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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. Gosling [a,*], Francis E. Mayle [b], Nicholas J. Tate [c], Timothy J. Killeen [d,e]

[a] Department of Earth and Environmental Sciences, CEPSAR, The Open University, Walton Hall, Milton Keynes, MK7 6AA, UK
[b] School of Geosciences, University of Edinburgh, Drummond Street, Edinburgh, EH8 9XP, UK
[c] Department of Geography, University of Leicester, Leicester, LE1 7RH, UK
[d] Centre for Applied Biodiversity Science, Conservation International, 2501 M Street, NW, Suite 200, Washington, DC 20037, USA
[e] Museo de Historia Natural "Noel Kempff Mercado", Avenida Irala 565, Casilla 2489, Santa Cruz de la Sierra, Santa Cruz, Bolivia

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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.

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

* Corresponding author. Tel.: +44 1908 655147; fax.: +44 1908 655151.
E-mail address: W.D.Gosling@open.ac.uk (W.D. Gosling).

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(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 and Horn, 1996; Bush and Rivera, 1998, 2001; Bush, 2000), 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 km^2 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' (Fig. 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 Bignoniaceae are by far the most dominant families, whilst the

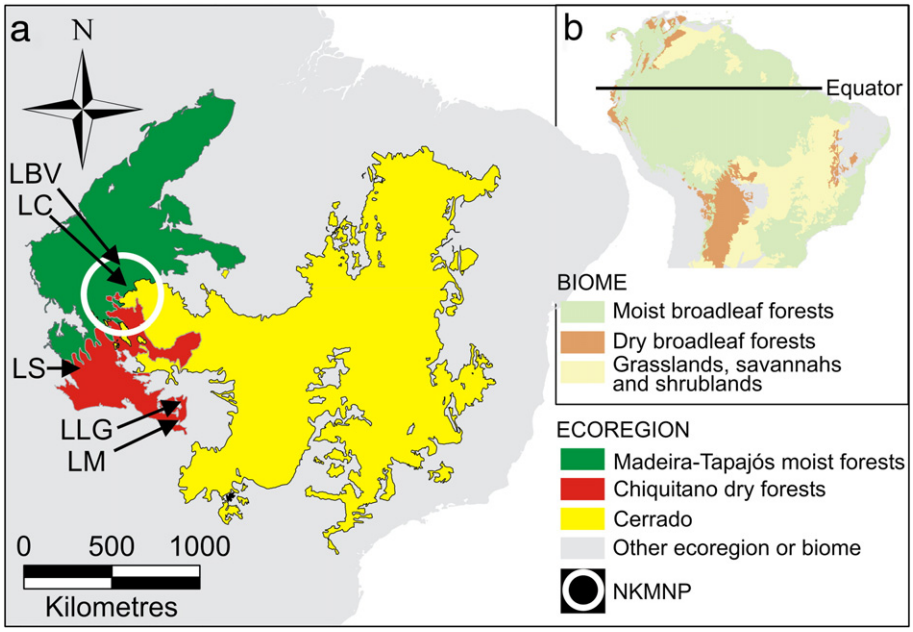

Fig. 1. Modern day vegetation distribution patterns in relation to the study site: a) ecoregion, b) biome. NKMNP = Noel Kempff Mercado National Park, LBV = Laguna Bella Vista, LC = Laguna Chaplin, LM = Laguna Mandioré, LS = Laguna Socórros, LLG = Laguna La Gaiba. Biomes and ecoregion definitions follow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