eight taxa are represented in both the vegetation and pollen rain of this SDTF (Table 3), together comprising 74.2% of total stems ≥10 cm d.b.h. and 84.4% of total basal area. Of these twenty-eight taxa, by far the most important in the pollen rain, when expressed as a percentage abundance of the plot TLP, are: *Anadenanthera* (25.3%), Moraceae (21.3%) and Arecaceae undif. (7.3%). Other significant taxa (≥1% pollen abundance) are: *Schefflera* (3.2%), *Melastomataceae/Combretaceae* (1.8%).
Apuleia leocarpa (1.2%) and Myrtaceae (1.0%). All of these taxa, except
Melastomataceae/Combretaceae (p/v = 0.3), are over-represented in the pollen rain
relative to their abundance in the vegetation: Moraceae (p/v = 36.2), Schefflera (16.1),
Anadenanthera (3.6), Apuleia leocarpa (2.1), Arecaceae (1.3) and Myrtaceae (1.3).
Three of these pollen taxa are also important in the vegetation: Anadenanthera (7.0% of
stems ≥10 cm d.b.h.), Melastomataceae/Combretaceae (5.7%) and Arecaceae (5.7%).
Six taxa are present in the modern pollen rain at significant levels (>3%) during at least
one year but are not recorded in the floristic inventory of the SDTF plot because they
are grasses, herbs or small trees (Figure 2a): Asteraceae (Asteroide/Cardue) undif.,
Piper, Poaceae, Ferdinandusa eliptica, and Pteropsidia (trilete) undif. Other non-
arboreal pollen types (NAP) are also present (>1%) during the 2000 field season.

5.2.3. Cerradão

The cerradão plot contains eleven species that comprise at least 1% of the
vegetation cover (excluding grasses) that are absent from the modern pollen rain, the
most important of which are: Caraipa aff. densifolia (10.4% cover), Ouratea boliviana
(4.3%), Roupala montana (4.0%), Similax aff. rufescens (2.8%), Erythroxylum
suberosum (1.8%), Manihot caerulescens (1.8%) and Pouteria ephedrantha (1.5%)
(Table 2).

Eighteen taxa are identified as present in both the pollen rain and the plot
vegetation (Table 4). Superficially, it appears that the palynological representation of
the vegetation is excellent with 89.4% of the vegetation cover represented in the pollen
rain. However, the overwhelming majority of the cover (78.8%) comprises various
species of Poaceae; consequently, only 50.0% of the non-grass cover within the plot is
represented in the pollen rain. The three taxa most abundant in the pollen rain are also
the three most abundant in the flora; however, the degree of over- and under-
representation of these taxa in the pollen relative to the vegetation is marked: Myrtaceae
(p/v = 2.2), Melastomataceae/Combretaceae (0.8) and Poaceae (0.2) (Table 4). The
most palynologically abundant taxa that are absent from the vegetation inventory of the
plot are Moraceae (23.0% total plot TLP), *Solanum* (6.6%) and Arecaceae undif.
(3.8%), as well as *Alchornea*, *Cecropia* and *Celtis*.

6. Discussion

6.1 Pollen-vegetation relationships

6.1.1 Ecosystem trends in pollen accumulation rates

The most striking pollen-vegetation relationship from the study plots is the
difference in PAR at the ecosystem level. Regardless of which year the pollen traps
were collected from, traps from the METF received more pollen per unit area than those
from the SDTF, which in turn accumulated more pollen than those from the *cerradão*
(Figure 2b). There are two possible reasons for this: i) the traps within the different
plots are differentially retaining the pollen, or ii) the quantity of pollen rain within the
ecosystems is different. If the first hypothesis is correct, this would suggest that traps
within drier environments are not retaining pollen as well as those in moister
environments, i.e. dry fibres allow grains to be blown out of the trap and/or drier
conditions cause oxidation and breakdown of those pollen grains retained. Therefore,
more damaged grains would be found in traps within the drier ecosystems, i.e. *cerradão*
> SDTF > METF. However, higher quantities of damaged grains are found within the
METF compared to either of the other two ecosystems (Figure 2b). In addition, METF
pollen taxa are found within other ecosystems’ pollen rain where no parent vegetation is
present (e.g. Moraceae, *Cecropia*) but not *visa versa* (e.g. Poaceae), which suggests that
METF is a more productive system with more widespread pollen dispersal. This hierarchy of PAR values (METF > SDTF > cerradão) suggests that in this setting the gross pollen productivity of an ecosystem can be used to provide basic information regarding the vegetation structure, i.e. closed canopy vs. open canopy vs. savannah (cerradão). Consistent patterns in inter-annual variation of PARs from forest ecosystems may also hint at a broader link between ecosystem pollen productivity and climate and raise concerns over the representativeness of pollen trap data gathered over a single year (Gosling et al., 2005).

6.1.2 Palynologically silent taxa

Each of the study plots contained taxa identified as important components of the flora that were not represented in the modern pollen rain. A total of nine such species were present within the METF flora, eight species within the SDTF, and eleven species within the cerradão. Gosling et al. (2005) demonstrated that the palynologically silent taxa in METF could be explained through reference to the predictive hierarchy based on flower structure and pollen strategy established by Bush and Rivera (2001). The strength of this relationship is further supported by our data from SDTF and cerradão. For example important components of the flora found to be absent from the pollen rain of SDTF and cerradão either have flower structures or pollination strategies associated with low pollen productivity. For example, in SDTF Bauhinia, Simira and Guazuma, are all hermaphroditic (Jardim et al., 2003), while in cerradão Pouteria is entomophilous (Pennington, 2004) and Caryocar is zoophilous (Mori, 2004).

6.1.3 Under-representation of taxa in the pollen rain
The p/v value for each taxon is a rough guide to the degree of its over- or under-representation in the pollen rain. In the METF, taxa that are under-represented in the pollen rain relative to their floristic abundance were shown, in the main, to hold to the hierarchy established by Bush and Rivera (2001) (Gosling et al., 2005). *Acacia* (8 stems) and cf. *Cupania* (one stem) are exceptions, as they have monoecious flowers (plants have separate male and female flowers), which are usually indicative of high pollen productivity, but in this case they are poorly represented in the pollen rain (0.04% and 0.06% total plot TLP, respectively), although this may be due to the stems of these two taxa being distant from the traps, especially with regard to the single stem of *Cupania* (Table 2 in Gosling et al., 2005).

In the SDTF plot nineteen taxa are under-represented in the pollen rain relative to their abundance in the vegetation (Table 3), of which thirteen have hermaphroditic flowers, four are monoecious (*Sterculia, Diolodendron, Sebastiana, Astronium*), and two are dioecious (plants have either male or female flowers) (Flacourtiaceae, *Lippia*) (Table 3). Dioecious plants are usually regarded as high pollen producers due to the need to disperse pollen between plants. However, under-representation of *Lippia* in the pollen rain may be due to its very small flower size and insect pollination (Atkins, 2004), while entomophily may also explain the under-representation in the pollen rain of *Sterculia, Diolodendron, Sebastiana*, and *Astronium* (Table 3).

There are fourteen under-represented taxa in the pollen rain of the cerradão plot relative to the flora. Of these, four are hermaphroditic (Melastomataceae/Combretaceae, *Ormosia, Mimosa, cf. Eriotheca*), five are dioecious (*Davillia, Apocynaceae, Flacourtiaceae, Alibertia/Amaioua, Lafoensia*), four may be dioecious or monoecious (Poaceae, *Matayba, Crotalaria, Galactica*), and one is monoecious (Cyperaceae) (Table 4). Twelve of these taxa are probably under-represented because they are zoophilous or
entomophilous and consequently do not produce or disperse much pollen. However, Poaceae and Cyperaceae do not conform to the predicted hierarchy of Bush and Rivera (2001) as they have pollination strategies and flower structures usually associated with high pollen productivity, i.e. they are both anemophilous (wind pollinated) and monoecious/dioecious. However, since both these families can reproduce asexually, through clonal spread, their low pollen values may reflect greater investment in this vegetative mechanism relative to sexual reproduction via flowers.

In the light of the hierarchy of Bush and Rivera (2001), the low abundance of grass pollen in the cerradão plot seems surprising (p/v = 0.2), even if one allows for clonal spread, although these data are not anomalous when compared with a pollen rain study of cerradão in Brazilia, Brazil (Ledru, 2002), which revealed similarly low grass pollen percentages (< 20%). In addition, the comprehensive study across the different structural formations within the Cerrado (sensu lato) ecoregion by Ledru (2002) found a gradation in the representation of grasses in the modern pollen rain, with Poaceae reaching higher pollen percentages in the more open cerrado (sensu stricto) and campo cerrado formations (>50% pollen), as one might expect. The cerradão data presented here and by Ledru (2002) raise the possibility of an ecosystem with grass comprising >50% cover not being dominated by grasses in their fossil pollen assemblages, indicating that caution must be exercised when interpreting the significance of Poaceae (or its absence) in the fossil pollen record.

6.1.4 Over-representation of taxa in the pollen rain

Three taxa, all tall trees, were found to be over-represented in the pollen rain of all three ecosystems: Moraceae, Cecropia and Schefflera. In the METF plot Moraceae comprises 64.3% TLP and 16.0% of the total stems in the plot (≥10cm d.b.h.), with the
anemophilous genus *Pseudolmedia* the most abundant tree (89 stems) and prolific pollen producer (p/v = 4.0, Table 2 in Gosling *et al.*, 2005). In the SDTF plot Moraceae comprises only three stems (≥10 cm d.b.h.), belonging to *Ficus eximia* (cleistogamous and wasp pollinated), *Sorocea guilleminiana* and *Maclura tinctoria* subsp. *tinctoria* (both wind pollinated). However, Moraceae pollen comprises 21.3% of the SDTF plot’s TLP (p/v = 36.2), demonstrating the overwhelming pollen productivity and dispersal of *Sorocea* and *Maclura* (both dioecious, anemophilous species) compared with the other taxa within this plot. With regard to the cerradão plot, Moraceae was entirely absent from the vegetation inventory but comprised almost a quarter (23.0%) of the plot TLP, demonstrating both the low pollen dispersal of the savannah tree taxa, as well as the effective long-distance transport of Moraceae pollen from METF several kilometres away. Furthermore, the relatively open structure of the savannah woodland would have been conducive to the deposition of wind-blown or rained-out Moraceae pollen in the traps.

*Cecropia* is found in all the ecosystems’ pollen rain (Figure 2) and vegetation (Killeen, 1998) although it is only recorded in the flora of the METF plot studied here. In the METF plot *Cecropia* reaches 4.4% total plot TLP and 0.4% stems (p/v = 12.3), whereas in the SDTF and cerradão plots it reaches 1.6% and 2.8% total plot TLP, respectively. *Cecropia* is, like Moraceae, monoecious/dioecious and anemophilous, so this over-representation can be explained through its anticipated effective long-distance dispersal, probably both within and between ecosystems.

*Schefflera* is present in the vegetation of all three plots at low levels (METF: two stems, SDTF: one stem, and cerradão: three occurrences) and is well represented in the pollen rain, which generates high p/v values for all three ecosystems: METF = 19.2, SDTF = 16.1, cerradão = 9.1. Although this taxon has hermaphrodite flowers (Jardim *et
al., 2003), which are not typical of anemophilous taxa (Frodin, 2004), its high over-representation in the pollen rain can probably be attributed to its ‘messy’ pollination syndrome (Horn and Ramirez, 1990), whereby its very open flower structure, with large numbers of exposed anthers, results in easily dispersed pollen, possibly indicating a degree of anemophily. In addition, four other palynologically important taxa (i.e. >3% TLP) were found to be over-represented within the pollen rain relative to their abundance in the plot vegetation, probably because they also have messy pollination syndromes: Hyeronima (METF), Anadenanthera (SDTF), Arecaceae undif. (SDTF), and Myrtaceae (cerradão).

6.2 Palynological differentiation between ecosystems

The greater pollen productivity and effective dispersal of pollen from the METF, compared with that from SDTF and cerradão (Figure 2b), highlights the difficulty of differentiating ecosystems where a regional patchwork of vegetation exists. The different proportions of Moraceae in SDTF vs. METF is borne out in both the pollen trap and lake surface pollen samples (Figure 2a). The lakes within the Madeira-Tapajós evergreen forest ecoregion contain Moraceae values of 53.9% and 40.0%, which are several fold higher than those recorded for the lakes within the Chiquitano dry forest ecoregion, which are 7.3%, 4.5% and 12.4% (Figure 2a). These data suggest that TLP values of >40% Moraceae are required to identify METF. They also show that double figure percentages of Moraceae pollen can be found in SDTF and cerradão due to long distance transport from METF and/or from a few individuals locally. However, it is also true that Moraceae pollen PAR drops off very rapidly once outside the METF, i.e. c. 8,900 grains cm$^{-2}$ within the forest but only c. 300 grain cm$^{-2}$ in the cerradão plot c. 1 km away (Figure 2b); although, as a percentage of the pollen rain, the values remain
relatively high (23.0% plot cerradão) due to the much lower overall pollen productivity
of this ecosystem.

*Schefflera* was identified as a good indicator of the *Cerrado* ecoregion by Ledru
(2002) because of its prolific pollen production and dispersal. Our pollen data support
the finding of Ledru (2002) that *Schefflera* is a high pollen producer, although its
presence (and over-representation) in the pollen rain of, not only the cerradão (one
component of the *Cerrado* ecoregion), but also SDTF and METF, demonstrates that it
cannot be considered an indicator-taxon of the *Cerrado*. Four other taxa are also found
in the pollen rain of all three plots (≥1%), i.e. Arecaceae, *Alchornea*,
Melastomataceae/Combretaceae and *Celtis* (Figure 2), although none can be considered
diagnostic of any particular ecosystem.

Poaceae has been shown to be proportionally more significant in the pollen rain
the more open the vegetation is, i.e. *cerradão* > SDTF > METF (Figure 2a). This pattern
is true for both artificial pollen trap and lake sediment data, although Poaceae pollen is
much more abundant in the lakes than the vegetation plots (Figure 2a). The high
proportion of Poaceae (and Cyperaceae) pollen in the lake sediments is due to the
presence of open and wetland savannah in the regional vegetation mosaic and the
abundance of these two taxa around the lake shores. It should also be borne in mind that
the relative contribution of aquatic taxa to the overall lake pollen assemblage is likely to
depend upon the pollen productivity of the terrestrial ecosystem in the lake catchment,
i.e. aquatics are more likely to mask the pollen signal from low pollen producing
cerrado or SDTF ecosystems rather than highly productive METF. This reinforces the
assertion of Bush (2002) that interpretation of Poaceae in the fossil record is often
problematic and it may be appropriate, in some cases, to exclude it from the TLP sum.
The most striking ecosystem-specific taxon is *Anadenanthera* which was restricted to SDTF, occurring in all three year’s plot data, with a total plot TLP value of 25.3%, and all three SDTF lakes, ranging from 1.9 to 8.9%. Once Poaceae and Cyperaceae are excluded from the lake TLP sums (as they likely reflect aquatic/wetland rather than terrestrial vegetation), *Anadenanthera* becomes more important, with recalculated values of 4.5%, 16.5% and 9.3% (Figure 2a).

Five other taxa were found to be restricted to one of the study plots (>1%): *Hyeronima* (METF), *Apuleia leocarpa, Ferdinandusa eliptica* (both SDTF), *Borreria* and *Solanum* (both cerradão). In addition, Myrtaceae was found in both SDTF and cerradão, but was over three times more abundant in the latter. However, the appearance of these taxa in the pollen rain of the plots was not consistent from one year to the next and they were also absent from the lake samples (Figure 2a), suggesting caution when considering these as potential ecosystem-indicator taxa. That said, *Borreria* was identified by Salgado-Labouriau (1973) as an important component of the vegetation and pollen rain elsewhere in the *Cerrado* ecoregion, so may be a good, regionally applicable, indicator of open ground; however it should be noted that *Borreria* can be found in a variety of ecological settings usually where the canopy opens out (Croat, 1978).

The separation of the arboreal (AP) and non-arboreal components (NAP) of tropical forests palynologically is not an easy task because many families or genera have species with a variety of growth forms, e.g. trees, shrubs, lianas (Gentry, 1993c). However, taxa identified as generally (Gentry, 1993c) or locally (Killeen, 1998) not being represented by trees have been categorised as non-arboreal (Figure 2) (although we recognise that some herbaceous taxa become woody or epiphytic in forested settings, which might result in an over-estimate of NAP in METF). SDTF is found to
have a higher proportion of NAP than the other two ecosystems, not withstanding grasses. Within the SDTF plot, Asteraceae, Bromeliaceae, *Piper* and fern spores are particularly important components of the NAP. Our finding of higher NAP in SDTF relative to METF is generally supported by the lake data (Figure 2a): METF lakes – 0.0% and 1.4% NAP, SDTF lakes – 1.6%, 3.0% and 4.0% NAP.

Together, all these data demonstrate that the pollen rain signals from modern METF, SDTF and *cerradão* ecosystems of NKMNP are not easily distinguished by the presence/absence of individual taxa, with *Anadenanthera* the possible exception. Therefore, an ‘assemblage approach’, in conjunction with a series of abundance thresholds, is best used, whereby associations of taxa that occur together in certain proportions, are indicative of a particular vegetation type; e.g. METF = > 40% Moraceae pollen, SDTF = *Anadenanthera* in association with Bromeliaceae undif. (probably *Pseudoananas sagenarius*), *Acacia*, *Apuleia leiocarpa* and/or *Ferdinandus* *eliptica*, *cerradão* = Poaceae in association with taxa such as *Machaerium* type, *Myrtaceae*, *Borreria* and/or *Solanum*.

### 6.3 Comparison with previous modern pollen studies

The extent of spatial applicability of the pollen assemblages found in NKMNP is examined through comparison with modern pollen studies from comparable vegetation types elsewhere in South America. With respect to *terra firme* METF, the Moraceae/Urticaceae pollen type is remarkably consistent in its percent abundance in the pollen rain (up to c. 60%) at NKMNP (LF-1), Cuyabeno (Ecuador), and the vicinity of Manaus (Brazil) (Bush *et al.*, 2001), demonstrating the importance of this taxon in the pollen rain of METF across a broad swathe of Amazonia. However, <30% Moraceae/Urticaceae pollen at Caxiuanã (Behling and da Costa, 2000) suggests that our
METF data may be less representative of eastern Amazonia, even though four
floristically important taxa of METF in NKMNP are also found in the pollen rain of this
site (Euterpe, Melastomataceae/Combretaceae, Moraceae/Urticaceae, and Sloanea).
Clearly, the broader scale applicability of our METF data depends upon the particular
region of Amazonia in question, which is unsurprising given the floristic heterogeneity
across Amazonia (ter Steege et al., 2006).

Our SDTF modern pollen assemblage has marked differences from previous
pollen rain studies of SDTF in: i) montane Colombia, where dominant taxa are
Pithecolobium, Schinus, Tara, Dodonaea, Clusia, and Escallonia (Grabandt, 1980), and
ii) Costa Rica, where there is 50% Anacardium type pollen and c. 5% Quercus and
Weinmannia (Rodgers III and Horn, 1996). None of these taxa are present in the
floristic inventory or pollen rain of our SDTF plot.

The pollen rain signal from the cerradão of NKMNP is similar to that found in
other modern pollen study sites from the Cerrado ecoregion (Salgado-Labouriau, 1973;
Salgado-Labouriau, 1978; Ledru, 2002) in two respects. Firstly, many key elements of
the flora are poorly represented, or absent, from the pollen rain and secondly, high
pollen input from nearby vegetation associations has been demonstrated to significantly
‘dilute’ the local pollen rain produced by the cerrado vegetation. Ledru (2002)
identified Byrsonima and Schefflera pollen as good cerrado indicators. In our study
both these taxa are also found in the cerradão pollen rain, although the Byrsonima
pollen was found to be indistinguishable from Machaerium (on the basis of the local
reference material collected from the study area). However, it is likely that this pollen
type most likely originates from Machaerium, as it is more abundant than Byrsonima in
the wooded vegetation of NKMNP; consequently, we refer to this pollen as
“Machaerium type”. The latter is well represented in the pollen rain of our cerradão
plot relative to its abundance in the vegetation survey (Table 4), which supports the
findings of Ledru (2002), even though it is only present in low abundance (2.0% TLP,
Figure 2a). In contrast to Ledru’s (2002) findings, our study shows that *Schefflera*
pollen has little ecological significance, because palynologically indistinguishable
species of this genus are present in all three ecosystems.

6.3 Implications for fossil pollen records

Changes in the geographic distribution, and floristic and structural characteristics,
of Amazonia’s forests since the last glacial period have long been debated (e.g.
Colinvaux *et al.*, 2000; Prado, 2000; Haffer and Prance, 2001; Cowling, 2004). The
modern pollen data presented here indicate that separation of different forest and
savannah ecosystems is possible, even where no major turnover in the pollen taxa is
identified, i.e. through examining changes in the abundance of certain taxa (e.g.
Moraceae) and/or relative changes in PAR or NAP components within an individual
fossil pollen record.

The fossil pollen records from Lagunas Bella Vista (LBV) and Chaplin (LC)
(Mayle *et al.*, 2000; Burbridge *et al.*, 2004) are now re-examined. During the last glacial
period (LBV >13,000 cal yr BP, and LC c. 50,000 – 11,400 cal yr BP) *Machaerium*
type, *Astronium, Paullinia/Roupala, Serjania* and Myrtaceae are found to be present.
These taxa are found in the pollen rain of SDTF and *cerradão* today but not in the
proportions found in the fossil records, suggesting that during this period the region was
dominated by a dry forest and savannah mosaic unlike those seen today.

*Anadenanthera* appears in these fossil records during the Holocene (LBV c.
10,800 – 1550 cal yr BP, and LC 10,160 – 650 cal yr BP) and occurs with fern spores
and grasses, which suggests that there are similarities with the SDTF formation seen
today. However, the absence of other dry forest taxa identified in our pollen rain study
suggests that these Holocene dry forests were compositionally different from the
modern Chiquitano dry forest.

Moraceae/Urticaceae pollen reaches 40% c. 1550 cal yr BP at LBV and c. 650 cal
yr BP at LC, associated with rises in Celtis, indicating the arrival, and dominance of,
METF in the catchment of these lakes, confirming the interpretation by Mayle et al.
(2000). This rainforest expansion is the earliest pollen assemblage in these fossil records
which is closely analogous with the modern pollen trap data.

In Laguna Chaplin the transition from a fossil pollen assemblage containing dry
forest elements (Anadenanthera) to one dominated by evergreen forest elements
(Moraceae) is accompanied by a relative increase in pollen influx rates (Burbridge et
al., 2004). The differential pollen productivity demonstrated between SDTF and METF
in the pollen traps means that this can now be interpreted as supporting evidence for the
late Holocene transition from a seasonally open SDTF to a permanently closed-canopy
METF. The absence of any change in sedimentology, or significant change in
sedimentation rates, during this transition (Burbridge et al., 2004) supports our
interpretation that this PAR shift was driven by a change in forest floristic composition
and structure rather than any change in sediment focusing, catchment in-wash, or lake
area.

Re-examination of these fossil records in the light of the modern pollen data
clearly demonstrates that the modern vegetation associations are relatively recent and
suggests that major reorganisation of vegetation assemblages in these ecotonal areas
should be anticipated for future climate changes, potentially similar in magnitude to
those seen earlier in the Holocene. Despite our finding that the majority of the LBV and
LC fossil pollen assemblages do not have an exact analogue match to the ecosystems
studied here, a clearer understanding of how the modern ecosystems are represented in
the pollen rain has allowed us to glean further insights into these palaeoenvironmental
records. This approach should be coupled with consideration of modern ecological
tolerances of the taxa involved (e.g. Bush et al., 2004; Punyasena et al., 2007, 2008;
Silman, 2007) to extract the maximum information from fossil pollen records, including
assemblages without modern vegetation analogues.

7. Conclusions

There is high inter-annual variability in the pollen rain collected in the traps may
indicate a close link between climate and pollen productivity and suggest that pollen
trap data from a single year should be viewed with caution (Gosling et al. 2005). In
addition, no one element of the pollen rain was found to be indicative of any particular
modern day vegetation association, except for perhaps Anadenanthera in the SDTF and
>40% Moraceae in the METF. Consequently, to achieve a robust differentiation of these
ecosystems in the fossil record, analysis of an assemblage of pollen taxa and their
occurrence in certain proportions must be identified to indicate the presence of an
ecosystem, with particularly characteristic associations being: i) METF –
Moraceae/Urticaceae (>40%), Cecropia (>3%), Hyeronima, and Celtis, ii) SDTF –
Anadenanthera (>3%), Apuleia leocarpa, Ferdinandusa eliptica and non-arboreal
components Asteraceae, Bromeliaceae, Piper and fern spores, iii) cerradão (densely
wooded savannah) – Poaceae, Myrtaceae, Borreria, Solanum plus Asteraceae and fern
spores.

Comparison between the pollen trap and lake surface sample data highlighted the
importance of understanding the catchment area from which samples are taken to
facilitate an accurate interpretation. Factors to be considered are likely pollen inputs
Re-examination of records from Lagunas Bella Vista and Chaplin in the light of the modern pollen data show that, while dry forest elements (*Anadenanthera*) are present at these sites during the Holocene, the fossil pollen assemblages as a whole are not perfect analogue matches with the modern pollen rain of the present-day Chiquitano SDTF of eastern Bolivia. This finding is probably a reflection of both the landscape-scale mosaic of vegetation being sampled in the pollen rain collected in the lakes, and the likely reorganisation of species within forest communities over centennial-millennial timescales. The modern pollen data confirm the arrival of a closed canopy evergreen forest in NKMNP during the last few thousand years (>40% abundance of Moraceae and increased PARs).

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Captions

**Table 1.** List of taxa representing $\geq 1\%$ of the total number of stems $\geq 10$ cm d.b.h. in the AC-2 plot in 1997, ranked by abundance of stems. Species highlighted in **bold** are not identified in the pollen data. Basal area calculated from the d.b.h. as measured in 1997. Ceas. = Caesalpinioideae, Mim. = Mimosoideae, and Pap. = Papilionoideae. Total number of stems = 512, total basal area = 192,733 cm$^2$. Raw data can be downloaded from [www.salvias.net](http://www.salvias.net).

**Table 2.** List of taxa representing $\geq 1\%$ cover (excluding grasses) along line transect survey in the FC-2 plot (500 m transect survey, 1993), ranked by number of occurrences. Species highlighted in **bold** are not identified in the pollen data. Abbreviations as Table 1 plus ex. = excluding. Total number of occurrences recorded = 1,541, total number of occurrences recorded excluding grasses = 326. Raw data can be downloaded from [www.salvias.net](http://www.salvias.net).

**Table 3.** List of taxa that are present in both the pollen rain and vegetation of the AC-2 plot in 1997 (stems $\geq 10$ cm dbh). $p/v = \%$ plot TLP / $\%$ of total stems of all taxa in plot surveyed. Flower structure and pollinator data from (Bush, 1995; Jardim *et al.*, 2003; Atkins, 2004; Beck, 2004; Fryxell, 2004; Lohmann, 2004; Mitchell, 2004; Webster, 2004). H = Hermaphrodite, M = Monoecious, D = Dioecious, A = Anemophilous, E = Entomophilous.

**Table 4.** List of taxa that are present in both the pollen rain and vegetation of the FC-2 plot (500 m transect survey, 1993). $p/v = \%$ plot TLP / $\%$ cover. Flower structure and
pollinator data from (Gentry, 1993c; Bush, 1995; de Almeida et al., 1998; Beck, 2004; Daly, 2004; Davis, 2004; Graham, 2004; Kubitzki, 2004; Rapini, 2004; Thomas, 2004). Abbreviations as Table 3.

Figure 1. Modern day vegetation distribution patterns in relation to the study site: a) ecoregion, b) biome. NKMNP = Noel Kempff Mercado National Park, LBV = Laguna Bella Vista, LC = Laguna Chaplin, LM = Laguna Mandioré, LS = Laguna Socórros, LLG = Laguna La Gaiba. Biomes and ecoregion definitions follow (Olson et al., 2001), base data from http://geodata.grid.unep.ch.

Figure 2. Pollen and spore summary pollen diagrams: a) percentage, and b) pollen accumulation rate (PAR). Identified pollen types ≥1% in any one sample are shown. Artificial pollen trap data are shown for the following vegetation study plots: Los Fierros 1 (LF-1) METF, Acuario 2 (AC-2) SDTF, and Los Fierros cerrado (FC-2) (wooded savannah). The pollen rain is collected between September 1998 – September 1999 (-99), September 1999 – September 2000 (-00), and September 2000 – September 2001 (-01). Diagonally striped bars show the mean value of all three years data for each plot. Surface sediment (0-1 cm depth) pollen spectra are shown for Laguna Bella Vista (LBV), Laguna Chaplin (LC), Laguna Mandioré (LM), Laguna Socórros (LS) and Laguna La Gaiba (LLG). LBV and LC pollen data are from Mayle et al. (2000) and Burbridge et al. (2004). Pollen of the Arecaceae genera Attalea and Euterpe (grey bars) are combined to create the Arecaceae undif. curve for LF-1, AC-2 and FC-2 to allow comparison with the lake surface sediment samples where these genera have not been differentiated. Machaerium type pollen encompasses Dalbergia (Fabaceae Pap.) and Byrsonima (Malpighiaceae) pollen. Other NAP (non-arboreal pollen) = Herbs/shrubs
(Alismataceae *Alisma*, Anacardiaceae *Alternanthera*, Araceae undif., Asteraceae
(Lactuceae) undif., Euphorbiaceae *Acalypha, Chamaesyce, Croton, Sebastiana*,
Fabaceae (Pap.) *Crotalaria*, Lamiaceae *Hyptis*, Loranthaceae *Psittacanthus*, Onagraceae
*Ludwigia*, Polygonaceae *Polygala*); weeds (Ambrosiineae *Ambrosia*, Anthemideae
*Artemisia*, Lythraceae *Cuphea*, Polygonaceae *Polygonum*); lianas/vines (Dilleniaceae
*Davilla*, Euphorbiaceae *Daleschampsia, Hevea*, Fabaceae (Pap.) *Clitoria, Galactia,*
Hippocrataceae *Anthodon*, Malpighiaceae *Banisteriopsis, Dicella*, Sapindaceae
*Paullinia*). * = Moraceae and Total PAR shown at 25% of all other curves. “Number of
traps” indicates the number of individual pollen trap samples (each with TLP \(\geq 100\)
grains) which are combined to give the aggregate pollen sum (TLP).

**Figure 3.** Photographs of pollen reference material from the collection at the University
of Leicester and University of Edinburgh. a-d) Araliaceae *Schefflera vinosa* (ex.
*Didymopanax vinosus*), e) Arecaceae *Attalea marpia*, f) Arecaceae *Euterpe precatoria,*
g-h) Bromeliaceae *Aechmea castellnavii*, i-k) Cecropiaceae *Cecropia concolor*, l-o)
Euphorbiaceae *Alchornea glandulosa*, p-r) Euphorbiaceae *Hyeronima alchorneoides*.

**Figure 4.** Photographs of pollen reference material from the collection at the University
of Leicester and University of Edinburgh. a-c) Fabaceae (Caesalpinioideae) *Apuleia*
*leiocarpa*, d-e) Fabaceae (Mimosoideae) *Acacia aroma*, f-g) Fabaceae (Mimosoideae)
*Anadenanthera colubrina*, h-k) Fabaceae (Papilionoideae) *Machaerium acutifolium*, l-o)
Melastomataceae *Miconia chamssois*, p-s) Combretaceae *Combretum* sp., t-w)
Moraceae *Helicostylis tomentosa*, x-y) Myrtaceae *Psidium guianense*, z-A) Piperaceae
*Piper aduncum*, B-E) Rubiaceae *Borreria latifolia*.
Figure 5. Photographs of pollen reference material from the collection at the University of Leicester and University of Edinburgh. a-d) Rubiaceae Ferdinandusa elliptica, e-h) Sapindaceae Serjania glabrata, i-k) Solanaceae Solanum apaense, l-m) Ulmaceae Celtis pubescens, n-o) Ulmaceae Trema micantha.

Figure 6. Photographs of pollen reference material from the collection at the University of Leicester and University of Edinburgh. a-d) Asteraceae Chromolaena squalida, e-f) Asteraceae Lessingianthus adenophylles, g-i) Cyperaceae Cyperus gigantes, j-k) Cyperaceae Oxycaxyum cubense, l-m) Poaceae Mesosetum cayennense.

Figures in attached files
<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Number of stems</th>
<th>% of total stems</th>
<th>Total basal area (cm²)</th>
<th>% of total basal area</th>
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**Clusiaceae**

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**Melastomataceae**

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**Poaceae**

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<td><em>Andropogon selloanus</em> (Hack.)</td>
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**Melastomataceae**

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**Fabaceae – Pap.**

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**Poaceae**

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**Flacourtiaicceae**

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**Myrtaceae**

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**Poaceae**

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<td>Ichnanthus procurrens (Nees ex Trin.) Swallen</td>
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**Poaceae**

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<tbody>
<tr>
<td><em>Manihot caerulescens</em> Pohl</td>
<td>6</td>
<td>0.39</td>
<td>1.84</td>
</tr>
</tbody>
</table>

**Fabaceae – Pap.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aeschynomene oroboides</em> Benth.</td>
<td>6</td>
<td>0.39</td>
<td>1.84</td>
</tr>
</tbody>
</table>

**Bombacaceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Eriotheca gracilipes</em> (K. Schum.) Robyns</td>
<td>5</td>
<td>0.32</td>
<td>1.53</td>
</tr>
</tbody>
</table>

**Myrtaceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Myrcia regnelliana</em> O. Berg.</td>
<td>5</td>
<td>0.32</td>
<td>1.53</td>
</tr>
</tbody>
</table>

**Sapotaceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pouteria ephedrantha</em> (A. C. Sm.) Radlk.</td>
<td>5</td>
<td>0.32</td>
<td>1.53</td>
</tr>
</tbody>
</table>

**Apocynaceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hancornia speciosa Gomes</td>
<td>4</td>
<td>0.26</td>
<td>1.23</td>
</tr>
</tbody>
</table>

**Caryocaraceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Caryocar brasiliense</em> Cambess. var intermediate</td>
<td>4</td>
<td>0.26</td>
<td>1.23</td>
</tr>
</tbody>
</table>

**Combretaceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Buchenavia aff. fomentosa</em> Eichler</td>
<td>4</td>
<td>0.26</td>
<td>1.23</td>
</tr>
</tbody>
</table>

**Clusiaceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Kielmeyera rubiflora</em> Camb.</td>
<td>4</td>
<td>0.26</td>
<td>1.23</td>
</tr>
</tbody>
</table>

**Fabaceae – Mim.**

<table>
<thead>
<tr>
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<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Mimosa</em> sp. 3</td>
<td>4</td>
<td>0.26</td>
<td>1.23</td>
</tr>
</tbody>
</table>

**Fabaceae – Pap.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bowdichia virgilioides</em> Kunth</td>
<td>4</td>
<td>0.26</td>
<td>1.23</td>
</tr>
</tbody>
</table>

**Icacinaceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Emmotum nitens</em> (Benth) Miers</td>
<td>4</td>
<td>0.26</td>
<td>1.23</td>
</tr>
</tbody>
</table>

**Poaceae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Axonopus canescens</em> (Nees) Kuhlm.</td>
<td>4</td>
<td>0.26</td>
<td>1.23</td>
</tr>
</tbody>
</table>

**TOTAL**

<table>
<thead>
<tr>
<th>Number of occurrences</th>
<th>% cover</th>
<th>% cover (ex. grasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1,435</td>
<td>93.12</td>
<td>440.18</td>
</tr>
<tr>
<td>(239)</td>
<td>(15.51)</td>
<td>(73.31)</td>
</tr>
</tbody>
</table>
Table 3

<table>
<thead>
<tr>
<th>VEGETATION DATA</th>
<th>POLLEN DATA</th>
<th>FLOWER</th>
</tr>
</thead>
<tbody>
<tr>
<td>POLLEN TAXA</td>
<td>No. stems ≥10 cm dbh</td>
<td>% of total stems of all taxa in plot (v)</td>
</tr>
<tr>
<td>Caesalpinia undif.</td>
<td>60</td>
<td>11.72</td>
</tr>
<tr>
<td>Flacourtiaceae</td>
<td>46</td>
<td>8.98</td>
</tr>
<tr>
<td>Tabebuia cf. roseo-alba</td>
<td>38</td>
<td>7.42</td>
</tr>
<tr>
<td>Anadenanthera</td>
<td>36</td>
<td>7.03</td>
</tr>
<tr>
<td>Arecaceae undif.</td>
<td>29</td>
<td>5.66</td>
</tr>
<tr>
<td>Melastomataceae/Combretaceae</td>
<td>29</td>
<td>5.66</td>
</tr>
<tr>
<td>Bigoniaceae</td>
<td>19</td>
<td>3.71</td>
</tr>
<tr>
<td>Machaerium type</td>
<td>18</td>
<td>3.52</td>
</tr>
<tr>
<td>Cordia</td>
<td>17</td>
<td>3.32</td>
</tr>
<tr>
<td>Sterculia</td>
<td>11</td>
<td>2.15</td>
</tr>
<tr>
<td>Malpighiaceae cf. Dicella</td>
<td>10</td>
<td>1.95</td>
</tr>
<tr>
<td>Rhamnidiaceae</td>
<td>10</td>
<td>1.95</td>
</tr>
<tr>
<td>Chorisia</td>
<td>9</td>
<td>1.76</td>
</tr>
<tr>
<td>Dilodendron</td>
<td>9</td>
<td>1.76</td>
</tr>
<tr>
<td>Spondias mombin</td>
<td>8</td>
<td>1.56</td>
</tr>
<tr>
<td>Sebastiana</td>
<td>7</td>
<td>1.37</td>
</tr>
<tr>
<td>Myrtaceae undif.</td>
<td>4</td>
<td>0.78</td>
</tr>
<tr>
<td>Tiliaceae cf. Luehea</td>
<td>4</td>
<td>0.78</td>
</tr>
<tr>
<td>Apuleia leocarpa</td>
<td>3</td>
<td>0.59</td>
</tr>
<tr>
<td>Moraceae</td>
<td>3</td>
<td>0.59</td>
</tr>
<tr>
<td>Serjania</td>
<td>3</td>
<td>0.59</td>
</tr>
<tr>
<td>Astronium cf. urundava</td>
<td>1</td>
<td>0.20</td>
</tr>
<tr>
<td>Schefflera</td>
<td>1</td>
<td>0.20</td>
</tr>
<tr>
<td>Hymenaea</td>
<td>1</td>
<td>0.20</td>
</tr>
<tr>
<td>Fabaceae (Mim.) cf. Samanea tubulosa</td>
<td>1</td>
<td>0.20</td>
</tr>
<tr>
<td>Amburana</td>
<td>1</td>
<td>0.20</td>
</tr>
<tr>
<td>Zanthoxylum</td>
<td>1</td>
<td>0.20</td>
</tr>
<tr>
<td>Lippia</td>
<td>1</td>
<td>0.20</td>
</tr>
<tr>
<td>TOTAL</td>
<td>380</td>
<td>74.22</td>
</tr>
</tbody>
</table>
Table 4

<table>
<thead>
<tr>
<th>POLLEN TAXA</th>
<th>No. of occurrences</th>
<th>% cover (v)</th>
<th>% plot TLP (p)</th>
<th>p/v</th>
<th>Structure</th>
<th>Pollinator</th>
</tr>
</thead>
<tbody>
<tr>
<td>Poaceae</td>
<td>1,215</td>
<td>78.84</td>
<td>12.29</td>
<td>0.16</td>
<td>M/D</td>
<td>A</td>
</tr>
<tr>
<td>Melastomataceae/Combretaceae</td>
<td>55</td>
<td>3.57</td>
<td>2.85</td>
<td>0.80</td>
<td>H</td>
<td>E</td>
</tr>
<tr>
<td>Myrtaceae undif.</td>
<td>22</td>
<td>1.43</td>
<td>3.15</td>
<td>2.20</td>
<td>H</td>
<td>E</td>
</tr>
<tr>
<td><em>Ormoxia</em></td>
<td>15</td>
<td>0.97</td>
<td>0.03</td>
<td>0.03</td>
<td>H</td>
<td>E</td>
</tr>
<tr>
<td><em>Davillia</em></td>
<td>12</td>
<td>0.78</td>
<td>0.12</td>
<td>0.15</td>
<td>D</td>
<td>E</td>
</tr>
<tr>
<td>Apocynaceae undif.</td>
<td>11</td>
<td>0.71</td>
<td>0.03</td>
<td>0.04</td>
<td>D</td>
<td>E</td>
</tr>
<tr>
<td>Flacourtiae undif.</td>
<td>11</td>
<td>0.71</td>
<td>0.06</td>
<td>0.08</td>
<td>D</td>
<td>E</td>
</tr>
<tr>
<td><em>Mimosa</em></td>
<td>7</td>
<td>0.45</td>
<td>0.12</td>
<td>0.27</td>
<td>H</td>
<td>E</td>
</tr>
<tr>
<td>Asteraceae (Asteroide/Cardue) undif.</td>
<td>5</td>
<td>0.32</td>
<td>1.47</td>
<td>4.59</td>
<td>M/D</td>
<td>E</td>
</tr>
<tr>
<td>Bombacaceae cf. <em>Eriotheca</em></td>
<td>5</td>
<td>0.32</td>
<td>0.06</td>
<td>0.19</td>
<td>H</td>
<td>E</td>
</tr>
<tr>
<td><em>Matayba</em></td>
<td>5</td>
<td>0.32</td>
<td>0.09</td>
<td>0.28</td>
<td>M/D</td>
<td>E</td>
</tr>
<tr>
<td>Cyperaceae</td>
<td>4</td>
<td>0.26</td>
<td>0.08</td>
<td>0.31</td>
<td>M</td>
<td>A</td>
</tr>
<tr>
<td><em>Schefflera</em></td>
<td>3</td>
<td>0.19</td>
<td>1.72</td>
<td>9.05</td>
<td>H</td>
<td>E</td>
</tr>
<tr>
<td><em>Machaerium</em> type</td>
<td>3</td>
<td>0.19</td>
<td>1.98</td>
<td>10.42</td>
<td>H</td>
<td>E</td>
</tr>
<tr>
<td><em>Alibertia/Amaioua</em></td>
<td>2</td>
<td>0.13</td>
<td>0.03</td>
<td>0.23</td>
<td>D</td>
<td>E</td>
</tr>
<tr>
<td><em>Crotalaria</em></td>
<td>1</td>
<td>0.06</td>
<td>0.03</td>
<td>0.50</td>
<td>M/D</td>
<td>E</td>
</tr>
<tr>
<td><em>Galactia</em></td>
<td>1</td>
<td>0.06</td>
<td>0.06</td>
<td>1.00</td>
<td>M/D</td>
<td>E</td>
</tr>
<tr>
<td><em>Lafoensia</em></td>
<td>1</td>
<td>0.06</td>
<td>0.03</td>
<td>0.50</td>
<td>D</td>
<td>E</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>1,378</strong></td>
<td><strong>89.42</strong></td>
<td><strong>-</strong></td>
<td><strong>-</strong></td>
<td><strong>-</strong></td>
<td><strong>-</strong></td>
</tr>
</tbody>
</table>
Figure 1
Figure 3