Characterization of Neotropical forest and savannah ecosystems by their modern pollen spectra

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Abstract

Controversy surrounds the Quaternary palaeoenvironmental history of Amazonia. It is unclear whether moist evergreen forest, savannah or seasonally dry forest dominated the Amazon basin at the last glacial maximum (c. 21,000 years B.P.). In part the uncertainty surrounding the palaeoenvironmental history of Amazonia stems from a poor understanding of the ecological significance of the fossil pollen records from the region. In order to improve interpretations of the fossil pollen record it is essential to better understand the nature of the pollen rain produced by modern ecosystems.

In this thesis, three Neotropical ecosystems equivalent to those alluded to above were characterised by their modern pollen rain. This was achieved by examining samples collected in artificial pollen traps located within permanent (50 x 200 m) vegetation plots in the Noel Kempff Mercado National Park area, Bolivia. In each plot 10 traps were sampled for one field season (September 1998 to September 1999, or September 2000 to September 2001) and 5 traps were sampled from two additional field seasons (between 1998 and 2001). Pollen counts of at least 100 grains were made for each trap. In total 318 pollen taxa were distinguished, of which 116 were identified. The characteristic pollen from each of the three ecosystems were determined through a series of steps: spatial and temporal variations were explored using Spearman's Rank correlations, the distinctive taxa of each ecosystem were identified using Principal Components Analyses (PCA), and the representativity of the pollen for each ecosystem was examined by comparing pollen and vegetation abundances. These analyses revealed a small number of taxa that can be used to characterize these ecosystems. Further PCA showed that it is possible to differentiate between the ecosystems by assessing the *relative proportions* of *Didymopanax*, *Alchornea*, *Anadenanthera*, Melastomataceae/Combretaceae, Moraceae/Urticaceae, Myrtaceae, Palmae, Pteropsidia (trilete), Poaceae and *Solanum*. These findings mean that it is now possible to detect these ecosystems in the fossil pollen record and consequently further information regarding the nature of the vegetation change in the Amazon basin can be gained.

Acknowledgements

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List of acronyms and abbreviations

BP	Years before present (1950)
Caes.	Caesalpinioideae
cf.	Compare (from the Latin *confer*)
CO_2	Carbon dioxide
Fab.	Fabaceae
ka	Thousands of years
LGM	Last Glacial Maximum
Mim.	Mimosoideae
MHNSC	Museo Histoia Natural “Noel Kempff Mercado”, Santa Cruz
NKMNP	Noel Kempff Mercado National Park
pa	Per annum
Pap.	Papilionoideae
PAR	Pollen accumulation rate (grains cm^{-2} $year^{-1}$)
PCA	Principal components analysis
ppmv	Parts per million by volume
T “number” - “year”	T = trap
e.g. T89-01	“number” = unique location number, e.g. 89
	“year” = year collected, e.g. 2001
Undiff.	Undifferentiated

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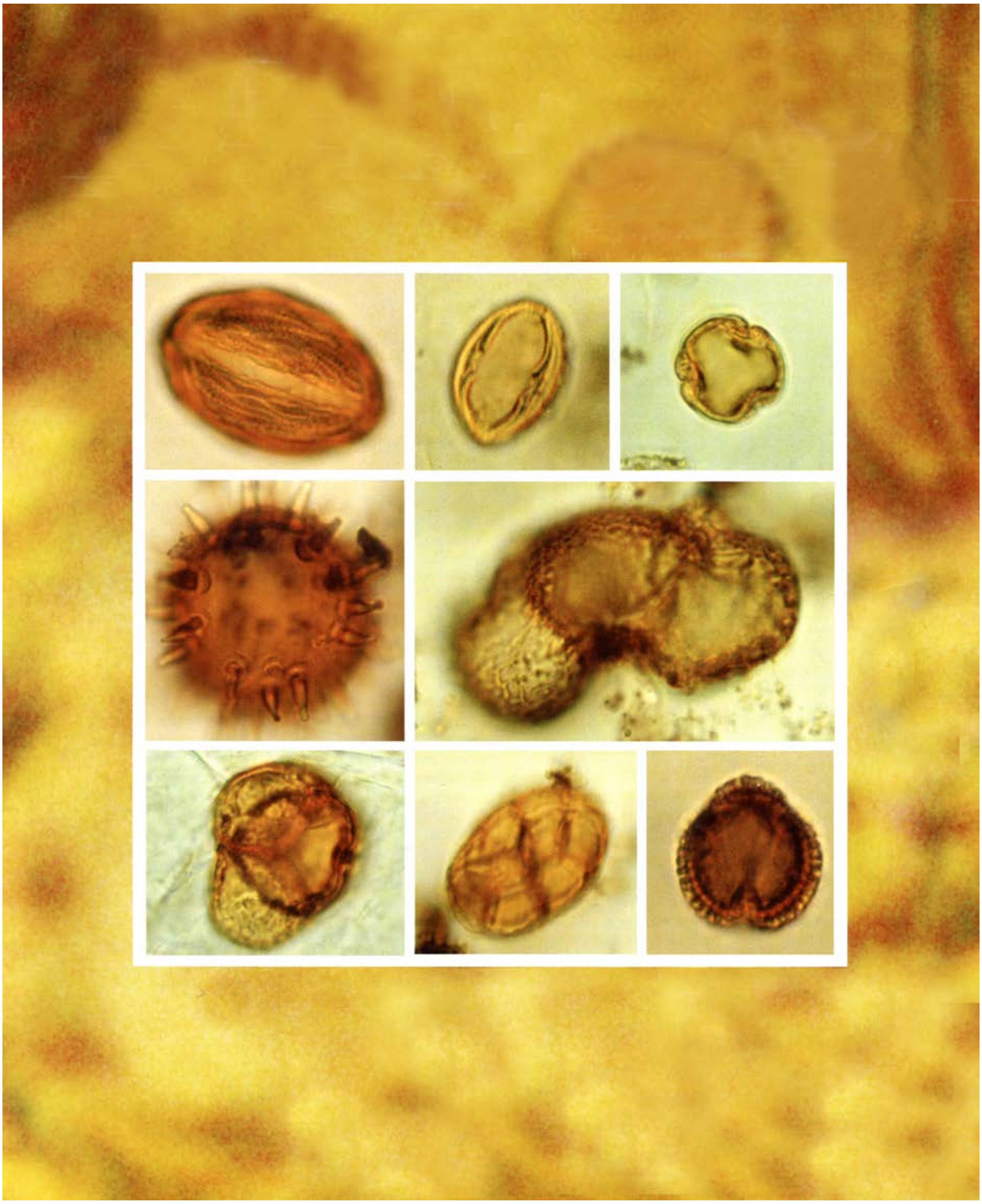


Chapter 1

Introduction

Frontispiece (previous page): Designed by K. Moore for "Leicester Latitude" magazine and subsequently modified by K. Price. Original photographs taken by R.E. Burbridge and the author.

Chapter 1

Introduction

In this short introductory chapter to the thesis there are two sections. Firstly, a brief rationale is given and the overall aim of the project is stated (section 1.1). Secondly, the structure of the thesis is outlined (section 1.2).

1.1 Rationale and overall aim

The palaeoenvironmental history of the Neotropics is poorly understood because of a lack of records and an inability to interpret those records that do exist. The first of these problems can only be addressed by identifying and investigating further sites in the Neotropics that contain long palaeoenvironmental records. This process is time consuming, costly and relies to a certain extent on luck in finding suitable sites. The second problem, however, stems from an insufficient knowledge of modern day ecology to fully interpret the palaeoecological records that do exist. Given access to Neotropical ecosystems, it is possible to advance the understanding of the modern environment and therefore advance this aspect of Neotropical palaeoecology.

The primary source of information for reconstructing the palaeoenvironments of the Neotropics has been the fossil pollen record (e.g. Leyden, 1985; Absy *et al.*, 1991; Colinvaux *et al.*, 1996; Bush *et al.*, 2000; Mayle *et al.*, 2000; Ledru *et al.*, 2001; Behling *et al.*, 2002; Weng *et al.*, 2002; Sifeddine *et al.*, 2003; Burbridge *et al.*, in press). Different interpretations of these records have contributed to the controversy concerning the kind of vegetation and climate that existed in Amazonia at the last glacial maximum (c. 21 ka BP). The three proposed scenarios can be summarised as follows: i) Amazonia became arid to such an extent that most of the basin was covered by savannah and evergreen forests were restricted to isolated refugia (Haffer, 1969; Haffer and Prance, 2001), ii) Amazonia became slightly drier resulting in the replacement of the evergreen forest by other ecosystems at the margins but a core area of evergreen forest was maintained over the majority of the basin (Colinvaux *et al.*, 1996; Colinvaux *et al.*, 2001), and iii) a drier climate over Amazonia lead to the replacement of evergreen forest with deciduous and semi-deciduous dry forest (Prado and Gibbs, 1993; Pennington *et al.*, 2000). These fundamental differences demonstrate the extent of controversy regarding past climate and vegetation change in this region. This in turn presents significant problems when trying to assess the possible impact of any future climate change.

Current interpretations of the fossil pollen records from the Neotropics are hampered by two interconnected problems: i) the huge species diversity of the region means that many families and genera are represented in a range of ecosystems, and ii) the pollen from these plants are often only identifiable to genus or family level. This means that divisions seen in the flora are not identifiable in the pollen. This has resulted in previous authors using a few key indicator taxa to distinguish ecosystems in the fossil pollen record. These divisions are crude when compared with the vast floristic diversity of the Neotropics. Therefore ecological information is lost because the fossil pollen data are not fully understood. To establish how to extract more ecological information from the fossil pollen record, a better understanding of the relationship between modern pollen assemblages and their parent vegetation is required. However, few such studies currently exist from the Neotropics. Therefore, the aim of this research is to characterise a range of Neotropical ecosystems by their modern pollen spectra and determine the extent to which they can be differentiated from each other.

1.2 Structure of thesis

Following this introduction chapter there are eight further chapters. In chapter 2 the rationale behind the need to characterise Neotropical ecosystems by their modern pollen spectra is explored in detail and the key aims of this project are stated. In chapter 3 the reasons for locating this study in and around Noel Kempff Mercado National Park, Bolivia are given. In chapters 4 and 5 the practical methodology applied in this investigation is explained and the results of methodological developments and pilot research are presented. The findings of this preliminary research are used to establish the exact focus of the main project. Then, in chapter 6, the detailed ecological backgrounds of the ecosystems studied for the main part of the thesis are reported. Following this, two results and discussion chapters contain the main body of the research. In chapter 7 the characteristic pollen rain from each of the ecosystems is determined. Then, in chapter 8, the extent to which these ecosystems can be differentiated on the basis of their characteristic pollen spectra is investigated. Finally, in chapter 9, a summary of the findings is presented, the extent to which the aims have been achieved is assessed and the implications for interpreting the palaeoenvironmental records of Amazonia are discussed.

Chapter 2

Understanding Amazonian palaeoenvironments

Chapter 2

Understanding Amazonian palaeoenvironments

The rationale, aim and structure of the thesis were introduced in chapter 1. The purpose of chapter 2 is to explain more fully the rationale for the research. To achieve this, the chapter is divided into two sections. The first section explains the need to accurately understand the palaeoenvironmental history of Amazonia and outlines the current thinking on the issue. This is accomplished in four sub-sections which focus on: i) the role of palaeoenvironmental understanding in anticipating the impacts of human induced climate change, with particular emphasis on Amazonia, ii) the nature of the evidence currently available for understanding environmental change in the Amazon basin and the reliance on fossil pollen records, iii) the controversies surrounding the interpretation of the palaeoenvironmental history from these fossil pollen records, and iv) the research that is required to achieve an improved understanding of the fossil pollen record. In the second section it is demonstrated how the study of modern pollen-vegetation relationships in the Neotropics can be used to better interpret the fossil pollen record from Amazonia. This is accomplished in three stages: i) the theory behind modern pollen-vegetation studies, ii) the current research from the Neotropics, and iii) the most appropriate location for conducting a modern-pollen study aimed at improving the understanding of Amazonia's palaeoenvironmental history. In the light of these considerations three specific research aims are presented in section 2.3.

2.1 The study of palaeoenvironments

Since the Industrial Revolution in 18th century Europe, human activity has had a greater and greater impact on the environment of planet Earth. During this period people became capable of modifying the systems that regulate the environment of the planet on a global scale. To understand how these modifications will affect the planet in the future, the past must be studied to provide evidence of how the consequences of global environmental change may impact on the planet (Diamond, 1998).

2.1.1 Future climate change

Human induced climate change is now widely accepted by the scientific community (Folland and Karl, 2001). However, the understanding of how this climate change will impact on the globe and human society is still poor (Schneider and Sarukhan, 2001). Anthropogenic activities, such as the burning of fossil fuels and deforestation, have lead to a significant shift in global carbon from geological and terrestrial stores into the atmosphere (Prentice, 2001), which has resulted in a measured increase in global atmospheric CO_2 concentrations of c. 80 ppmv in the last two hundred years (Ciais, 1999; Park, 2001). These emissions, coupled with the release of other 'greenhouse gases', are expected to increase global mean temperatures possibly by as much as 3.5 ^{o}C by the year 2080 (Cubasch and Meehl, 2001; Prather and Ehhalt, 2001). However, despite much funding and research, there is yet to be a consensus of opinion among scientists as to the consequences for the earth (e.g. Melillo *et al.*, 1993; Cox *et al.*, 2000; Dale *et al.*, 2000; Grace and Rayment, 2000). One of the main concerns is the effect of any climate change on terrestrial ecosystems and any possible feed-backs from a change in vegetation cover back into the climate system (Dale *et al.*, 2000). Uncertainty primarily arises due to a poor understanding of how the vegetation and the atmosphere interact (Eltahir, 1996). This means that it is difficult to say how changes in climate will affect vegetation. To explore these interactions numerous computer models have been developed to simulate the ways in which the planet might react to different anthropogenically modified futures (e.g. Cox *et al.*, 2000; Grace and Rayment 2000; McAvaney, 2001). Each of these computer models paints a different picture of the future dependant on the information placed into it. This has led to further uncertainty about the way in which the human modified Earth will evolve.

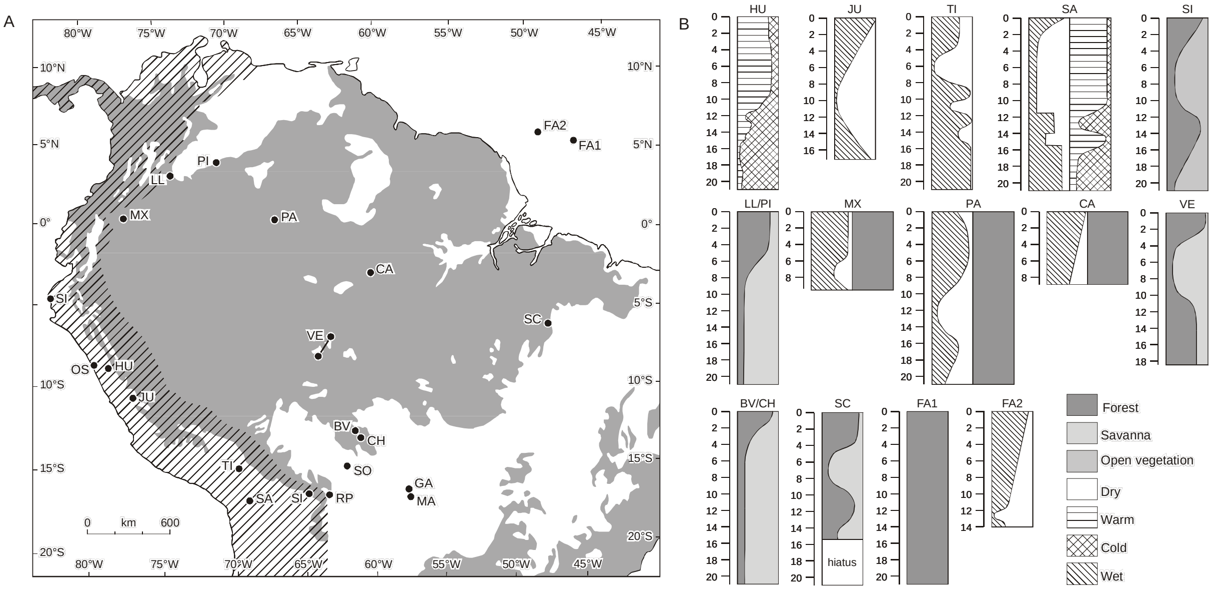
Modellers have turned to the empirically-based palaeoclimatic record to validate predictions of future climate change. Theoretically, if a model can be run backwards in time to successfully simulate the independently substantiated climate record, then it can be run forwards in time with more confidence. This area of research was the subject of a European Science Foundation conference, entitled “Achieving Climate Predictability using Palaeoclimatic Data” chaired by Jean Claude Duplessy (2001), which aimed to bring together palaeoenvironemental researchers and climate modellers. As a result of the conference, North Africa and Amazonia where identified as areas where the palaeoclimatic history was so poorly understood as to hinder the development of such models.

Amazonia is an integral part of the global carbon cycle. Today it is one of the largest terrestrial carbon stores on the planet and as a consequence of this any climate change, past or future, is likely to effect its role in this cycle (Seiler and Conrad, 1987; Grace *et al.*, 1995; Keller *et al.,* 1997; Philips *et al.,* 1998; Prentice and Lloyd, 1998; Houghton *et al.*, 2000; Tian *et al.*, 2000; Behling, 2002; Mayle *et al.*, in press). Ciais (1999) and Park (2001) demonstrate that palaeofluctuations in CO_2 levels between glacial and interglacial periods were of a comparable magnitude (c. 80 ppmv) to those occurring due to human activity. An understanding of these palaeofluctuations could therefore be used to gain an insight into how any future change in CO_2 levels might affect the globe. If Amazonia’s role in carbon cycling and environmental change can be better understood then it may be possible to: i) predict how Amazonia is likely to respond to increased atmospheric CO_2, and ii) determine how a deforested Amazon Basin might effect the build up of CO_2 in the atmosphere. The next two sections detail the palaeoenvironmental evidence available from the region and the problems that have been encountered in interpreting them.

2.1.2 The Amazonian palaeoenvironmental record

Figure 2-1a illustrates the small number of sites that have been investigated in Amazonia and highlights their sparse distribution. Figure 2-1b demonstrates the fragmentary nature of the palaeoenvironmental records that do exist. These figures demonstrate the lack of data available to build palaeoenvironmental reconstructions of the Amazon basin. It is this lack of data which has forced researchers to extrapolate between sites in an attempt to understand the palaeoenvironments of the region. These generalised interpretations are liable to be revised as new data become available.

In addition to the paucity of the palaeoenvironmental record for Amazonia, a generally poor understanding of Amazonian ecology hinders the interpretation of the palaeoenvironmental record that does exist. It has long been recognised that a good understanding of ecology is required to maximise the information that can be extracted from the palaeorecord (West, 1964). The massive ecological diversity of Amazonia and the regions inaccessibility mean that, to date, only a relatively small proportion of the area has been studied (Tanner *et al.* 1998). As a result of this lack of understanding, only a limited number of indicator taxa are commonly used to identify ecosystems palynologically, e.g. Moraceae/Urticaceae to identify forest and Poaceae to identify savannah. This method of interpretation is a simplification of the massive ecological diversity found across Amazonia (Dinerstein *et al.*, 1995; Olson *et al*., 2001), which means that much potential vegetation and climate information is lost in the interpretation of the fossil pollen signal. For example, little palynological differentiation of forest types has been attempted even though many occur under different environmental conditions.



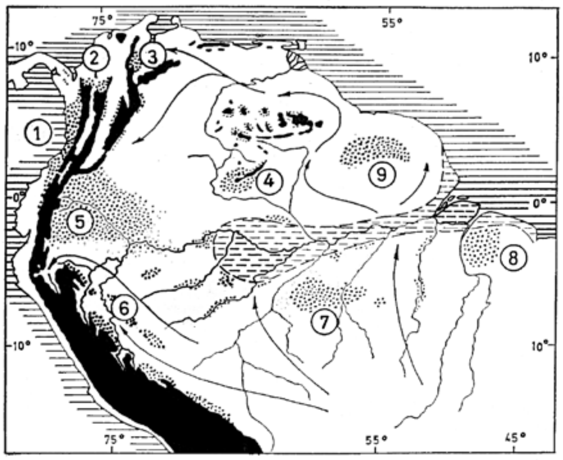
Source: Mayle *et al.* (in press)

Figure 2-1: Fossil pollen records from South America. Fossil pollen cores are scarce and unevenly distributed across the Amazon basin. Key for sites: HU, Huascaran ice-core (Thompson *et al.* 1995, 9°07’S, 77°37’W); JU, Lake Junin (Seltzer *et al.* 2000, 11°S, 76°W); TI, Lake Titicaca (Baker *et al.* 2001a, 17°S, 69°W); SA, Sajama ice-core (Thompson *et al.* 1998, 18°06’S, 68°53’W); SI, Siberia (Mourguiart and Ledru 2003, 17°50’00”S, 64°43’08”W); PI, Laguna El Pinal (Behling and Hooghiemstra 1999, 4°08’N, 70°23’W); MX, Maxus 4 (Weng *et al.* 2002, 0°27’S, 76°37’W); PA: Lake Pata (Colinvaux *et al.* 1996, Bush *et al.* 2002, 0°16’N, 66°41’W); CA, Lago Calado (Behling *et al.* 2001, 3°16’S, 60°35’W); VE, Porto Velho/Humaita (de Freitas *et al.* 2001, 8°43’S, 63°58’W to 7°38’S, 63°04’W); BV, Laguna Bella Vista (Mayle *et al.* 2000, Burbridge *et al.* submitted, 13°37’S, 61°33’W); CH, Laguna Chaplin (Mayle *et al.* 2000, Burbridge *et al.* submitted, 14°28’S, 61°04’W); SC, Serra dos Carajas (Absy *et al.* 1991, Sifeddine *et al.* 2001, 6°35’S, 49°30’W); FA1, Amazon Fan (Haberle and Maslin 1999, 51°2.7’ N, 47°1.8’W); FA2, Amazon Fan (Maslin and Burns 2000, 5°45’N, 49°06’W); GA, Laguna La Gaiba (17°47’00”S, 57°43’00”W); MA, Laguna Mandioré (18°05’31”S, 57°33’46”W); SO, Laguna Socórros (16°08’30”S, 63°07’00”W); RP, Rio Piray (Servant *et al.* 1981, 17°55’S, 63°15’W); OS, Ostra (Andrus *et al.* 2002, 8°55’S); SI, Siches (Andrus *et al.* 2002, 4°40’S).

2.1.3 Theories of vegetation change in Amazonia

In the light of sparse, fragmentary and poorly understood palaeoenvironmental data, large question marks still hang over the environmental evolution of Amazonia. A key question currently under debate is: What was Amazonia like at the Last Glacial Maximum (LGM)? There are two theories, which disagree over how wet the Amazon was during this time and the relative distribution of different ecosystems (figure 2-2).

a) The forest refuge hypothesis

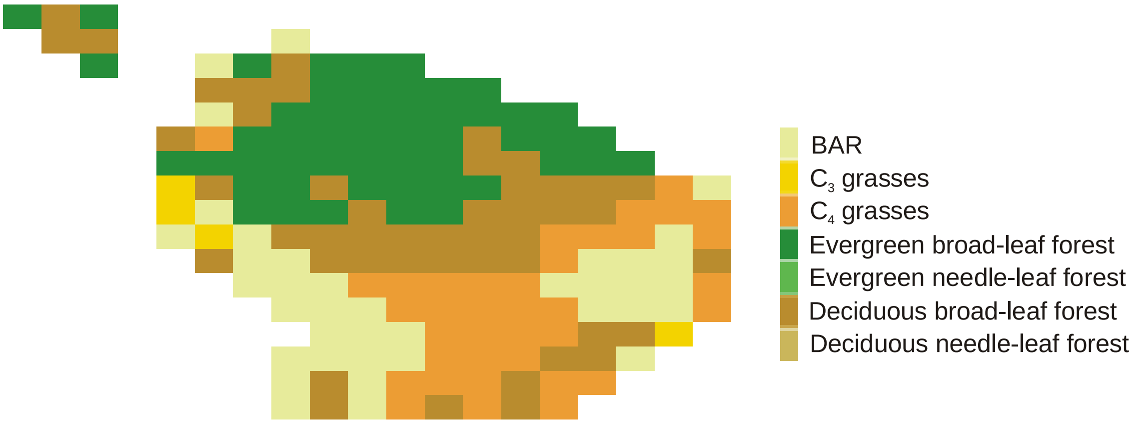


1. Chocó refuge
2. Nechí refuge
3. Catatumbo refuge
4. Imerí refuge
5. Napo refuge
6. East Peruvian refuge
7. Madeira-Tapajós refuge
8. Belém refuge
9. Guiana refuge

Hatched area = interglacial Amazonian embayment (sea level raised by about 50 meters)
Black areas = elevations above 1000 meters

Source: Haffer (1969)

b) The continuous forest hypothesis



Source: Mayle *et al.* (in press)

Figure 2-2: Amazonia at the Last Glacial Maximum (c. 21 ka BP). a) Haffer's fragmented Amazon based on areas of high diversity, and b) a shrunken but not fragmented distribution of Amazon forest predicted by a dynamic global vegetation model (Mayle *et al.*, in press).

The first of these is the 'Refugia Hypothesis', first put forward by Haffer (1969). Haffer (1969) presented a theory that suggested that during the Pleistocene Amazonia was subjected to a number of dry periods, which coincided with glaciation at high latitudes. These, he envisaged, resulted in the fragmentation of the Amazonian forest into a number of much smaller forest "refugia", surrounded by expanded savannahs and arid areas occupying most of the basin (figure 2-2a). Haffer (1969) used this theory to explain the high diversity and endemism of avifauna in Amazonia, but did not present any palaeoenvrionmental data to support this argument. Subsequently, palaeoenvironmental data have been presented in support of an arid Amazon during the last glacial period. Work by van der Hammen (1974 and 1991), Absy and van der Hammen (1976) and van der Hammen and Hooghiemstra (2000) have shown alternations between forest and grassland cover during the Pleistocene from pollen records in Amazonia. Also, lake level lowstands have been recorded during the Pleistocene at the Sabana de Bogata (van’t Veer and Hooghemstra, 2000) and Lake Titicaca (D’Agostino *et al.*, 2002) in the Andes and in the lowlands at Lake Valencia (Salgado-Labouriau, 1980) and sediment hiatuses at Carajas (Absy *et al.*, 1991) and Laguna Bella Vista (Mayle *et al.* 2000) which could be interpreted as indicative of drier climate conditions that may have favoured savannah ecosystems. Also, Damuth and Fairbridge (1970), Brown and Ab’Saber (1979) and Ab’Saber (1982) have interpreted geomorphological data as evidence of a drier climate. The Haffer hypothesis has been recently further developed by Haffer and Prance (2001) who have proposed orbital forcing as a sufficient mechanism to create an arid Amazonia. Haffer and Prance (2001) presented data from multiple sources (biotic, palaeobotanic, geomorphological and climatic) that suggest that during the proposed arid periods Amazonia was covered in a patchwork of vegetation, which included forest “refugia”. Further supporting evidence comes from Andean ice core records where lower nitrate levels during the last glacial stage were interpreted as evidence of reduced forest cover in Amazonia (Thompson *et al.*, 2000).

Colinvaux (1987 and 1991), Salo (1987), Colinvaux *et al.*, (1996), Colinvaux and de Oliveira (2000) and Colinvaux *et al.*, (2000) have argued strongly that there is insufficient evidence to support a dry Amazonia hypothesis. Firstly, the reliability of the biogeographical data used by Haffer to formulate the original hypothesis has been questioned by Nelson *et al.* (1990)

who suggested that some of the results might have been an artefact of the sampling density. In addition to this, palaeoenvironmental evidence from long cores collected from areas of lowland Amazonia that the Haffer hypothesis predicted would be savannah, such as Lake Pata (Colinvaux *et al.,* 1996), show no evidence of vegetation change during the Pleistocene. Where vegetation change has been recorded in the fossil pollen record (e.g. Absy *et al.*, 1991; Mayle *et al.*, 2000) Salo (1987) has argued that it is as a result of shrinkage of the region at the margins and that any climate change was insufficient to result in the fragmentation of the ecosystems. Modelling of global vegetation dynamics (Turcq *et al.*, 2002; Mayle *et al.*, in press) supports this theory of shrinkage at the margins. Both predict a reduced, but not fragmented, broadleaf evergreen forest in the Amazon Basin at the LGM (figure 2-2b). There is also no evidence of vegetation change in records from the Amazon fan, which should record a homogenised signal for the whole of the basin (Haberle and Maslin, 1999; Hoorn, 2001). These factors raise concerns over Haffer's theory. Therefore, an alternative environmental history is required to explain the high levels of endemism in the Amazon. Colinvaux *et al.* (2000) suggested that despite some re-assortment of taxa due to a cooler and drier climate during glacial periods that: "*The overwhelming property of the Amazon ecosystems in the face of… documented global change was stability.*" (p. 164). In the light of this interpretation Colinvaux (1987 and 1998), Bush (1994), Cowling and Sykes (1999) and Cowling *et al.* (2001) have proposed alternative mechanisms for generating high endemism in Amazonia. This research suggests that many complex processes are factors in the creation of high endemism, including the disturbance of the ecosystems and the creation of special environmental conditions by changes in temperature and CO_2.

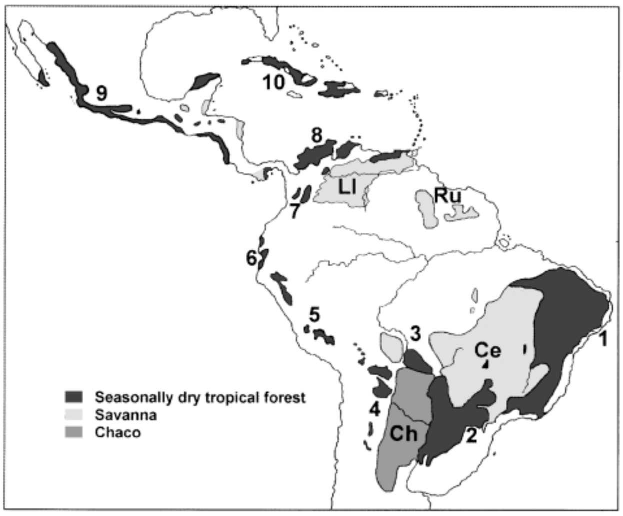
What all this research shows is that the current understanding of palaeo and modern ecology of Amazonia is unable to provide a conclusive environmental history of the region and that there is likely to be considerable revision of these hypotheses as further data become available. The Haffer hypothesis in its original format has been shown to conflict with the study of long palaeoenvironmental records, which fail to show evidence of savannah expansion in the predicted areas. On the other hand however, Colinvaux *et al.*'s (2000) assertion that Amazonia is likely to have been relatively stable since the start of the Pleistocene seems premature given the absence of comprehensive or consistent palaeoenvironmental data.

There is strong palaeoenvironmental evidence that suggests that some significant vegetation change is likely to have occurred in the Amazon during the Pleistocene. Baker *et al.* (2001) finds evidence for a wetter altiplano during the LGM, while Thompson *et al.* (2000) suggested, from Andean ice core records, that during the last glacial stage lower latitudes (9^{o}S) were drier and higher latitudes (18^{o}S) were wetter. If such change was happening on a in the Andes it seems likely that there would be an impact on the numerous fragile ecosystems of the Amazon basin. This response is likely to have been complex and probably not uniform given the vastness and diversity of Amazonia. Bush *et al.* (2002) suggested that the response of Amazonia to climate change is not likely to be uniform given the vast area and range of influences. In addition to this there are problems with the nature of the long records from the Amazon fan - these are supposed to record any change across the catchment area. Viewed critically, the argument for no change from these records is less than convincing because it is highly possible that evergreen rain forest would survive along the course of the major rivers even if it were fragmented elsewhere. The signal collected in the Amazon fan would therefore be naturally biased towards the evergreen rain forest signal because its main source area for the pollen is the river system.

Another question that can be levelled at the continual forest hypothesis is: What *type* of forest? Colinvaux *et al.* (2000) have talked about continual forest cover but have evaded addressing the issue of the nature of the forest type, although they do stress the increased presence of Andean taxa. Both Liu and Colinvaux (1985) and Bush *et al.* (2000) have documented forest change in the Amazon basin, but interpretation of the change is difficult due to the diversity and limited understanding of the forest types. Intriguingly, modern biogeographic studies also point towards a Quaternary change in the forest types across Amazonia. Studies have revealed species distribution patterns across the Neotropics that suggest significant changes in their distribution ranges in the past (Prado and Gibbs, 1993; Pennington *et al.*, 2000; Prado, 2000). Prado and Gibbs (1993) have shown that the discrete patches of dry forest, which currently exist across south of Amazonia, may once have been interlinked. This has been shown by the identification of a number of species that are common to many of the forest patches across the continent (Prado and Gibbs, 1993). To allow these species to spread across the continent the forest units must at some point have been interlinked. The importance of this observation is that an expanded dry forest across southern Amazonia would suggest a drier climate (Prado and Gibbs, 1993; Pennington *et al.*, 2000; Prado, 2000) (figure 2-3).

However, dry forests have not been widely identified in the palaeoenvironmental record. This paradox in the evidence could be caused by two things: i) either that the records which do exist do not cover, either in space or time, the areas into which the dry forest expanded, or ii) that it is currently impossible to distinguish this type of tropical forest from other types of forest palynologically.

The ability to recognise and reliably document the palaeoenvironmental history of the dry forest is paramount to the understanding of Amazonian response to climate change. For example, a failure to differentiate between moist evergreen forest and deciduous or semi-deciduous dry forest would result in a severe misinterpretation of the climatic conditions. To resolve the controversies concerning the palaeoenvironmental history of Amazonia a better understanding of the fossil pollen record is required.



1. Caatingas
2. Misiones nucleus
3. Bolivian Chiquitano region
4. Piedmont nucleus
5. Bolivian and Peruvian interAndean valleys
6. Pacific coastal Ecuador
7. Columbian interAndean valleys
8. Caribbean coast of Columbia and Venezuala
9. Central America
10. Antilles savannas

Ce. Cerrado
Ll. Llanos
Ru. Rupununi
Ch. Chaco

Source: Pennington *et al.* (2000)

Figure 2-3: The Pleistocene dry forest arc. Floristic similarities have been shown between these disjunct dry forest regions (Prado and Gibbs, 1993; Pennington *et al.*, 2000). These authors envisaged that to achieve this widespread distribution across the continent that the dry forest regions must have been more extensive and interlinked during the Pleistocene.

2.1.4 Research agenda

Two routes of scientific investigation must be pursued to achieve an improved understanding of Amazonia’s palaeoenvironmental history. Firstly, further locations need to be found in Amazonia with long palaeoenvironmental records. Analysis of additional records will clarify the spatial extent of changes and remove the necessity for long distance extrapolations. This requires the identification of sites where long records are present. The field work required to discover and retrieve such records is often hit and miss, making developments in this area slow, difficult and expensive. Secondly, the nature of Amazonian modern pollen rain needs to be better understood so that more detailed and reliable interpretation of the fossil pollen records that do exist can be made. This area of Neotropical palynology can now be actively investigated because it is possible to gain access to a range of different ecosystems to study the pollen rain and its parent vegetation.

2.2 Modern pollen-vegetation studies

It has been repeatedly shown that, through the understanding of modern pollen-vegetation relationships, the fossil pollen record can be better interpreted and more reliable palaeoenvironmental reconstructions produced, e.g. Fagerlind (1952), Davis (1963), West (1964), Wright, (1967), Delcourt *et al.*, (1983), Hicks and Birks (1996), Huntley (1996), Hicks (2001), Bush (2002) and Markgraf *et al*. (2002).

2.2.1 Theory

Modern pollen-vegetation studies establish the relationship between the modern vegetation and the pollen that it produces (Birks and Gordon, 1985). The aim is to distinguish the different types of vegetation using only the pollen that they are producing. Once a characteristic pollen spectrum has been established for a vegetation type it can then be sought in the palaeoenvironmental record. In figure 2-4 the theoretical linkage between modern vegetation and palaeoenvironmental reconstruction achieved through pollen analysis is demonstrated.

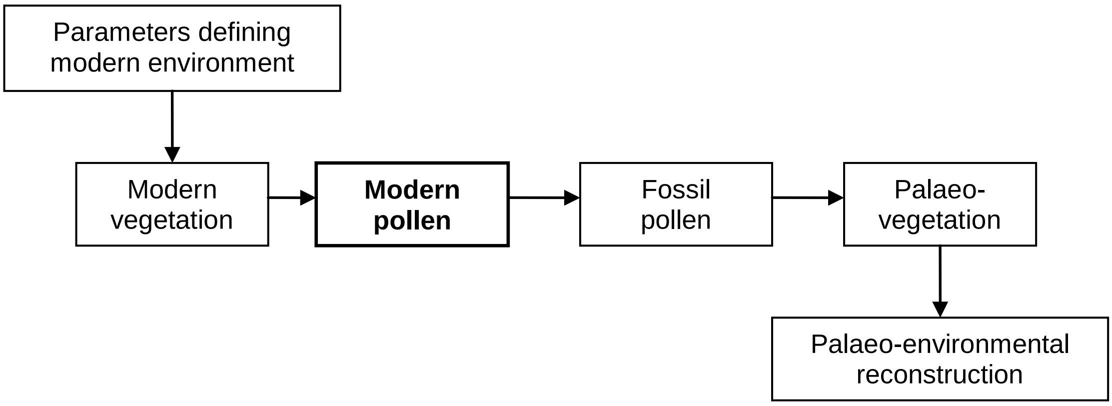


Figure 2-4: Linking modern and past vegetation. An understanding of modern pollen-vegetation relationships bridges the gap between the fossil pollen record and modern vegetation.

The relationship between the modern pollen rain and the surrounding vegetation is an extremely complex one, with many variables affecting the production, dispersal and deposition of grains (Faegri, 1966; Tauber, 1967; Frankel and Galune, 1977; Regal, 1982; Birks and Gordon, 1985). This complexity has now been researched in most ecosystems across the globe although there is a strong bias in the studies towards ecosystems that occur at temperate northern latitudes; e.g. Castledine and Gordon (1978), Anderson and Brubaker (1986), Anderson *et al.* (1991), Barboni and Bonnefille (2001) and Vermoere *et al.* (2001). These various studies have demonstrated that each environment presents its own unique set of problems for the collection of modern pollen rain and as a consequence of this many different sampling methodologies have evolved.

2.2.2 Modern pollen in the Neotropics

The studies that have been carried out in the Neotropics have employed a variety of techniques to collect modern pollen rain from a range of environments (table 2-1).

Reference	Methodology	Ecosystem(s) studied
Salgado-Labouriau (1978)	Glycerin trap	*Terra firma* savannah
Grabandt (1980)	Moss samples	Altitudinal transects[1]
Layden (1985)	Ekman grab samples	Deciduous and semi-deciduous dry forest
Liu and Colinvaux (1985)	Surface samples	Moist *terra firma* evergreen forest
Bush (1991)	Mud/water interface samples	Moist *terra firma* evergreen forest; Deciduous and semi-deciduous dry forest
Rull (1991)	Surface samples	Moist inundated evergreen forest; Seasonally inundated savannah
Behling *et al.* (1997)	Funnel trap (Bush, 1992)	Moist *terra firma* evergreen forest
Bush and Rivera (1998)	Funnel trap (Bush, 1992)	Deciduous and semi-deciduous dry forest
Bush *et al.* (2001)	Funnel trap (Bush, 1992)	Moist *terra firma* evergreen forest
Bush and Rivera (2001)	Funnel trap (Bush, 1992)	Deciduous and semi-deciduous dry forest
Weng *et al.* (in press)	Moss polsters	Altitudinal transect[2]

Table 2-1: Modern pollen-vegetation studies from the lowland Neotropics. 1 = transects include Neotropical forest, the páramo, savannah, xerophytic formations, mangrove forest, beach and shore formations, meadows and aquatic formations. 2 = transect ranges 340 - 3530 m elevation and includes 5 distinct vegetation zones.

Table 2-1 lists the different methodologies applied in the various studies. The nature of the way in which modern pollen is captured by these different methods will affect the results; e.g. samples taken from a mud/water interface are likely to contain pollen from the water bodies' catchment area while funnel traps collect only the pollen rain deposited from the air at that location. These methodological differences mean that it is difficult to apply more than one modern pollen study to the interpretation of any one fossil pollen core because there may be inherent biases in the different methods. This is particularly unfortunate in the Neotropics where modern pollen studies typically only deal with one or two ecosystems (table 2-1), but fossil pollen records often record more than one or two changes (e.g. Mayle *et al*., 2000). Greater inter-study comparability would be also particularly useful in the Neotropics because of the small number of studies that have been carried out (table 2-1). This dearth of information means that the interpretation of the fossil pollen record is based mainly upon the ecological characteristics of the ecosystems and does not take into account variations in pollen levels caused by differential production rates and/or dispersal mechanisms.

In the light of these deficiencies in the modern pollen studies from the Neotropics and given the need to better understand the fossil pollen record of the region (discussed in section 2.1), a strategy that allows a range of Amazonian ecosystems to be characterised by their modern pollen spectra is required. The key problem with the studies that do exist is their limited scope and the lack of inter-study comparability. Therefore, more ecosystems must be studied using a standard methodology. Ideally samples should be taken from across Amazonia from all the ecosystems present. However, this would be a huge logistical and financial undertaking. Therefore, to make the sampling of ecosystems as manageable and affordable as possible it is necessary to identify sites where many ecosystems are accessible.

2.2.3 Focus on ecotones

Ecotones are transition zones in the landscape where two or more ecosystems meet or merge into one another (Matějka, 1992; Risser, 1995). These locations are usually created where the climatic limits of a number of ecosystems are reached or there is a change in another ecologically critical factor such as soil type or hydrology (Risser, 1995). This means that at ecotones numerous ecosystems are present in a relatively small area. Therefore, the expense and time invested in one field trip can yield samples from multiple environments rather than just one, improving the cost effectiveness of the research. These practical considerations are of great consequence when working in Amazonia where much of the area is not easily accessible without the aid of a plane, boat or 4x4 truck.

For these practical reasons ecotones are very attractive areas for carrying out modern pollen research. In addition to this, interest from ecologists and palaeoecologists in ecotones means they are areas where information complimentary to a modern pollen study is often available.

Ecologists tend to work at ecotones for two main reasons: i) they provide an opportunity to study many ecosystems within a relatively small area, and ii) they allow ecosystem interactions to be investigated (Kent *et al.*, 1997; Smith *et al.*, 1997). Palaeoecologists are interested in working at ecotones because the vegetation in these areas is at the limit of its ecological tolerance, i.e. the point where conditions change from favouring one ecosystem too favouring another. The delicate balance between the dominance of one ecosystem over another at ecotones means that when conditions change (e.g. climate) it is at these marginal locations where the impact upon the vegetation occur first (Crumley, 1993; Neilson, 1993; Noble, 1993; Peteet, 2000).

2.3 Research aims

To facilitate a better interpretation of the fossil pollen records from Amazonia a greater understanding of the modern pollen-vegetation relationships of the ecosystems that are likely to have responded to past climate change is required. To achieve this, the modern pollen of those Neotropical ecosystems that are likely to have responded to past climate change in Amazonia must be studied, ideally at a location where ecological and palaeoecological data already exist.

In the light of the current controversies surrounding the palaeoenvironmental history of the Amazon basin, three key research aims have been identified that will aid the interpretation of the fossil pollen record and are achievable within a three year PhD. The overall aim is to facilitate a better understanding of the fossil pollen record by discovering how a range of present day Neotropical ecosystems are represented by the pollen they produce. This will allow fossil pollen assemblages to be related back to the vegetation that produced them with more confidence. In doing this it is hoped that more light will be shed on the true nature of

Amazonia's palaeoenvironmental history. To achieve the overall aim three things need to be established:

i) A repeatable and reliable methodology for sampling modern pollen rain in tropical environments (chapter 4).
ii) Characteristic pollen spectra need to be identified from a range of lowland Neotropical ecosystems (chapter 7).
iii) The extent to which these characteristic pollen assemblages can be used to differentiate ecosystems from one another (chapter 8).

2.4 Summary

In this chapter the purpose and rationale of the research carried out in this PhD has been presented. Firstly, the research was placed within the context of existing studies from related diciplines. In section 2.1.1 the inadequately understood role of Amazonia in the global environment was highlighted and attention was drawn to the necessity to improve this understanding if an assessment is to be made of the human impacts on these systems. It was demonstrated that to improve this understanding, knowledge of past changes to the region were desirable. In section 2.1.2 the sparse nature of the paleoenvironmental record from Amazonia was demonstrated and the reliance on a few fossil pollen records emphasised. In section 2.1.3, the controversies that have arisen from different interpretations of the record were discussed. This focused on two key areas: i) the validity of Haffer's refugia hypothesis (Haffer, 1969), and ii) the possible misidentification of different forest types in the fossil pollen record. Then in section 2.1.4 the two avenues of research required to achieve a better understanding of the palaeoenvironmental record from Amazonia were identified: i) the need for further long fossil pollen records, and ii) the need for an improved understanding of modern ecology. It was then suggested that the latter of these two areas could be addressed through the application of a modern pollen-vegetation study.

In the second half of the chapter the scope of modern pollen-vegetation studies in the Neotropics was discussed. Firstly, in section 2.2.1 details of the theory behind such studies were presented. Then, in section 2.2.2, the absence of a comprehensive modern pollen-vegetation research from the lowland Neotropics was highlighted. In 2.2.3 the practicalities of carrying out such a study in the Neotropics were discussed and ecotonal regions were identified as prime locations. Then in the light of the current controversies surrounding Amazonia’s palaeoenvironmental history and the particular lack of information regarding modern pollen rain in the lowlands three key aims were identified as the purpose of this PhD research: i) to establish a reliable and repeatable methodology for sampling modern pollen rain in tropical environments, ii) to determine the characteristic pollen assemblages from a range of lowland Neotropical ecosystems, and iii) to discover the extent to which these pollen assemblages could be used to differentiate the ecosystems.

This chapter has established a detailed rationale for modern pollen-vegetation study into Amazonia and culminates with three specific research aims that this thesis will address. The following chapter argues that Noel Kempff Mercado National Park, Bolivia, is an ideal location for carrying out such a modern pollen study.

Chapter 3

Noel Kempff Mercado National Park, Bolivia

Chapter 3

Noel Kempff Mercado National Park, Bolivia

In chapter 2 it was established that modern pollen-vegetation studies carried out at ecotones in the Neotropics are necessary to extract an accurate palaeo-vegetation reconstruction from the fossil pollen record. This chapter goes on to detail the suitability of Noel Kempff Mercado National Park (NKMNP), Bolivia for such a study (figure 3-1). The suitability of the park is demonstrated in two stages. Firstly, it is made clear how the high diversity of pristine ecosystems accessible in, and around, NKMNP fulfils the criteria laid out in chapter 2 for collecting modern pollen rain and relating modern pollen studies to the fossil record (section 3.1). The vegetation studies carried out in NKMNP are considered and it is shown how they can be integrated with the modern pollen data to identify the pollen-vegetation relationships and so help explain the fossil pollen record. This examination of the modern ecology of the park is followed by a brief review of the fossil pollen data that exist from the region (section 3.2). Then, in section 3.3, the reasons for using NKMNP for a modern pollen-vegetation study are explained.

3.1 Park ecology

There are two good ecological reasons for using NKMNP as a location for a modern pollen-vegetation study. Firstly, NKMNP is largely undisturbed by human activity, primarily due to its remote location in the north-east corner of Santa Cruz province, Bolivia (figure 3-1). The only human activity that is known in the region of the park is: i) from subsistence agriculture practiced by the inhabitants of a number of small villages, and ii) from the selective logging for Mahogany (*Swietenia macrophylla*). This took place until 1995 in the west of the park.

However, structural damage from this logging has been shown to have been low (Gullison and Hardner, 1993; Panfil and Gullison, 1998). The park therefore contains almost pristine vegetation, which means that any pollen signal extracted from the modern pollen rain will be, as close as is possible given some natural re-assortment of taxa in the past is likely, an analogue of those ecosystems that are found in the fossil record prior to human disturbance. Secondly, as depicted in figure 3-2, NKMNP contains a highly diverse range of vegetation within its c. 15 000 km2 area (the reasons for this high diversity are discussed below). The floristic composition of this vegetation is very well understood because Killeen (1998) and Panfil (2001) have investigated in detail the vegetation of the park and have categorised it into five distinct ecosystems that they subdivided into twenty-two different plant communities (figure 3-2). The ecosystems have been identified as critically endangered (Dinerstein et al., 1995) and this has led to the park being designated as a World Heritage Site (UNESCO, 2001).

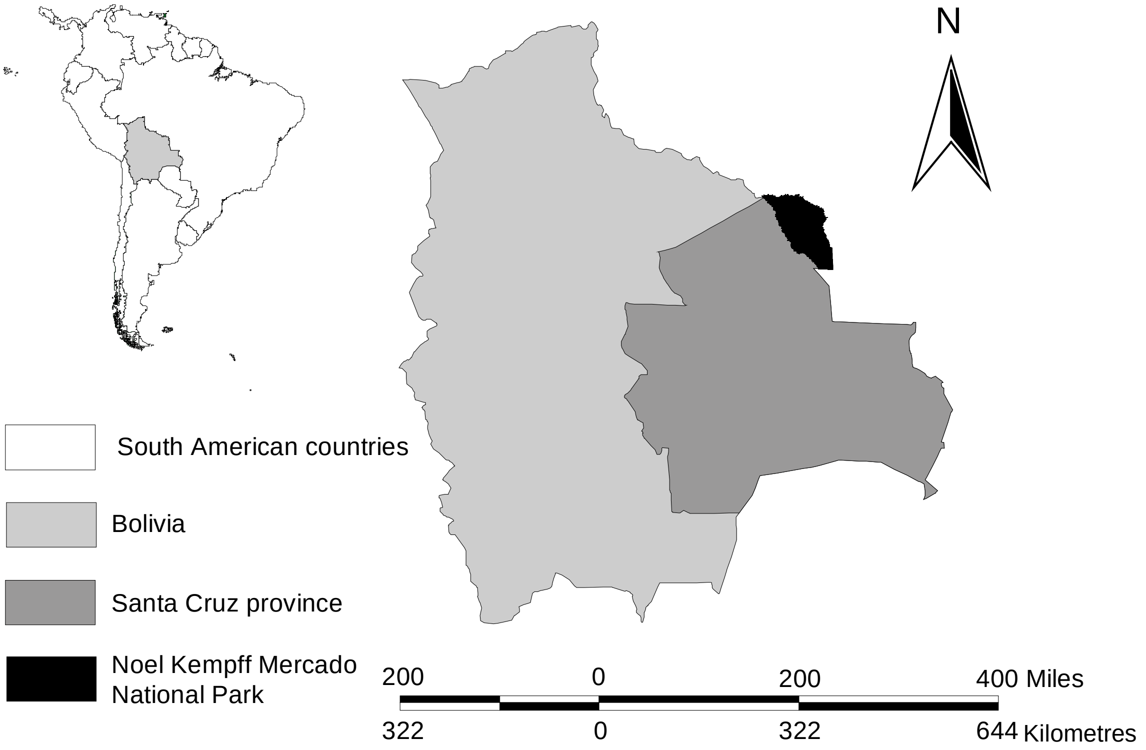
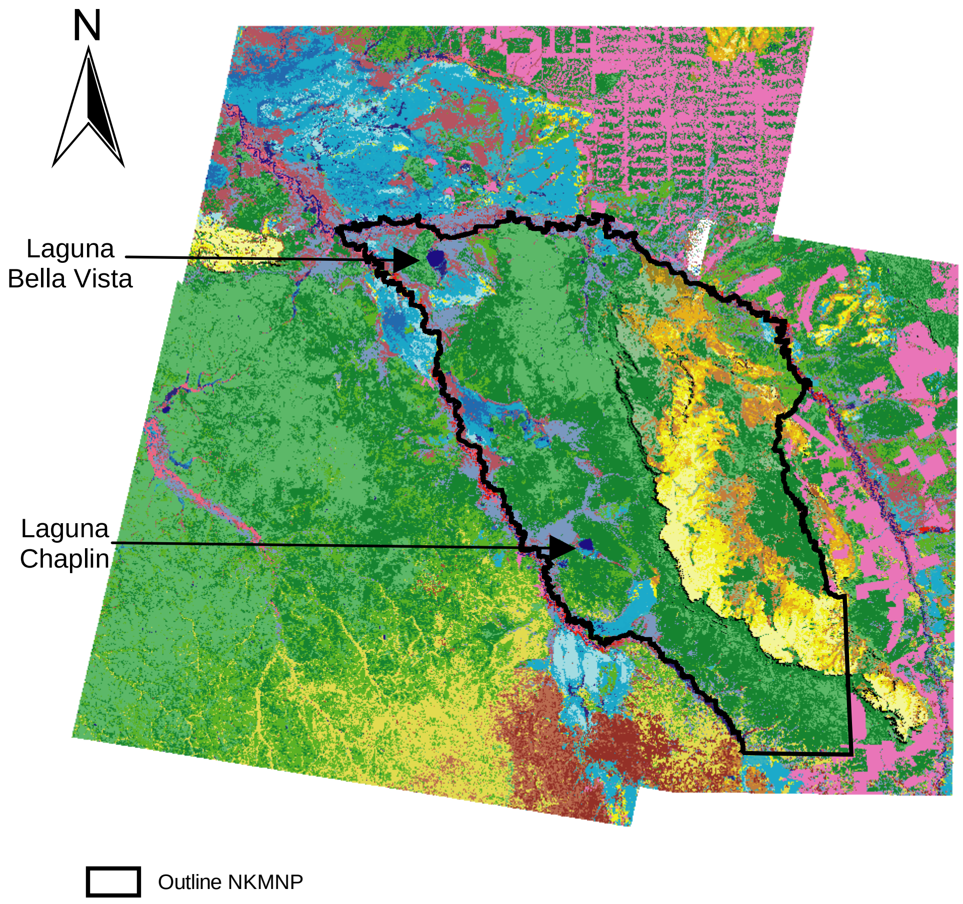


Figure 3-1: The location of Noel Kempff Mercado National Park. Covering c. 15,000 km^2 NKMNP is located in the northeastern corner of Santa Cruz province, Bolivia. The park's international border abuts the Brazilian states of Rondônia to the north and Mato Grosso to the east.



Vegetation classifications (ECOSYSTEMS, Plant communities)

MOIST *TERRA FIRMA* EVERGREEN FOREST
- 🟩 Tall *terra firma* evergreen forest
- 🟩 Evergreen *terra firma* liana forest
- 🟩 Dwarf *terra firma* evergreen forest
- 🟩 Evergreen *terra firma* mixed liana forest

MOIST INUNDATED EVERGREEN FOREST
- 🟦 Tall inundated evergreen forest
- 🟪 Low inundated evergreen forest
- 🟥 Tall riverine evergreen forest
- 🟪 Pioneer riverine evergreen forest

SEASONALLY INUNDATED SAVANNAH
- 🟦 Pampa aguada^
- 🟦 Pampa termitero^^
- 🟦 Inundated scrubland
- 🟦 Savannah marsh
- 🟪 Palm marsh
- ⬛ Marsh

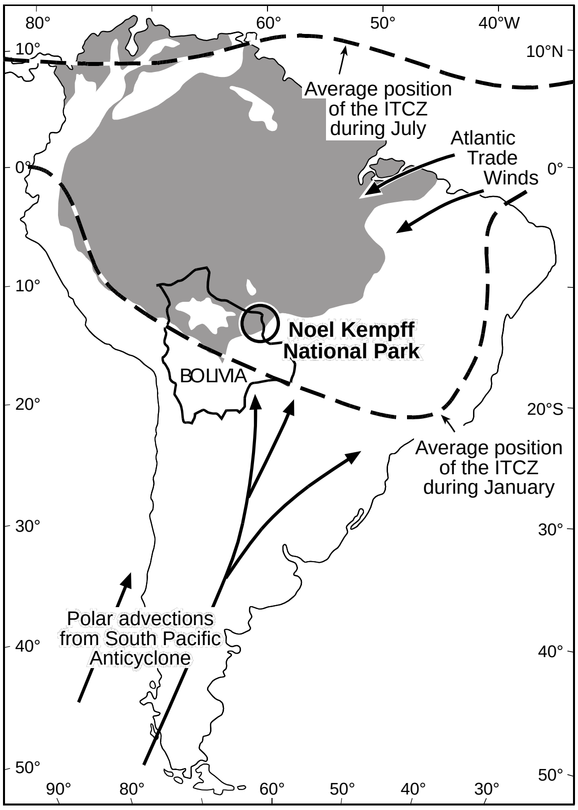
DECIDUOUS AND SEMI-DECIDUOUS DRY FOREST
- 🟥 Inundated semi-deciduous dry forest
- 🟫 Semi-deciduous dry forest
- 🟨 Deciduous dry forest
- 🟩 Semi-deciduous palm forest

TERRA FIRMA SAVANNAH
- 🟨 Campo limpo, campo rupestre, campo sujo, campo húmido*
- 🟨 Campo cerrado**
- 🟧 Cerrado (*sensu stricto*)***
- 🟫 Cerradão****

OTHER CLASSIFICATIONS
- 🟦 Rivers and lakes
- 🟪 Agricultural land

Figure 3-2: Vegetation distribution across Noel Kempff Mercado National Park. Some plant communities have Spanish names, rough English translations are as follows: * = open savannah, ** = shrubby savannah, *** = open woodland, **** = closed woodland, ^ = seasonally inundated open savannah and ^^ = seasonally inundated shrub savannah/termite savannah. Data from Landsat^{TM} (T.J. Killeen, unpublished data).

The primary, but not sole, reason for the high ‘beta’ (between habitat) diversity within NKMNP is the climatic situation of the region. The climate of the park is governed, in the main, by the movement of the Inter Tropical Convergence Zone (ITCZ) around the equator (Servant *et al.*, 1993) (figure 3-3). During the austral summer (October - February) the park is subjected to the humid Atlantic Trade Winds brought south by the ITCZ moving to between 10^{o} - 15^{o}S (Paegle, 1987; Ronchail, 1989). Opposed to this, in the austral winter (June - August), the park is dominated by cold high-pressure systems called “*surazos*”. During the austral winter these *“surazos”* are able move up from the south because the ITCZ has retreated towards the equator, resulting in a drier climate during the austral winter (Paegle, 1987; Ronchail, 1989). The close proximity of the southerly limit of the ITCZ means that the park is subjected to a range of climatic conditions that control the general type of vegetation that can survive in the park. This is because rainfall is sufficient to support moist evergreen forest in the north while the dry season in the south is long enough to favour savannahs and deciduous and semi-deciduous dry forests (figure 3-2).



Source: Mayle *et al.* (2000)

Figure 3-3: Annual movement of the Inter Tropical Convergence Zone. The movement of the ITCZ across South America is shown in relation to the moist evergreen forest of the Amazon basin (shaded grey), the Andes (marked by cs), Bloivia (outlined) and the NKMNP (circled).

However, climatic parameters alone are not responsible for the massive diversity of ecosystems found within the NKMNP. Killeen and Schulenburg (1998) have cited the

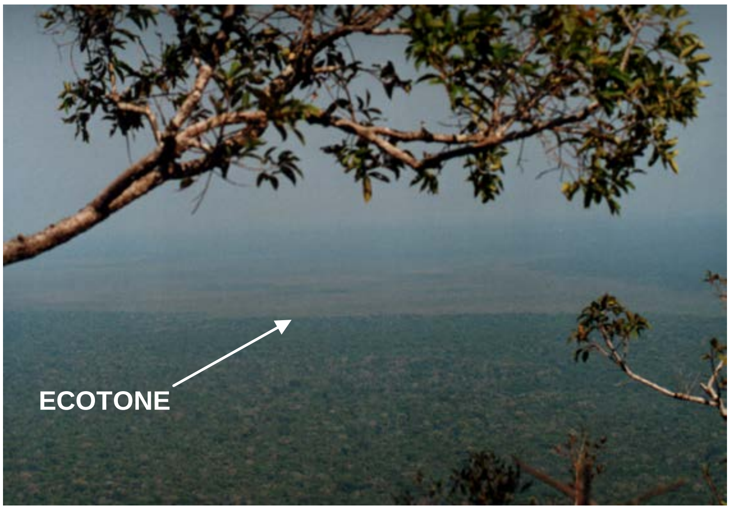


Figure 3-4: The lowland expanse of the Noel Kempff Mercado National Park. Taken from the Huanchaca plateau looking west, note evergreen forest - savannah ecotone.

variation in the geology and geomorphology as the main reason for the parks considerable habitat diversity. Situated on top of the 1.2 - 1.4 billion year old Precambrian Brazilian Shield, the park can be divided into two starkly different types of landscape (O'Connor *et al.*, 1987; Litherland and Power, 1989). To the west is a lowland plain that undulates between 200 - 300 m above mean sea level (a.m.s.l.). From amid this plain protrude granite inselburgs that reach up to a further 10 - 15 metres (figure 3-4).

Within the lowlands a range of hydrologic and topographic conditions exist that supports a variety of plant communities (figure 3-2). In contrast to the lowland area, the Huanchaca plateau rises steeply to 900 m a.m.s.l. in the east and its c. 7000 km^2 expanse spans the Bolivian - Brazilian border and supports a range of ecosystems similar to those found in the lowlands but adapted for life high on the plateau (figures 3-4 and 3-5).

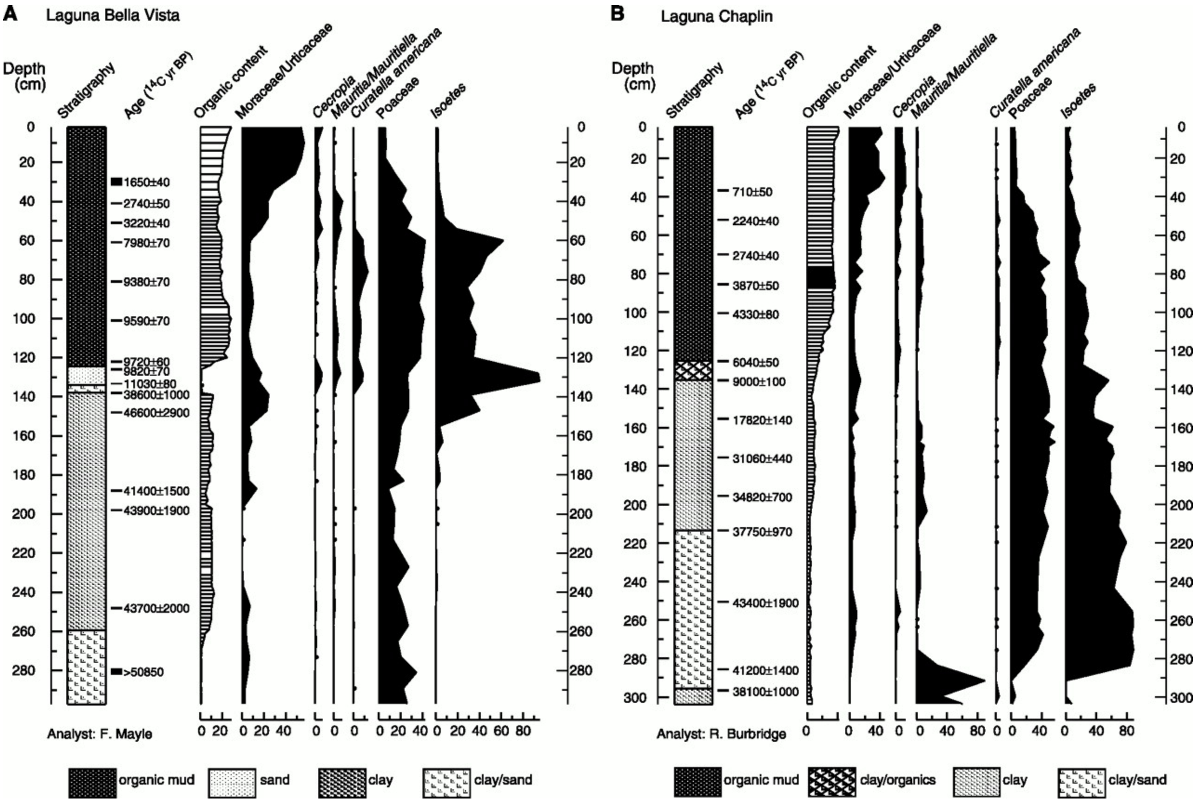
Figure 3-5: The Huanchaca plateau. Looking south along the Hunachaca plateau.

NKMNP is an ideal location for carrying out a modern pollen study because it contains a wide range of pristine ecosystems within a relatively small area (in comparison to the size of the Amazon basin) which can be accessed via old logging roads. In addition to this, detailed information is available on the precise floristic make up of each of the distinct ecosystems as a result of vegetation studies carried out by Killeen (1998) and Panfil (2001). These studies provide detailed vegetation data from 32 permanent vegetation plots at 8 locations within and bordering the park. These authors described and analysed the floristic composition of each of the ecosystems and show how the various areas can be differentiated ecologically. Further data (T.J. Killeen, *pers. comm.*, 2001) has identified and located all the plants found within each plot >10 cm d.b.h. (diameter breast height). The collection of modern pollen rain from the vegetation study plots means that an extremely detailed pollen-vegetation study is possible. Details of how these plots were set up can be found in chapter 4. This availability of vegetation data to use in conjunction with the modern pollen study is unique in terms of modern pollen studies from lowland Amazonia. A detailed understanding of how the modern pollen relates to the vegetation will allow the signals found in the fossil pollen record to be confidently related back to a vegetation type that is likely to have produced them. The principles of this relationship have been stated in chapter 2 (section 2.2.1). The direct relevance of such a study to the fossil pollen record that already exists from NKMNP is the subject of the next section.

3.2 Park palaeoecology

Palaeoecological studies from NKMNP show that there has been significant vegetation change over the last 50,000 years which, it is presumed, is in response to changes in climatic conditions (Mayle *et al.*, 2000; Burbridge, 2001; Panfil, 2001; Burbridge *et al.*, in press). Reconstruction of the vegetation history has been carried out for two lakes in NKMNP, Laguna Bella Vista in the north and Laguna Chaplin in the south (figure 3-2). The results of these investigations are detailed in Mayle *et al.* (2000), Burbridge (2001) and Burbridge *et al.* (in press). These studies, using well dated high resolution analysis of the fossil pollen, have shown that the moist evergreen forest arrived in the north of the park c. 3000 years ago (Laguna Bella Vista) but did not reach the south until around 700 years ago (Laguna Chaplin) (figure 3-6). This is demonstrated by identifying how far back the moist evergreen forest signal stretches down the core and therefore back through time. This is achievable because both lakes are currently surrounded by evergreen forest so the surface samples are assumed to contain pollen representative of this type of ecosystem. From this it is reasonable to assume that so long as this signal persists back in time, down through the core, that a similar vegetation type surrounded the lake.

However, once the pollen signal no longer matches that of the evergreen forest then interpretation becomes more difficult because little is known of how different ecosystems are manifest in the pollen that they produce. Inferences are drawn from the fossil pollen record regarding the nature of the vegetation that surrounded the lakes prior to the evergreen forest based upon known habitat preferences of particular indicator taxa, such as *Curetella americana* seen as characteristic of savannahs (figure 3-6). This method of interpretation is difficult in Amazonia because many families of Amazonian plants occur in a wide range of ecosystems and often it is only possible to identify pollen down to family level. This means that by using this method of interpretation differences between ecosystems are often invisible to the palynologist. From this fossil pollen evidence it is clear that there are significant shifts in vegetation type prior to the arrival of the evergreen forest in NKMNP (figure 3-6) but the exact nature of these changes remains unknown. An insight into the nature of these changes can be gained by improving the understanding of how nearby ecosystems, which are the ones likely to have preceded the evergreen forest because of their close proximity, are represented palynologically. Therefore it is anticipated that a study of the modern pollen of NKMNP will directly help the interpretation of the fossil pollen records from NKMNP.



Source: Mayle *et al.* (2000)

Figure 3-6: Summary pollen diagram from Laguna Bella Vista and Laguna Chaplin. The dominance of Moraceae/Urticaceae and low percentages of Poaceae indicated how far back in time the moist evergreen forest persisted.

3.3 Justification for using park

NKMNP is an ideal location to carry out a modern pollen-vegetation study that is aimed at improving the understanding of palaeoenvironmental change in Amazonia for four reasons. Firstly, because of the remote location of the park the vegetation present has not been affected much by human activity and therefore the ecosystems should provide a good analogue of those in the past. Secondly, it is located on the ecotone of moist evergreen forest, deciduous and semi-deciduous dry forest, and savannahs. All these vegetation types can therefore be accessed within a relatively small region. Thirdly, floristic studies carried out in and around the park mean that extremely detailed vegetation data is available for correlation with the pollen rain data. Finally, two of the longest fossil pollen records from anywhere in Amazonia have been obtained from within the park (chapter 2, figure 2-2). This means that any improved methods of interpretation developed will be directly applicable to these important records.

3.4 Summary

In this chapter it has been shown that NKMNP is an ideal location for carrying out a modern pollen study with the aim of better understanding Amazonia's palaeoenvironmental history. In section 3.1 three key points about the ecology of the park were highlighted: i) the pristine nature of the vegetation, ii) the high habitat diversity of the park, and iii) the detailed research that has been carried out on the vegetation. In section 3.2 a brief summary of the palaeoenvironmental history of the park was given and the presence of two of the longest fossil pollen records from Amazonia was emphasised. In the next chapter details of the methodological techniques used to carry out a modern pollen study in NKMNP are presented.

Chapter 4

Methodology

Chapter 4

Methodology

In chapter 3 the suitability of Noel Kempff Mercado National Park (NKMNP) as a location for carrying out a modern pollen study was demonstrated. Now, in chapter 4, the practical techniques applied to collect the pollen rain from the ecosystems of the park are outlined. These methods are repeatable, reliable and allow the accurate collection of modern pollen rain from tropical environments and therefore fulfil aim one of this PhD thesis (as defined in chapter 2, section 2.3). This chapter starts with the practical considerations taken to allow the collection of pollen from a variety of ecosystems (section 4.1). In section 4.2 the developments and modifications to the pollen trapping mechanism (Bush, 1992), are explained and justified. In section 4.3 the preparation protocol used to extract the pollen from the traps is presented. Problems with this protocol are highlighted and a possible alternative strategy for use in future work is also mentioned. The final part of the practical methodology is that for the pollen identification, which is detailed in section 4.4. The final section, 4.5, highlights the problems with formulating a sampling strategy for extracting a reliable pollen rain signal from a Neotropical ecosystem. In doing this it is demonstrated that pilot research (chapter 5) was required to answer fundamental questions about the nature of the pollen rain prior to commencing the main project (chapter 6 onwards).

4.1 Field methods

32 permanent vegetation study plots were set up in and around NKMNP between 1993 and 1996 by T.J. Killeen with the aid of the Museo de Historia Natural “Noel Kempff Mercado”, Santa Cruz (MHNSC) with the aim of obtaining a detailed understanding of the vegetation of

this remote and diverse area of Amazonia (outline in chapter 3, section 3.1) (Killeen, 1998). Seventeen of these permanent vegetation study plots were sampled annually from 1998 to 2001 for their pollen rain (appendix I); traps were set up and collected by F.E. Mayle between 1997 and 1999, and by the author and F.E. Mayle in 2000 and 2001. These plots were selected for three reasons: i) they had been identified as representative of the five key Neotropical ecosystems contained within the park, ii) detailed ecological data existed for them, and iii) they were accessible with the logistical support of the MHNSC. These plots were typically 500x20 metres in size (for full details of locations and sizes see appendix I). Ten pollen traps were placed within each plot and replaced every 12 months (for trap details see section 4.2). The traps were, where possible, placed at 50 metre intervals along the centre of each plot to allow any spatial patterns in the distribution of the pollen rain to be sampled. The loss of some traps was anticipated, so multiple sites were used for each ecosystem. However, recovery rates were excellent (92 % of all traps placed in the field were at least partially recovered), resulting in the collection of many more samples than could be analysed during a three year PhD (appendix II). Some samples were lost in the field for a variety of reasons including animal attack and fire damage (figure 4-1).

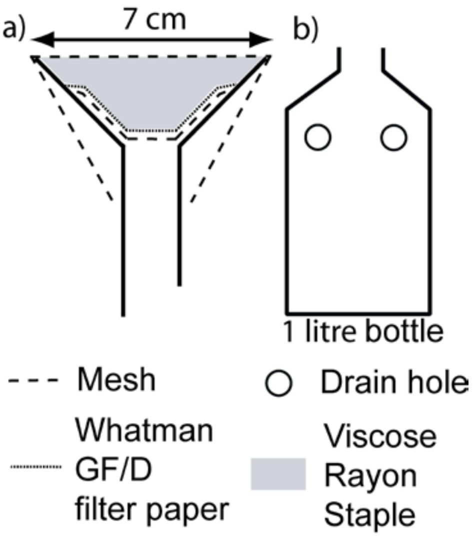
a) Tapir attack **b) A burnt out savannah plot**

Figure 4-1: Damage to pollen traps. a) Sometimes it was possible to recover fragments of a sample after an animal attack. b) When fire swept through the Los Fierros, Campo Cerrado plot during the 1999-2000 field season it destroyed all the traps.

4.2 The pollen trap

Constructed pollen traps were chosen to sample the modern pollen rain in NKMNP because: i) they allowed the pollination biology of the ecosystems to be investigated in terms of pollen accumulation rates (PARs) and inter-annual variability, and ii) the traps could be located within the ecosystems to optimise the spatial resolution of sampling. Funnel traps, as described by Bush (1992), were used because of their: i) portability, ii) simplicity, iii) cheapness, and iv) because they could cope with the high rainfall of the region (F.E. Mayle, *pers. comm.*, 2000). They had also been employed in some other Neotropical studies allowing a degree of comparability (chapter 2, table 2-1).

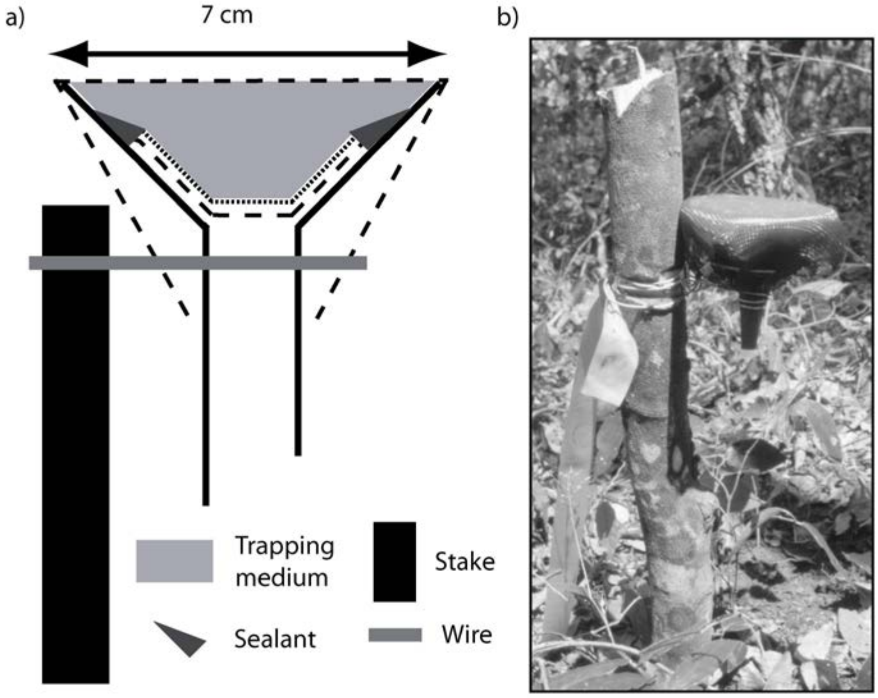
Using the description of Bush (1992) (figure 4-2) the traps placed into the field in 1998, by F.E. Mayle, consisted of a funnel (70 mm diameter) containing a glass fibre filter paper and viscose rayon staple, held in place by a coarse mesh, mounted in a plastic bottle and placed on the ground. Bush (1992) states that a plastic bottle should be present under the funnel to catch and store rainfall, thus providing a source of moisture for the fibres during dry periods, anticipated to improve retention of pollen in the fibres and prevent oxidation (M.B. Bush, *pers. comm.*, 2000). However, while collecting traps from NKMNP during the dry season, it was found that fibres remained dry even when the bottles were full of water. Clearly the evaporation of water alone is insufficient to keep the fibres moist in these environments. Regardless of this, even in the dry samples no evidence of oxidation was found.



Source: Gosling *et al.* (2003)

Figure 4-2: Schematic of a funnel trap. a) Funnel section of trap, which in the field is mounted in to, b) the bottle section.

Therefore, the bottle half of the trap was considered superfluous to requirements and was consequently omitted from those traps set in 1999-2000 and 2000-2001 (figure 4-3).



Source: Gosling *et al.* (2003)

Figure 4-3: Schematic of a modified funnel trap. a) Modifications to pollen trap set up from those shown in figure 4-2, b) pollen trap deployed in NKMNP. Other symbols as figure 4-2.

The traps were usually mounted, using a wire, to a stake that had been driven into the ground (figure 4-3). The use of stakes allowed the location of the traps to be determined, made them easily visible and less likely to be damaged by animals, burnt, or covered by leaf litter or other dead vegetation. The stakes raised the traps 0.5 metres above the maximum level of seasonal inundation, ensuring that the traps would not be submerged or washed away during the rainy season. As far as was possible, the height at which the pollen rain was sampled was consistent. In the few locations where it was not possible to mount the traps on stakes they were either attached to plant stems within the ecosystem or positioned on the ground as per Bush (1992). When the traps had to be positioned in either of these ways, consistency in the distribution pattern was paramount and, when attached to vegetation, the species was noted so that any swamping of the trap by the pollen from a ‘host’ plant could be accounted for (see appendix II). Upon collection, the fibre, filter and mesh were separated from the funnel and sealed in a plastic grip-lock bag. These were kept in darkness at 3 ^{o}C to prevent microbial growth.

4.3 Laboratory methods

The traps contained viscose rayon staple as the trapping medium. This was prepared using the standard pollen preparation procedures as described in Faegri and Iversen (1989), Moore *et al.* (1991) and Bennett and Willis (2001), with some important modifications (see below). These modifications adapted the method for specific use with pollen traps that use fibre as the medium of collection and follow the ‘wash’ methodology recommended by Behling *et al.* (1997) and Bush and Rivera (1998). This method is also described, and shown to be effective, by Gosling *et al.* (2003). The use of a ‘washing’ methodology is necessary as no effective chemical procedure has been found that is capable of destroying the viscose rayon staple while leaving the pollen in a countable state (Bush, 1992; C. Alison, *pers. comm.*, 2000).

4.3.1 Extraction from viscose rayon staple

i) Add 5% Potassium Hydroxide (KOH) / Sodium Hydroxide (NaOH) to the bag containing the viscose rayon pad (50ml is usually sufficient to saturate the fibre). Leave overnight to allow the pollen to be freed from the fibre. This makes the sample alkaline which takes any humic acids within the sample into solution.

ii) Dissolve exotic marker pollen, e.g. *Lycopodium* tablet(s), in 7% Hydrochloric acid (HCl) and add the solution to the bag if PAR is to be calculated.

iii) Wash repeatedly with copious quantities of water to separate the pollen from the fibre. Then filter the sample through a Whatman GF/D filter paper (or other glass fibre equivalent) using a buchner funnel with suction. Multiple filter papers may be needed for large samples, as the filter paper can become clogged. Vigorous teasing and kneading of the wool is required to free material. Typically 4-5 washes are sufficient to remove all organic material. Discard the filtrate and use tweezers to transfer the filter papers into 50ml centrifuge tubes. The filter papers now hold all the material washed from the fibre.

4.3.2 Separation of 'washed' sample from buchnar funnel filter paper(s)

i) Use conc. (40%) Hydroflouric Acid (HF) to dissolve the glass fibre filter paper(s) and also remove any silicates that may have entered the sample. This procedure can be carried out over two hours by heating the sample in the HF to 90^{o}C, or overnight cold. It may be necessary to repeat this process if a number of filter papers have been used or there is a large quantity of silicates in the sample. Centrifuge the sample for five minutes at 3000 rpm and decant the supernatant.

ii) Once all fragments of filter paper and silicates have been removed, place sample in 7% HCl and heat to 90^{o}C for 20-30 minutes to remove silicate residues and fluorosilicates. (Heating increases solubility). Then centrifuge and decant.

iii) Wash sample in water, using a ‘whirlimix’ and stirring rod to ensure that the entire sample is mobilised and washed effectively. Centrifuge and decant.

4.3.3 Final treatment

i) Acetolyse the sample following the standard procedure described in Moore *et al.* (1991) and mount onto slides.

4.3.4 Alternative laboratory method

During the course of this research a detailed investigation was undertaken to try and discover a method of processing viscose rayon staple that allowed the trapping medium to be completely removed (W.D. Gosling, unpublished data). By destroying the trapping medium one can have complete confidence in the recovery of the entire sample. Unfortunately, no method could be found that did not severely degrade the quality of the pollen sample recovered. However, experimentations with cotton fibre as the trapping medium produced favourable results both in the field and laboratory and it is therefore recommended for any future study (Gosling *et al.*, 2003; Appendix III). Due to time constraints and practical considerations it was not possible to use cotton fibre as the trapping medium in this project.

4.4 Pollen analysis and identification

Once processed, the samples were placed in silicon oil and mounted on washed, cleaned and polished microscope slides 76x26 mm, 0.8-1.0 mm thick and sealed with wax under cover slips 20x40 mm of thickness number 1.5. They were then analysed using a Nikon LABOPHOT microscope typically at 400x magnification but switching to 1000x for fine detail and small grains. The pollen was photographed with a Nikon FM camera using an eight second exposure of a 200 ASA print film. For small grains and fine detail a Tamron 2x tele-converter lens was fitted to provide additional magnification. To compensate for the reduced light levels caused by this additional magnification, the exposure time was increased to about eleven seconds

Identification was based primarily on Roubik and Moreno (1991) and the reference collection held at the University of Leicester of ~1000 taxa. F.E. Mayle has been building up this collection since 1995 with the assistance of R.E. Burbridge, S. Punyasena and the author. This collection is based primarily on samples held in the herbarium of the MHNSC, although a few were obtained from the Royal Botanic Gardens, Edinburgh. Other texts used in the identification process were Heusser (1971), Salgado-Labouriau (1973), Markgraf and D'Antoni (1978), Hooghiemstra (1984), Colinvaux *et al.* (1999), Velásquez (1999) and Wille (2001).

4.5 Sampling problem

In all, 458 traps from 17 plots representing five ecosystems encompassing nine plant communities were collected from NKMNP between 1999 and 2001. With each trap sample taking between three and six days to process and analyse it was impossible to study all of them during the course of this three year PhD. Therefore, a sampling strategy had to be devised to meet the second aim of the project - the characterization of each ecosystem by its modern pollen spectra (as defined in chapter 2, section 2.3). To achieve this aim, firstly, the heterogeneity of the pollen rain from each plot had to be determined, i.e. would it be possible to look at one trap from each plot and use it to characterize the ecosystem, or were there intra-plot spatial variations in the pollen rain that required further investigation to reliably characterize the ecosystem palynologically. To address this question a pilot study was set up. This pilot study and its implications for the main study are the subject of the next chapter.

4.6 Summary

In this chapter the practical methodology applied in this PhD thesis has been discussed and methodological advances made outlined. In section 4.1 the nature of the vegetation study plots and the trap distribution strategy, established by F.E. Mayle in 1997, were described. Then, in section 4.2, the type of pollen trap used was detailed and modifications by the author were outlined. Then, in section 4.3, the advances made by the author to the sample preparation protocol were explained and an alternative methodology also developed presented. In section 4.4 the process of analysis and identification of the pollen was described. Finally, in section 4.5, the sampling problem presented by the nature of modern pollen rain collected from the NKMNP was described and the necessity for pilot research explained. This pilot research is the subject of the next chapter.

Chapter 5

Pilot research

Chapter 5

Pilot research

In the previous chapter the practical methods used to collect, process and analyse the modern pollen rain from Noel Kempff Mercado National Park (NKMNP) were presented. It was also shown in chapter 4 that more pollen traps were collected than could be processed and analysed during the course of a three-year PhD. To determine which of the traps collected were required to characterize the modern pollen rain from each of the ecosystems the research presented in this chapter was carried out. This research was designed to answer two fundamental questions about the nature of the pollen rain: i) how spatially variable is the pollen rain, and ii) how much does the pollen rain vary from year to year? It was the answers to these questions, the pollen preservation, the traps recovered and the time constraints of the PhD that governed the number of traps which were sampled and from where. In section 5.1 the preliminary investigation into the pollen rain of the five ecosystems sampled is detailed. The results of this are then used to construct a strategy for investigating the extent of spatial variation in the pollen rain within three of the ecosystems (section 5.2). In the light of this research a workable sampling strategy was formulated for the main part of the project, which includes investigation of inter-annual variability (section 5.3).

5.1 Preliminary investigation

Variations of pollen rain within tropical ecosystems have been well documented (e.g. Islebe and Hooghiemstra, 1995; Elenga *et al.,* 2000; Marchant & Taylor, 2000; Vincens *et al.,* 2000). Therefore, it was suspected that there would be spatial variation in the pollen rain sampled from within the five key ecosystems found in, and around, NKMNP. The extent of the variation determined the number of samples that needed to be studied to extract a characteristic pollen signal from each ecosystem and in turn, due to the time constraints, controlled the number of ecosystems that could be studied. This preliminary investigation was designed to identify the degree to which the pollen rain within each of the five ecosystems varied.

5.1.1 Strategy

Traps were taken from five plots representative of each of the five key ecosystems (highlighted grey in table 5-1). These plots, rather than other plots from the same ecosystem, were sampled because they had superior trap recovery rates (see appendix II). Traps were sampled from the 1998-1999 field season because they were the only ones available at that stage of the project. To determine the extent of the variation, four well spaced samples were taken from well preserved traps (figure 5-1).

Ecosystem	Plant community	Plot name	Plot code
Moist *terra firma* evergreen forest	Evergreen *terra firma* liana forest	El Chore 1	CH-1
		El Chore 2	CH-2
	Tall *terra firma* evergreen forest	Los Fierros 1	LF-1
		Los Fierros 2	LF-2
Moist inundated evergreen forest	Tall inundated evergreen forest	Las Londras 1	LO-1
		Las Londras 2	LO-2
	Tall riverine evergreen forest	Monte Cristo 1	CR-1
		Monte Cristo 2	CR-2
Deciduous and semi-deciduous dry forest	Deciduous dry forest	Cerro Pilou 1	CP-1
		Cerro Pilou 2	CP-2
	Semi-deciduous dry forest	Acuario 1	AC-1
		Acuario 2	AC-2
Terra firma savannah	Campo cerrado*	Los Fierros, Campo cerrado	FC-1
	Cerradão*	Los Fierros, Cerradão	FC-2
Inundated savannah	Pampa aguada*	Toledo	PP
	Pampa termitero*	Los Fierros, Pampa termitero	FT

Table 5-1: Plots sampled. Four plant communities have Spanish names (*) for loose English translations see chapter 3, figure 3-2.

As no work had previously been carried out on appropriate sizes for pollen counts from lowland tropical ecosystems the guideline of c. 300 grains set out by Moore *et al*. (1991) for temperate taxa was used as a starting point. The use of this value is also suggested by Rull (1987) as appropriate for use in tropical highlands.

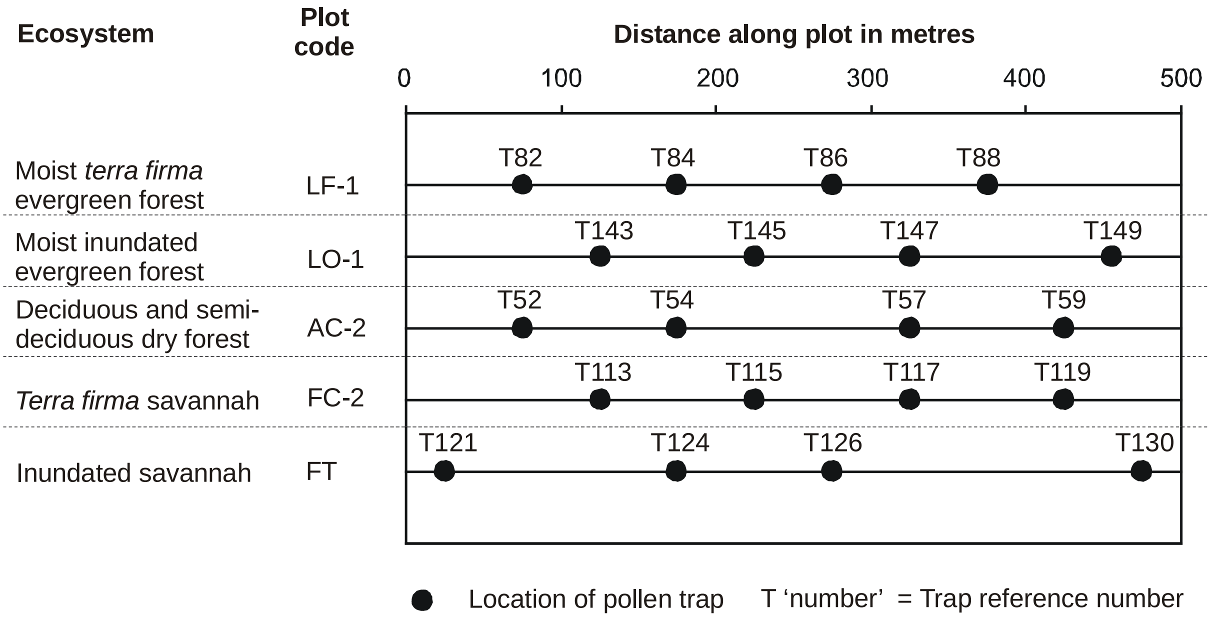


Figure 5-1: Traps sampled for preliminary investigation. All traps were collected during the 1998-1999 field season. Therefore, for reference in the text they are referred to as T 'number'-99, e.g. T82-99.

5.1.2 Results

The results are shown for the percentage occurrence of the abundant pollen types, i.e. those taxa occurring at >5% in at least one sample (figures 5-2). Two key trends are noticeable in these data: i) there are some discernible differences between the pollen rain collected from each ecosystems, and ii) there is a high degree of variation in the pollen rain collected within each ecosystem.

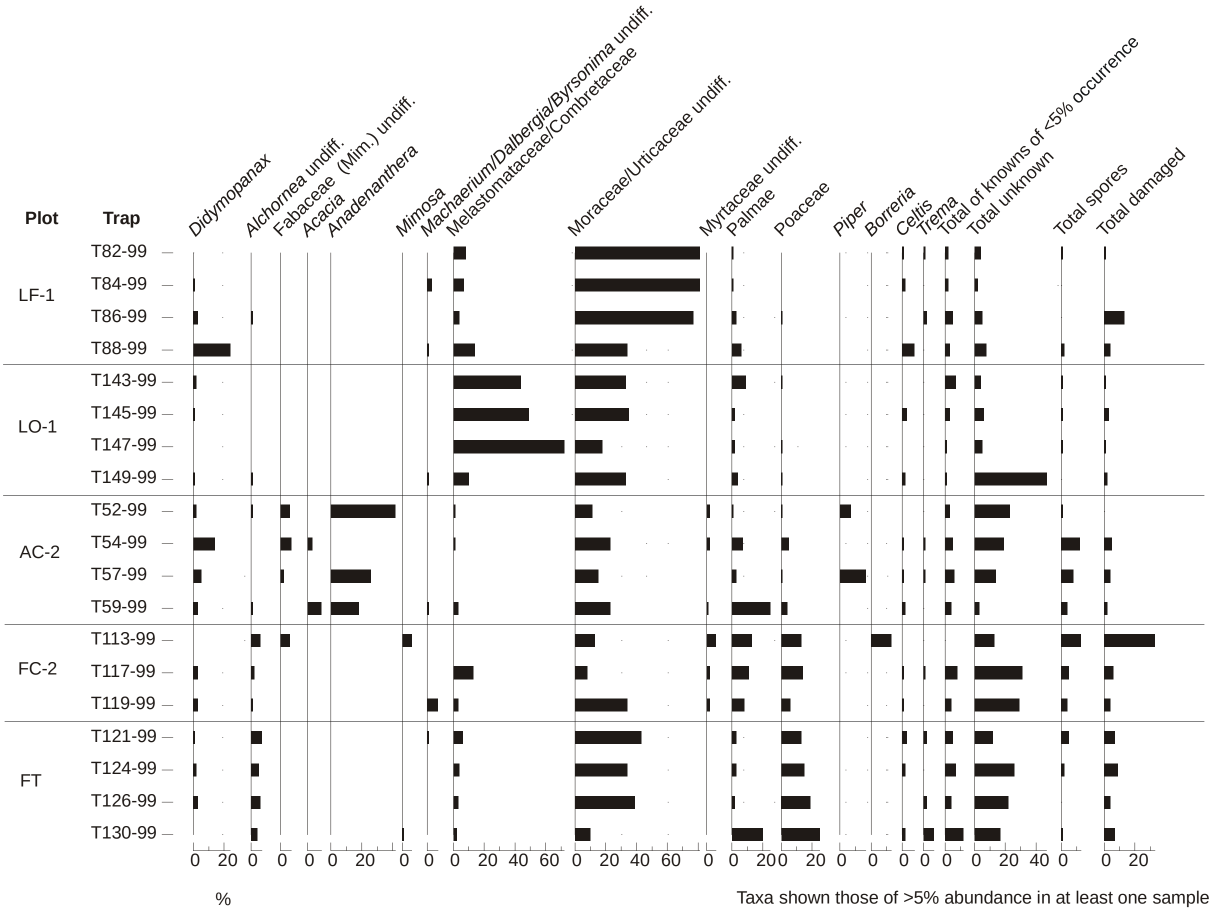


Figure 5-2: Spatial variation of pollen rain. Pollen percentage data. T113-99 and T115-99 both suffered termite damage in the field. This limited the pollen count from T113-99 to sixteen grains and rendered T115-99 uncountable. Ecosystems associated with plots are: moist *terra firma* evergreen forest = LF-1, moist inundated evergreen forest = LO-1, deciduous and semi-deciduous dry forest = AC-2, *terra firma* savannah = FC-2 and inundated savannah = FT.

The taxonomy used throughout this thesis follows Killeen *et al.* (1993), with modifications for pollen identification following Mayle *et al.* (2000). Full details of pollen taxonomy can be found in appendix IV. Key taxa are presented on plates and other identifications can be found on the CD enclosed. From the pollen percentages (figure 5-2) it can be seen that there is a great deal of variation between traps within each of the plots. In LF-1 Palmae rises through the plot suggesting that there may be a spatial bias in the distribution of this taxon. LO-1 shows a greater than 30% difference in the occurrence of Melastomataceae/Combretaceae. In AC-2 *Anadenanthera* and *Piper* are shown to have discontinuous distributions, fluctuating from 0-42% and 0-17% respectively. This possibly indicates that the pollen rain sampled by the trap is very localised. The two savannah plots, FC-2 and FT, show the constant presence of grass pollen (6-25%), but also show significant input from other taxa that vary markedly within these ecosystems, e.g. Moraceae/Urticaceae and Palmae. These data demonstrate that the pollen rain in all these plots is unevenly distributed. The high levels of intra-plot variability are borne out in the pollen accumulation rates (PARs) (equation 5-1; appendix V).

Influx of pollen to trap per year (I):

$$I = \frac{\text{exotic pollen added} \times \text{modern pollen counted}}{\text{exotic pollen counted}}$$

Pollen accumulation rate (PAR):

$$= I / \text{surface area of trap}$$

Equation 5-1: Pollen accumulation rates in grain cm^{-2} year^{-1}. After Stockmarr (1972).

The high level of intra-plot variability in the pollen rain in all the plots demonstrated that it was necessary to increase the spatial resolution of the sampling to be certain of understanding the extent of spatial variation found within each ecosystem. Therefore, a detailed investigation of the spatial variability of the pollen rain within the ecosystems was carried out.

5.2 Detailed investigation of spatial variability

To determine the full extent of spatial variability within any given plot it was decided that it was necessary to sample all ten, spatially distinct, traps from one year. To achieve this for all five ecosystems was deemed to be impossible within the time constraints of this PhD because to sample and process 50 pollen traps and achieve pollen sums of c. 300 would take between 150 and 300 days (based on three to six days per trap, chapter 4, section 4.5). To accomplish the aim of sampling all the spatially distinct traps available, within the time available, and to leave time to investigate the inter-annual variation in the pollen rain, both the number of ecosystems being investigated and the size of the pollen counts had to be reduced.

5.2.1 Strategy

The choice of ecosystems to be investigated in detail was decided by considering two criteria: i) how useful was an improved understanding of the ecosystem's modern pollen rain to answering questions concerning Amazonia's Quaternary environmental history, and ii) how extensive was the ecosystem in the modern vegetation, i.e. how widely applicable would the results be.

As was discussed in chapter 2 (section 2.1.3) there are two key debates surrounding the palaeoenvironmental history of Amazonia: i) did forest or savannah dominate the Amazon basin at the Last Glacial Maximum (LGM)? and ii) if the Amazon Basin was dominated by forest at the LGM what was the relative extent of dry forest vs. moist forest? To shed light on the first of these, at least one forest (either LF-1, LO-1 or AC-2) and one savannah (either FC-2 or FT) ecosystem needed to be studied. To help answer the second, a detailed look at either of the moist evergreen forest plots (LF-1 and LO-1) and the dry forest plot (AC-2) was required. Therefore, based on these palaeoecologial considerations it was necessary to consider at least three of the five ecosystems, one of which must be from the dry forest (AC-2), one from the moist evergreen forest (either LF-1 or LO-1) and one from the savannah (either FC-1 or FT). To determine which of the moist evergreen forest and savannah plots should be studied the wider distributions of their vegetation types were considered.

It is assumed that the ecosystems with the largest modern day extent are likely to be the best represented in the fossil pollen record because their size means that they have more chance of being recorded. In the case of the two moist forest plots, LF-1 was selected because the tall *terra firma* evergreen forest is much more spatially extensive than the inundated evergreen forest of LO-1 within the park (chapter 3, section 3.1) and the Amazon Basin as a whole. For the savannahs, the FC-2 plot, containing Cerradão, was selected because this vegetation association is part of the much larger Cerrado (*sensu lato*) ecoregion that covers large areas to the east of the park (this will be discussed in chapter 6). In contrast the inundated savannah of FT is restricted to local areas that are subjected to seasonal flooding. Full descriptions of the vegetation and the spatial extent of these three ecosystems are presented in the next chapter.

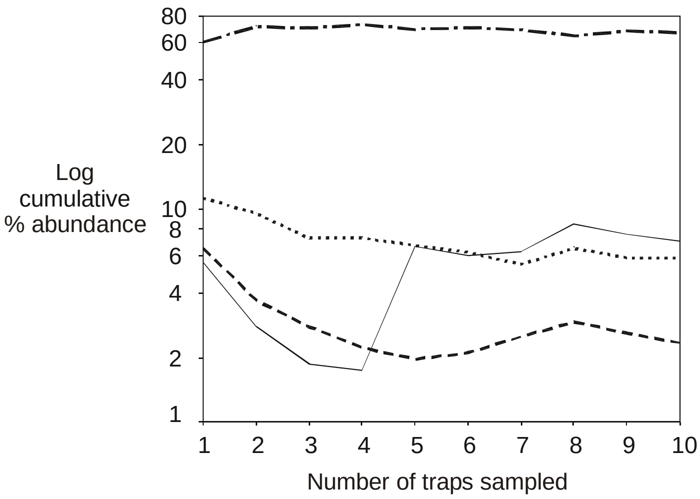
Once the minimum number of ecosystems to be studied had been decided it was necessary to determine appropriate pollen count sizes. To sample the ten spatially distinct traps from these three ecosystems with pollen counts of c. 300 pollen grains would require at least 90 days, which was deemed too long a time to allow sufficient remaining time to investigate inter-annual variations. So, to increase the speed of the analysis and given that the sampling unit of interest was the ecosystem, it was decided that pollen counts per trap would be reduced to c. 100 grains (i.e. 1000 grains per ecosystem). It was calculated that this would produce the data required to assess the intra-plot spatial variability to be collected in approximately 40 days (10 days to sample and process and 30 days to count).

Once it had been established which of the three ecosystems were to be sampled then it was necessary to select a specific field season’s worth of traps. For plots LF-1 and AC-2 it was possible to build upon the data already collected for the preliminary investigation because all ten traps had been successfully recovered for the 1998-1999 field season. However, for FC-2, two of the traps were missing from this field season, so consequently a different year had to be sampled for this ecosystem. In both the 1999-2000 and 2000-2001 field seasons there was full recovery of traps from FC-2 but there was significantly less damage to those traps collected in the latter year, therefore the 2000-2001 field seasons traps were sampled. For full details see appendix II. It is acknowledged that by sampling different years some of the comparability between the ecosystems is lost.

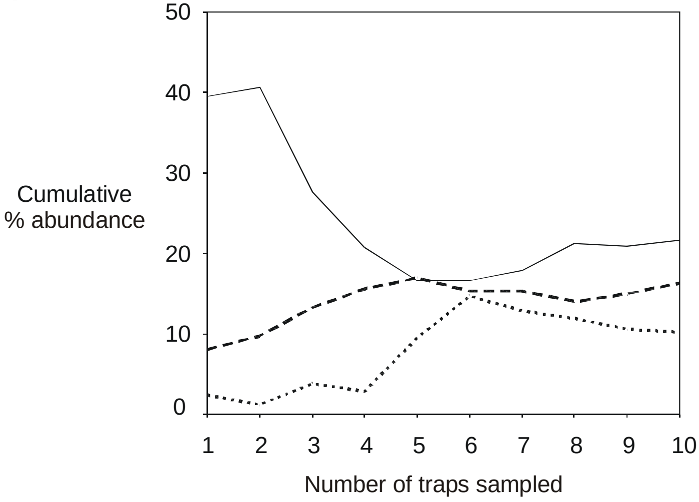
5.2.2 Results

To determine the quantity of pollen traps that were required to capture a consistent pollen signal from each of the ecosystems the cumulative percentage occurrence of abundant pollen types through each plot was investigated. This demonstrates that once five samples have been collected, consistent percentage abundance for most taxa were recorded (figure 5-3).

a) Los Fierros 1



b) Acuario 2



c) Los Fierros, Cerradão

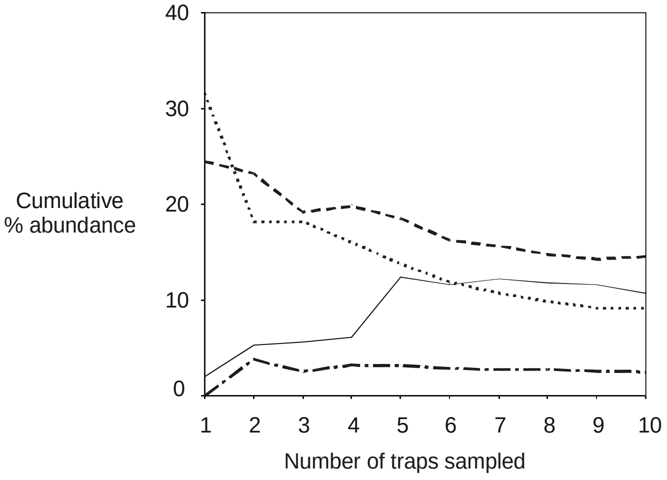


Figure 5-3: Sampling efficiency. Lines indicate the cumulative percentage occurrence of selected taxa. The taxa shown were selected to show variation in occurrence at different abundances.

5.3 Strategy for main project

In the light of this finding it was concluded that by sampling five traps from each of the remaining two years worth of traps, a good indication of the extent of inter-annual variation could be gained across the range of spatial variation in the ecosystem. The spatial position of the traps selected for analysis was determined using three criteria. Firstly, locations were identified where traps had been successfully retrieved from the field every year so that variation at the same location could be studied. Secondly, traps that had suffered the least physical damage were selected, and thirdly, a good spread of samples through the plot was aimed for. Traps sampled for pollen are highlighted in grey in table 5-2.

Trap locations 113 and 115 from the 1998-1999 field season (T113-99 and T115-99) contained poorly preserved pollen. The reason for this is unknown in trap T113-99 and it is suspected that termites damaged the pollen in trap T115-99. As a consequence of this, traps T116-99 and T119-99 were sampled to provide a set of five pollen counts for the 1998-1999 field season.

a) Los Fierros 1

Trap ID number	Recovered Y/N (comment)		
	1998-1999	1999-2000	2000-2001
81	Y	Y	Y
82	Y	Y	Y (d)
83	Y	Y	Y (d)
84	Y	Y	Y
85	Y	Y	Y
86	Y	Y	Y
87	Y	Y (d)	Y (d)
88	Y	Y	Y
89	Y	Y	Y (d)
90	Y	Y	Y

b) Acuario 2

Trap ID number	Recovered Y/N (comment)		
	1998-1999	1999-2000	2000-2001
51	Y (d)	Y	Y
52	Y (d)	Y	Y
53	Y	Y	Y (d)
54	Y (d)	Y	Y
55	Y	N	N
56	Y	Y	Y
57	Y (d)	Y	Y
58	Y (d)	Y (d)	Y (d)
59	Y (d)	Y	Y
60	Y (d)	N	N

c) Los Fierros, Cerradão

Trap ID number	Recovered Y/N (comment)		
	1998-1999	1999-2000	2000-2001
111	Y (d)	Y (d)	Y (d)
112	N	Y	Y
113	Y (pp)	Y (d)	Y
114	N	Y	Y
115	Y (d, pp)	Y	Y
116	Y (d)	Y (d)	Y
117	Y (d)	Y	Y
118	Y (d)	Y (d)	Y
119	Y	Y (d)	Y
120	Y (d)	Y (d)	Y

Table 5-2: Trap recovery rates and sampling strategy. Y = yes, N = No, (d) = damaged in field and (pp) = poor pollen preservation which meant it was necessary to sample additional traps. Full details of recovery from these and all the other plots can be found in appendix II.

5.4 Summary

In this chapter the preliminary analysis carried out to determine the sampling strategy for the main project has been presented. This analysis has revealed that there is a great deal of spatial variability within the pollen rain collected from all of the ecosystems sampled within, and around, NKMNP. Therefore, due to the time constraints of the PhD, it has been argued that only three of the five ecosystems from which pollen has been collected can be examined in detail during the course of this project. The three ecosystems that were chosen are the moist *terra firma* evergreen forest, the deciduous and semi-deciduous dry forest and the *terra firma* savannah. They were selected over the others because work by Haffer (1969), Colinvaux (1987) and Prado and Gibbs (1993) has raised questions about their palaeo-environmental histories. The extent of the modern distribution of these ecosystems and their vegetation are detailed in chapter 6.

In addition it has been demonstrated that five traps are sufficient to sample the variation in the pollen rain from within each ecosystem. In response to this, a strategy based on the available traps has been formulated to allow the assessment of inter-annual variations in the pollen rain. It is all these data that constitute the basis for determining the characteristic pollen signatures from each of the plots, presented in chapter 7.

Chapter 6

Ecosystem ecology

Chapter 6

Ecosystem ecology

In the previous chapter data was presented from pilot research. This research demonstrated that it was only possible to provide a detailed and accurate account of the modern pollen rain from three ecosystems in this thesis; the moist *terra firma* evergreen forest, the deciduous and semi-deciduous dry forest and the *terra firma* savannah. The regional applicability of studying these ecosystems is demonstrated in this chapter by describing the spatial extent and ecological character of each of these ecosystems.

The three ecosystems are examined at four spatial scales. They are, in descending size order: i) biome, ii) ecoregion, iii) ecosystem, and iv) plant community. The examination of these spatial scales is carried out in three sections. First, the relationship of the ecosystems to the wider, continental scale, biomes and ecoregions are considered (section 6.1). Then the ecosystems of the park are the focus of attention and variations within the park are highlighted (section 6.2). Finally, the vegetation composition of the individual study plots is examined (section 6.3).

6.1 Biogeographic context

Given the considerable floristic diversity of the Neotropics (Olson *et al.*, 2001), it is necessary to understand the spatial extent of the ecosystems found within Noel Kempff Mercado National Park (NKMNP). This is necessary to determine the area over which any results may be applicable, i.e. over what area the pollen rain from a given ecosystem found in NKMNP is likely to be representative (table 6-1). Figures 6-1a and b show the spatial distribution of the biomes and ecoregions to which the ecosystems studied belong.

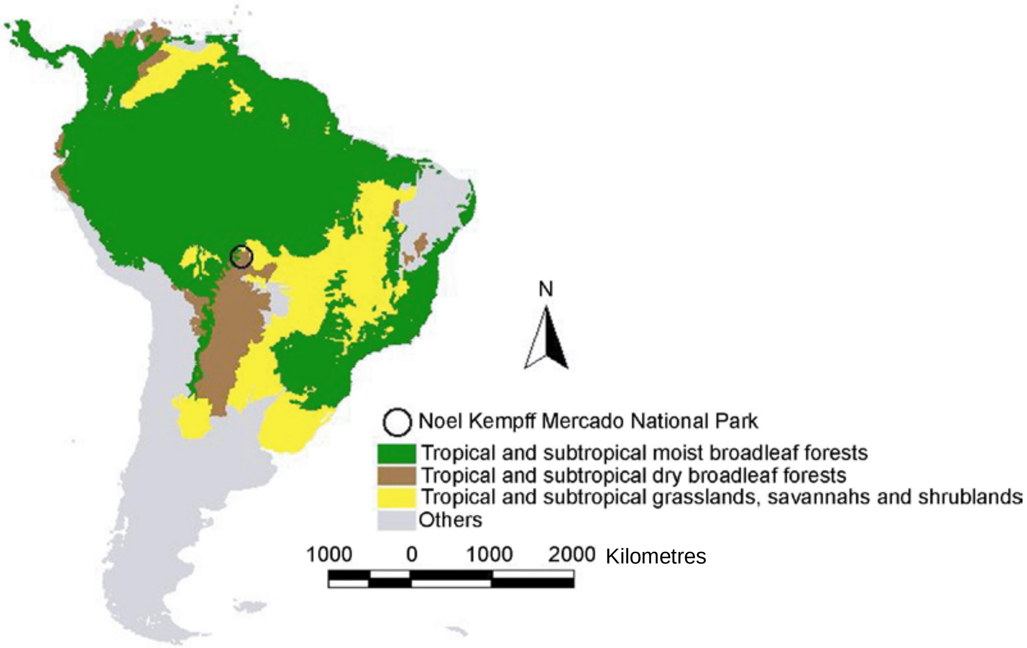
Large (continental) →	**Relative scale**	**→ Small (NKMNP)**
Biome^1	**Ecoregion^2**	**Ecosystem^3**
Tropical and subtropical moist broadleaf forests	Madeira-Tapajós moist forests	Moist *terra firma* evergreen forest
Tropical and subtropical dry broadleaf forests	Chiquitano dry forests	Deciduous and semi-deciduous dry forest
Tropical and subtropical grasslands, savannahs and shrublands	Cerrado (*sensu lato*)^4	*Terra firma* savannah

Table 6-1: Biogeographic hierarchy. Terminology adapted from 1 = Olson *et al.* (2001), 2 = WWF (2003), 3 = Killeen (1998) and 4 = Eiten (1972 and 1978).

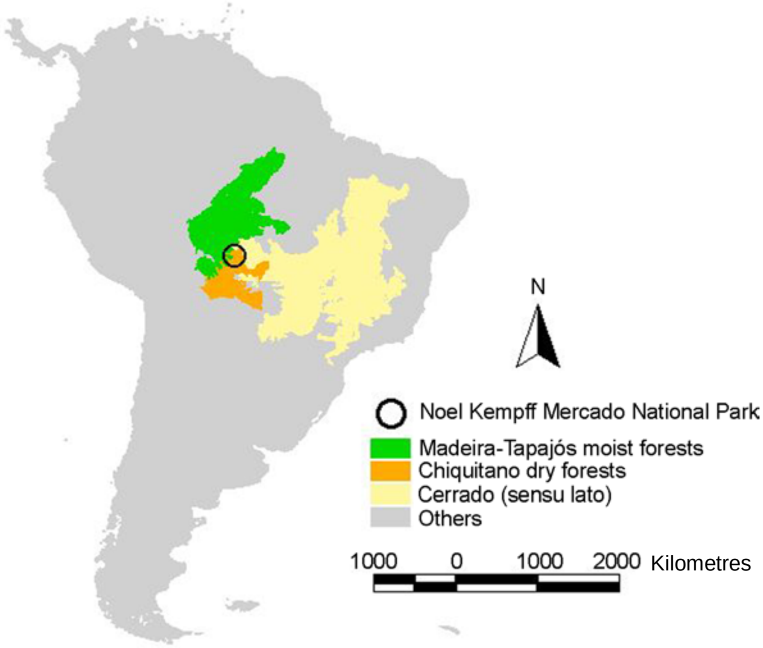
Olson *et al.* (2001) presented a hierarchical scheme that divided the terrestrial vegetation of the Earth into large scale units of ‘biomes’ comprised of associated ‘ecoregions’. These groupings were made on the basis of floristic, structural and climatic similarities between vegetation. This scheme provides a *“comprehensive coverage, a classification framework that builds on existing biogeographic knowledge, and a detailed level of biogeographic resolution.”* (Olson *et al.*, 2001, p. 933). This is particularly useful as it places the vegetation found in NKMNP in a global context. In addition, the data set and a detailed technical guide to the ecoregions is published by the World Wildlife Fund (WWF). This is downloadable through the United Nations Environment Network GEO data portal (United Nations, 2003) and has additional information published on the WWF website (WWF, 2003).

Each ecoregion is *“a geographically distinct assemblage of natural communities that share a large majority of their species, ecological dynamics, and similar environmental conditions, and whose ecological interactions are critical for their long term persistence.”* (Dinerstein *et al.*, 1995, p. 14). Ecoregions with vegetation similar to that found in NKMNP cover vast areas of lowland South America (figure 6-1b) and corresponding biomes cover significantly more (figure 6-1a). The degree to which the results of this thesis can be applied to these wider contexts is dependent on the diversity of the vegetation at these spatial scales. In the next three sub-sections broad descriptions of the ecosystems are given and their associated biogeographic regions are discussed.

a) Biomes



b) Ecoregions

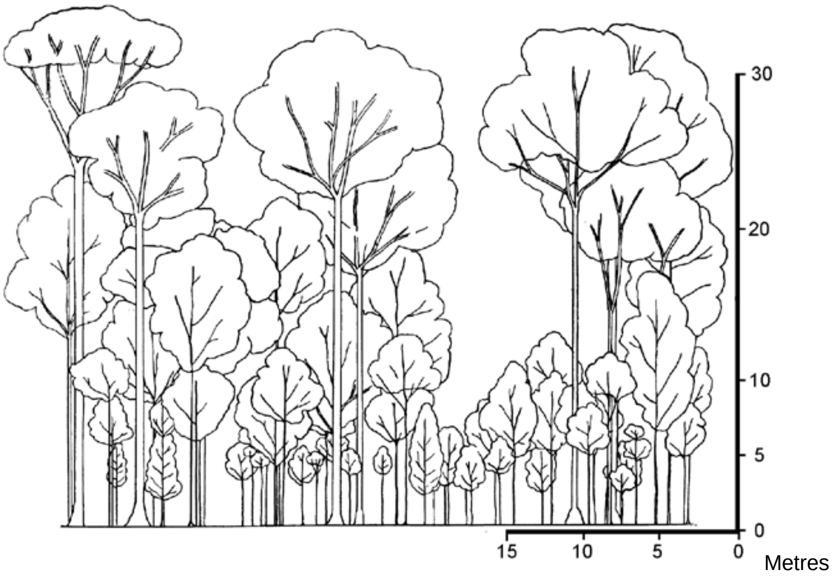


Modified from: Olson *et al.* (2001)

Figure 6-1: Spatial distribution of biogeographic units.

6.1.1 Moist *terra firma* evergreen forest ecosystem

The 'tropical and subtropical moist broadleaf forests' biome of South America covers a vast area of the continent and includes the largest extent of moist *terra firma* evergreen forest in the world, estimated to cover 3,303,000 km^2 in 1973 (Richards, 1996). Forests within this biome occur where the temperature in the coldest month does not go below 20^{o}C, mean annual precipitation exceeds 1000 mm pa and there are not more than four dry months in the year (UNESCO, 1981). There is a great deal of variation in the climate above these minimum thresholds but, despite this, the moist *terra firma* evergreen forests display a broadly similar structure (figure 6-2).



Modified from: Richards (1996)

Figure 6-2: Typical structure of tall *terra firma* evergreen forest. Tall *terra firma* evergreen forest is a major component of the moist *terra firma* evergreen forest found in the Madeira-Tapajós ecoregion.

As shown in table 6-1 and depicted in figure 6-1 the moist *terra firma* evergreen forest contained within NKMNP falls within the 'Madeira-Tapajós moist forest' ecoregion defined by Olson *et al.* (2001). The climatic parameters of this ecoregion vary as follows: i) rainfall in the extreme south and north is <2000 mm pa but reaches 4000 mm pa in the centre, and ii) mean annual temperature varies from 23^{o}C to 27^{o}C (Sears, 2003). This climatic variation means that the floristic composition of this ecoregion varies across its length. However, delimited to the north, west and east by three large rivers: the Solimões (Amazon), Madeira and Tapajós, and to the south by the ecotone with the Chiquitano dry forest, this ecoregion is sufficiently cut off from its neighbours to contain its own distinct flora (Sears, 2003). This includes the rare local endemic *Polygonanthus amazonicus,* the western limit of *Dinizia excelsa* and the eastern limit of *Theobroma cacao* (Sears, 2003). Common trees of the ecoregion belong to the Fabaceae (*Cournarouna speciosa*, three species of *Elizabetha* and two species of *Eperua*), Malpighiaceae (*Lophanthera lactescens*) and Polygalaceae (*Polygala scleroxylon*) (Sears, 2003). Consequently, although the moist *terra firma* evergreen forest pollen signal extracted from NKMNP is likely to be highly representative of the 'Madeira-Tapajós' ecoregion, extrapolation to moist forests elsewhere in Amazonia may be less secure. However, because of similarities in structure, climate and flora between this and other ecoregions within the 'tropical and subtropical moist broadleaf forests' biome (Dinerstein *et al*., 1995), and the restricted level to which taxa can be identified from their pollen alone (as discussed in chapter 2, section 2.1.2), it may be possible to apply the general characteristics of this moist *terra firma* evergreen forest to the wider biome with caution.

6.1.2 Deciduous and semi-deciduous dry forest ecosystem

The 'tropical and subtropical dry broadleaf forests' biome includes ecoregions scattered across South America (figure 6-1). In general the 'tropical and subtropical dry broadleaf forest' biome occurs when mean annual temperature is greater than 17^{o}C, the area is frost free, mean annual precipitation is between 250 and 2000 mm pa, potential evapotranspiration exceeds precipitation and there are four or five months of dry season each year (UNESCO, 1981; Murphy and Lugo, 1986). This wide range of climatic conditions means that this biome can be found under a variety of very different settings. This variability produces the great variety of deciduous and semi-deciduous dry forest that exist (Gentry, 1995). The common physiognomic factor that links these forests is that a proportion of the taxa are ‘facultatively deciduous’, i.e. they loose their leaves as a response to water stress during the dry season (Killeen and Schulenberg, 1998). These types of forests are broadly similar and have the typical structure seen in figure 6-3.

Figure 6-3: Typical structure of a semi-deciduous dry forest. The Chiquitano dry forest near Laguna Mandioré (Bolivia) in the dry season. This forest typically has a deciduous canopy layer that reaches c. 20 metres and an evergreen component in the under-story (R. Guillien, *pers. comm.*, 2001).

The ‘deciduous and semi-deciduous dry forest’ ecosystem located to the south of NKMNP comprises the northeastern-most extent of the ‘Chiquitano dry forests’ ecoregion of Bolivia (Parker *et al.*, 1993; Killeen *et al.*, 1998; Landivar, 2003). This ecoregion is described as the transition zone between the moist evergreen forests to the north and the drier forests to the south (Landivar, 2003). The ‘Chiquitano dry forests’ ecoregion (figure 6-2) has a distinct ecological character but varies locally, depending on drainage patterns. These variations mean that the region is composed of a number of distinct vegetation associations that are themselves ecologically discrete (Landivar, 2003).

The most wide-spread of these forest sub-types is the ‘soto/curupaú’ in which (in addition to those taxa listed in table 6-2) *Caesalpinia pluviosa*, *Machaerium scleroxylon*, *Amburana cearensis* and *Cedrela fissilis* are also important woody components (Landivar, 2003). In spite of a high level of internal variation, the ‘Chiquitano dry forest’ ecoregion has close florist affinities with other discrete dry forests regions across South America (Prado and

Gibbs, 1993). These broad floristic similarities between the Chiquitano dry forest and other parts of the 'tropical and subtropical dry broadleaf forests' biome means that palynological characterization of this region will make it possible to use the palynological signature of the 'Chiquitano dry forest' ecoregion to help with the identification of dry forests in the fossil pollen record from other floristically similar regions. In addition many of the dry forests have close ecological affinities and occur under similar climatic conditions to ecoregions classified within the 'tropical and subtropical grasslands, savannahs and shrublands' biome by Olson *et al.*, (2001) (see Prado and Gibbs, 1993).

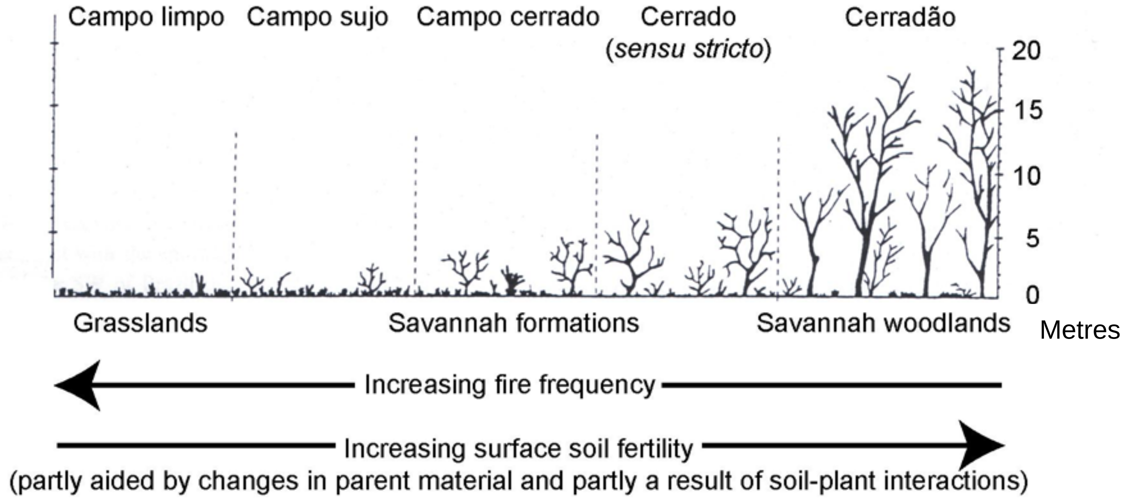
Forest sub-type	Characteristic vegetation
Cuchi/curupaú forest	*Astronium urundeuva - Anadenanthera macrocarpa*
Cuta/ajo-ajo forest	*Phyllostyllon rhamnoidies - Gallesia integrifolia*
Soto/curupaú forest	*Scinopsis brasiliensis - Anadenanthera macrocarpa*
Tajibo/tusequii forest	*Tabebuia heptaphylla - Machaerium hirtum*

Source: Landivar (2003)

Table 6-2: Variation within the 'Chiquitano dry forests' ecoregion. These four types of forest comprise the majority of the 'Chiquitano dry forests' ecoregion.

6.1.3 *Terra firma* savannah ecosystem

The Cerrado ecoregion, as mapped by Olson *et al*. (2001) (see figure 6-1), equates roughly to the Cerrado (*sensu lato*) mapped by Eiten (1972 and 1982). This region is a complex of xeromorphic woodland, scrub, savannah and grassfield vegetation that occurs under similar climatic conditions to the semi-deciduous dry forest (Eiten, 1972; UNESCO, 1981); i.e. precipitation 1000-2000 mm pa with up to five months of dry season and mean annual temperature ranging from 16^{o}C to 25^{o}C. The exact definition of this structurally diverse vegetation association is often confused. Therefore, to avoid confusion, definitions in this thesis follow the comprehensive guidelines on classification laid down by Eiten (1972). The terminology and how it relates to the varying vegetation structures is shown in figure 6-4.



Modfied from: Furley (1999)

Figure 6-4: The various structures of Cerrado (*sensu lato*). Soil fertility and fire frequency are the key factors in determining the type of Cerrado (*sensu lato*) that can grow.

From figure 6-4 the Cerrado (*sensu lato*) can be seen as a gradation of similar vegetation associations from open grasslands through to closed woodland. These distinct plant communities each have Spanish names (see figure 6-4) but differentiation between them is problematic due to the gradational nature of the transitions. The extent to which the woody taxa dominate different parts of this ecoregion is determined by fire, nutrient availability and water stress (Coutinho, 1982; Moreira, 2000; Hoffman and Moreira, 2002; Motta *et al.*, 2002; Oliveira-Filho and Ratter, 2002).

Despite this diversity in form at the plant community level, the Cerrado (*sensu lato*) ecoregion has a distinctive and diverse woody flora that can be used to characterise this region floristically (Oliveira-Filho and Ratter, 2002). Characteristic species include *Caryocar brasiliense*, *Qualea grandiflora*, *Byrsonima coccolobifolia* and *Tabebuia ochracea* (da Silva, 2003). However, there are strong regional differences in the herbaceous taxa (Filgueiras, 2002) and the vegetation of the region has been shown to be "*extremely heterogeneous*"

(Ratter *et al.*, 1996, p153). This suggests that applying the results of a palynological characterization from one area of this ecoregion to another must be done with caution.

6.2 Noel Kempff Mercado National Park ecosystem characteristics

The moist *terra firma* evergreen forest, deciduous and semi-deciduous dry forest and *terra firma* savannah ecosystems are all present within, and around, NKMNP because of its peculiar climatological, geological and geomorphic setting (as discussed in chapter 3). These ecosystems cover most of the park (figure 6-5). However, it should be noted that they are not the only ecosystems in the area and each can be sub-divided into a number of distinct plant communities (table 6-3; see chapter 3, figure 3-2).

Ecosystem	**Plant community***
Moist *terra firma* evergreen forest	• Tall *terra firma* evergreen forest • Dwarf *terra firma* evergreen forest • Evergreen *terra firma* liana forest • Evergreen *terra firma* mixed liana forest
Moist inundated evergreen forest	• Tall inundated evergreen forest • Low inundated evergreen forest • Tall riverine evergreen forest • Pioneer riverine evegreen forest
Deciduous and semi-deciduous dry forest	• Deciduous dry forest • Semi-deciduous dry forest • Semi-deciduous palm forest • Semi-deciduous inundated dry forest
Terra firma savannah	• Campo limpo, campo rupestre, campo sujo, campo húmido [open savannah] • Campo cerrado [shrubby savannah] • Cerrado (*sensu stricto*) [open woodland] • Cerradão [closed woodland]
Seasonally inundated savannah	• Pampa aguada [inundated open savannah] • Pampa termitero [inundated shrub savannah, termite savannah] • Inundated scrubland • Savannah marsh • Palm marsh • Marsh

Table 6-3: Composition of ecosystems in Noel Kempff Mercado National Park. Terminology modified from Killeen (1998) and Panfil (2001). * loose English translation given in [ ] where plant communities have distinct Spanish names. For spatial distribution see chapter 3, figure 3-2.

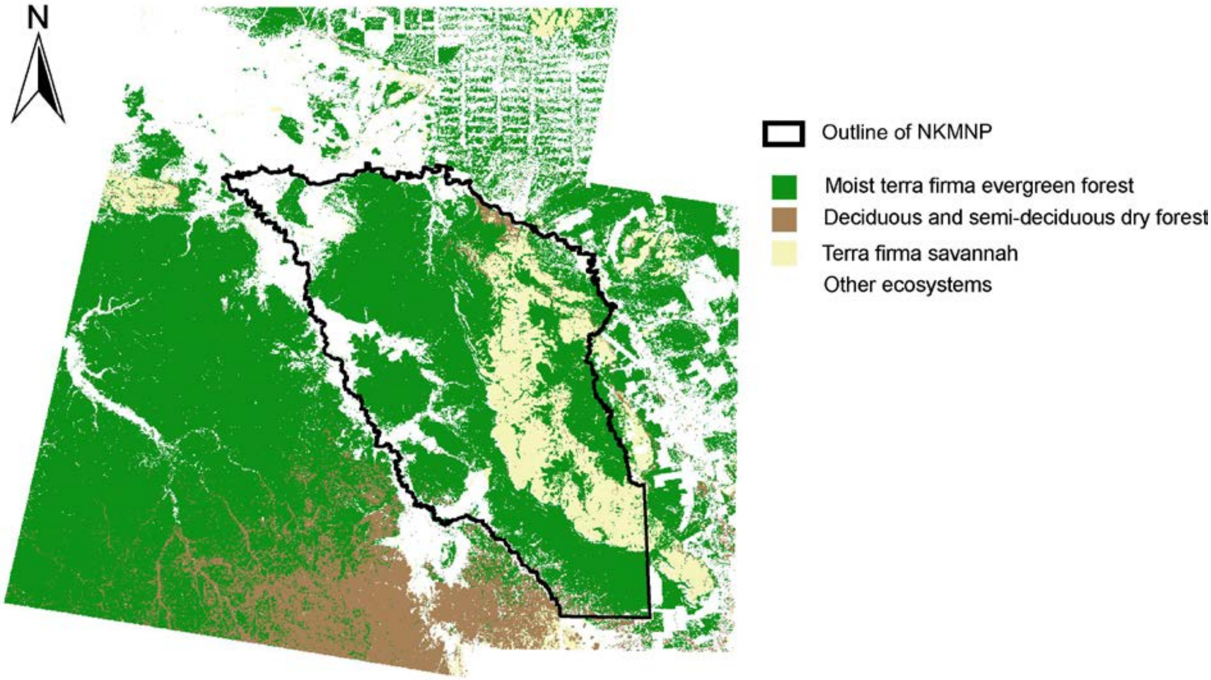


Figure 6-5: Distribution of the three ecosystems studied in Noel Kempff Mercado National Park. These three ecosystems include plant communities that cover the majority of the region. Data from Landsat^{TM} (T.J. Killeen, unpublished data).

6.2.1 Moist *terra firma* evergreen forest ecosystem

As was shown in figure 6-1 NKMNP contains the southernmost extent of the 'Madeira-Tapajós moist evergreen forest' ecoregion. The majority of this ecoregion is dominated by moist *terra firma* evergreen forest. In NMKNP this ecosystem consists of four different plant communities (table 6-3). These occupy the majority of the lowland, and a substantial portion of the Huanchaca plateau in NKMNP (figure 6-5). The lowland forest plant communities share many characteristics, namely: they are all found in well-drained areas with deep soil and maintain a closed canopy throughout the year with a continual shedding of leaves (figure 6-6).

In an ecological study Killeen (1998) showed that the following are the key characteristics of the vegetation within these types of forests. The most abundant tree is *Pseudolmedia laevis* (Moraceae), while *Qualea paraensis* (Vochysiaceae), *Erisma gracile* (Vochysiaceae), *Apuleia leiocarpa* (Caesalpinioideae) and *Moronobea coccinea* (Clusiaceae) are important species of emergent tree. In addition, discrete palm stands of either *Phenakospermum guianense, Astrocaryum aculeatum, Attalea marpia, Euterpe precatoria* or *Socratea exorrhiza*, exist throughout the forest, the species being determined by local drainage conditions. Some areas of forest can be distinguished by an abundance of lianas (table 6-3). The lianas thrive on areas of Tertiary laterite where their adaptation to water stress gives them a competitive advantage over trees. The moist *terra firma* evergreen forest found on the plateau is similar in composition to that found in the lowland. The key difference on the plateau is that there is moderately shallow lateritic soil, which restricts tree growth and as a consequence canopy height is no more than ten meters. This plant community has therefore been classified as dwarf evergreen forest (Killeen, 1998).

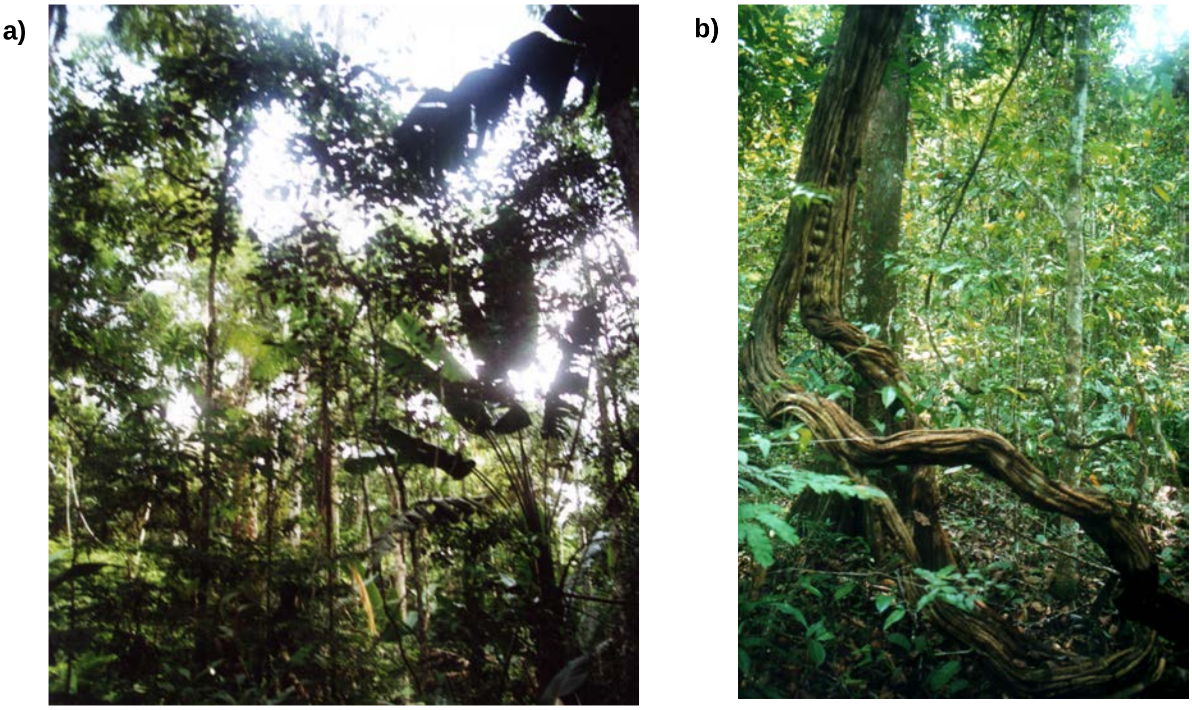


Figure 6-6: Tall *terra firma* evergreen forest within the Noel Kempff Mercado National Park. Los Fierros area. a) Clearing with palm, and b) large liana.

The different plant communities that comprise the moist *terra firma* evergreen forest found in and around NKMNP have broad compositional similarities. Therefore they are all representative of the wider 'Madeira-Tapajós moist evergreen forest' ecoregion. However, it is the ‘tall *terra firma* evergreen forest’ plant community that is the most spatially extensive within the ecoregion and therefore is probably the most representative of the vegetation found there.

6.2.2 Deciduous and semi-deciduous dry forest ecosystem

There are four plant communities within the deciduous and semi-deciduous dry forest ecosystem in and around NKMNP (table 6-3). The deciduous and semi-deciduous dry forests are located mainly towards the south of the park (figure 6-5) and represent the northernmost extent of the Chiquitano dry forest (figure 6-1) (Parker *et al.*, 1993; Killeen *et al.*, 1998). The lowland semi-deciduous forest occurs on an eroding peneplain, has a typical canopy height of between 15-20 metres and is structurally complex (Killeen, 1998).

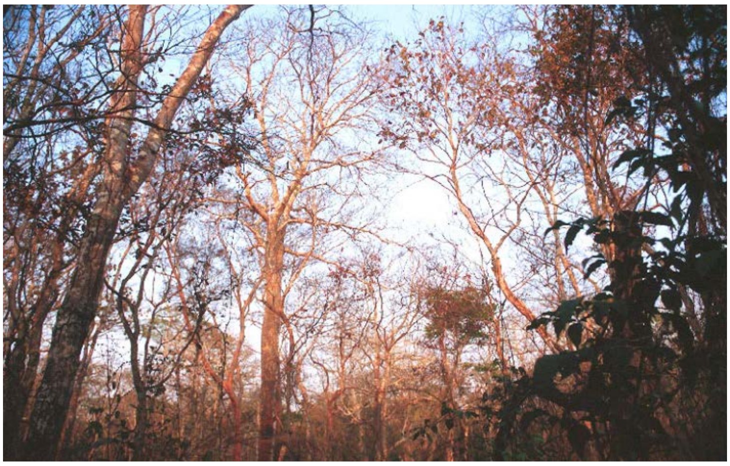


Figure 6-7: Semi-deciduous dry forest near Noel Kempff Mercado National Park. Acuario area. During the dry season many canopy trees loose their leaves due to water stress.

Parker *et al.* (1993) and Killeen (1998) showed that the dominant species within this type of forest are *Anadenanthera colubrina* (Fabaceae, Mimosoideae), *Casearia gossypiosperma* (Flacourtiaceae), *Amburana cearensis* (Fabaceae, Papilionoideae), *Combretum leprosum* (Combretaceae), *Tabebuia insignis* and *T. serratifolia* (Bignoniaceae), *Eriotheca roseorum* (Bombacaceae), *Poeppigia procera* (Fabaceae, Caesalpiniodeae) and *Aspidosperma cyclindrocarpon* (Apocynaceae). Therefore this forest type has broad floristic similarities to the ‘soto/curupaú’ vegetation association that dominates much of the Chiquitano dry forest (Landivar, 2003).

Other areas of semi-deciduous forest are markedly different in character. Edaphically controlled dry forests are present within areas of evergreen forest where granite inselburgs create favourable drainage conditions (figure 6-8a). To the south of the park “Cuci” palm (*Attalea speciosa*) forests occur (figure 6-8b) and on the plateau a type of dry forest with a close affinity to the cerradão exists. The main species present on the plateau are *Callisthene microphylla* (Vochysiaceae), *Copaifera langsdorfii* (Fabaceae, Caesalpiniodeae), *Terminalia fagifolia* (Combretaceae), *Commiphora leptophloeos* (Burseraceae), *Erythroxylum tortuosum* (Erythroxylaceae), *Acacia multipinnatum* (Fabaceae, Mimosoideae) and *Diospyros* sp. (Ebenaceae).

a) Edaphically controlled dry semi-deciduous dry forest

b) Cusi palm forest

Figure 6-8: Other types of dry forest near Noel Kempff Mercado National Park. a) Granite inselbergs created drainage conditions that favour semi-deciduous dry forest where the lowlands are covered by moist *terra firma* evergreen forest. Cerro Pilou area. b) Palm forests can be found in lowland areas. Campamento area.

The ‘deciduous dry forest’ and ‘semi-deciduous dry forest’ plant communities found to the south of NKMNP are part of the ‘Chiquitano dry forests’ ecoregion. These forests have compositional affinities with the ‘soto/curupaú’ vegetation type that dominates much of this ecoregion (see section 6.1.2). Consequently, the pollen rain collected from these forests are applicable to understanding the fossil pollen record from the ‘Chiquitano dry forests’ ecoregion.

6.2.3 *Terra firma* savannah ecosystem

Killeen (1998) divided the *terra firma* savannah of NKMNP into four different plant communities that encompassed seven different divisions of Cerrado (*sensu lato*) (figure 6-4). These different plant communities are found on a variety of thicknesses of well-drained soils to the southeast of the park and on the Huanchaca plateau (figure 6-5). The associated ecoregion ‘Cerrado (*sensu lato*)’ stretches south and east beyond the park (see figure 6-1).

The ground layer of all types of Cerrado (*sensu lato*) is always dominated by grass (Killeen and Hinz, 1992) but the density and composition of the woody taxa have been shown to vary over short distances within the park (Mostacedo and Killeen, 1997) (figures 6-9 and 6-10). The woody layer is extremely diverse (e.g. see Silberbauer-Gottsberger and Gottsberger, 1984; Ratter *et al.*, 1988; Ratter *et al.*, 1996; Castro *et al.*, 1998; Castro *et al.*, 1999; Furley, 1999). Even within NKMNP the floristic similarity between different

Figure 6-9: Cerrado (*sensu stricto*) in Noel Kempff Mercado National Park. Los Fierros area.

types of Cerrado (*sensu lato*) is low (Mostacedo and Killeen, 1997). However, a few species do occur across the full range of Cerrado (*sensu lato*) types in the vegetation around NKMNP. These are: *Byrsonima coccolobifolia* (Malpighiaceae), *Caryocar brasiliensis* (Caryocaraceae) and *Erythroxylum suberosum* (Erythroxylaceae) (Killeen, 1998). da Silva (2003) highlights the first two of these as distinctive Cerrado (*sensu lato*) species.

Figure 6-10: Cerradão in Noel Kempff Mercado National Park.

6.3 Study plot ecology

The flora of the three ecosystems discussed above has been studied in detail at thirty-two vegetation study plots in and around NKMNP (Mostacedo and Killeen, 1997; Killeen, 1998; Panfil, 2001). The three plots selected for this modern pollen study are Los Fierros 1, Acuario 2 and Los Fierros, Cerradão (table 6-4; figure 6-11); the reasons for this were discussed in chapter 4 and 5. The extent to which each of these plots are representative of the three ecosystems is discussed below.

Ecosystem	Plant community	Plot name	Plot code
Moist *terra firma* evergreen forest	Tall *terra firma* evergreen forest	Los Fierros 1	LF-1
Deciduous and semi-deciduous dry forest	Semi-deciduous dry forest	Acuario 2	AC-2
Terra firma savannah	Cerradão	Los Fierros, Cerradão	FC-2

Table 6-4: Vegetation of pollen study plots. For full plot details see appendix VI.

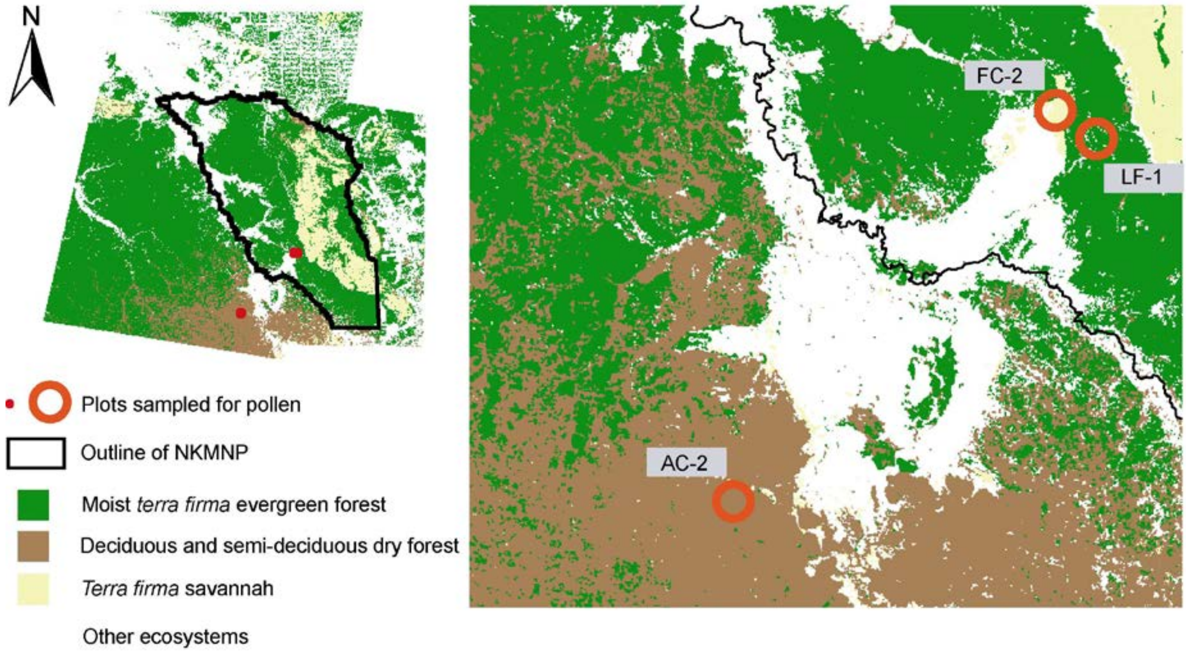


Figure 6-11: Pollen study plots in relation to ecosystems studied. Data from Landsat^{TM} (T.J. Killeen, unpublished data).

6.3.1 Tall *terra firma* evergreen forest plant community

The key findings of Panfil (2001)'s investigation of the vegetation of the LF-1 plot were that: i) the plot has a structure and diversity similar to the other moist *terra firma* evergreen forest plots within the park, and ii) that by using the Importance Value Index (IVI) described by Dallmeier *et al.* (1992), which takes into account relative density, relative dominance, and relative frequency of plants occurring within the plot (equation 6-1), the twelve ecologically most important species found within the plot >10 cm d.b.h. (diameter breast height) can be ranked (table 6-5).

Calculation of IVI for a taxon:

$$IVI = \Sigma[(ni / tni)*100]\ [(bi / bt)*100]\ \ [(fi / ft)*100]$$

where, *ni* is the number of individuals of a taxa
tni is the total number of individuals of all taxa
bi is the total basal area of a taxa
bt is the total basal area of all taxa
fi is the frequency occurrence of a taxa
ft is the total frequency occurrence of all taxa

Equation 6-1: Importance Value Index. The IVI allows the relative importance of taxa to be considered (Dallmeier *et al.*, 1992).

These data reflect the dominance of large evergreen trees from the

Vochysiaceae and Moraceae families and also demonstrate the importance of *Phenakospermum*, *Euterpe* and *Socratea* palm stands. The characteristic taxa shown in table 6-5 are very similar to those found in the other *terra firma* evergreen plots of the park (Panfil, 2001). These similarities mean that the LF-1 plot is typical of the 'tall *terra firma* evergreen forest' plant community found within NKMNP which, as was discussed in section 6.2.1, is extensive within the wider 'Madeira-Tapajós moist evergreen forest' ecoregion.

Family	*Genus*	*species*	IVI
Vochysiaceae	*Erisma*	*uncinatum*	38.0
Vochysiaceae	*Qualea*	*paraensis*	22.6
Moraceae	*Pseudolmedia*	*laevis*	20.9
Strelitziaceae	*Phenakospermum*	*guianensis*	19.8
Rubiaceae	*Capirona*	*decorticans*	15.6
Palmae	*Euterpe*	*precatoria*	14.3
Elaeocarpaceae	*Sloanea*	*eichleri*	10.5
Euphorbiaceae	*Hyeronima*	*oblonga*	10.5
Moraceae	*Pseudolmedia*	*macrophylla*	10.3
Rubiaceae	*Amaioua*	*guianensis*	8.1
Melastomataceae	*Miconia*	*pyrifolia*	6.6
Palmae	*Socratea*	*exorrhiza*	6.4

Source: Panfil (2001)

Table 6-5: The twelve most ecologically important species in Los Fierros 1.

6.3.2 Semi-deciduous dry forest plant community

Panfil (2001)'s investigation has shown two key things about the AC-2 plot. Firstly, it does not differ much in either structure or diversity to other nearby semi-deciduous dry forest, but it does differ in these respects from the other plant communities within the deciduous and semi-deciduous dry forest ecosystem. Secondly, that by using the IVI, the twelve ecologically most important species found in the plot, >10 cm d.b.h., can be determined (table 6-6).

These data characterize the plot as having a lower layer of short woody taxa, *Anadenanthera colubrina*, *Tabebuia roseo-alba*, *Combretum leprosum* and *Bauhinia rufa*, and an upper layer of larger trees not exceeding thirty metres in height. This includes the pot bellied *Chorisia integrifolia* (figure 6-12). These taxa are different from those shown to be important in the other dry forest nearby (Panfil, 2001). However, four species are prominent throughout the region *Caesalpinia floribunda, Anadenanthera colubrina, Tabebuia roseo-alba* and *Combretum leprosum* (Panfil, 2001). In addition, significant compositional differences can be seen between these and other types of dry forest within this ecosystem.

Family	*Genus*	*species*	IVI
Fabaceae (Caesalpiniodeae)	*Caesalpinia*	*floribunda*	36.9
Fabaceae (Mimosoideae)	*Anadenanthera*	*colubrina*	26.4
Bignoniaceae	*Tabebuia*	*roseo-alba*	19.8
Palmae	*Attalea*	*speciosa*	17.3
Flacourtiaceae	*Casearia*	*gossypiosperma*	15.0
Combretaceae	*Combretum*	*leprosum*	13.9
Sterculiaceae	*Sterculia*	*apetala*	10.9
Boraginaceae	*Cordia*	*alliodora*	9.8
Fabaceae (Caesalpiniodeae)	*Bauhinia*	*rufa*	9.8
Bombacaceae	*Chorisia*	*integrifolia*	9.6
Palmae	*Attalea*	*phalerata*	8.6
Sterculiaceae	*Guazuma*	*ulmifolia*	8.0

Source: Panfil (2001)

Table 6-6: The twelve most ecologically important species in Acuario 2.

Despite the diversity of the ‘deciduous and semi-deciduous dry forest’ ecosystem found in, and around, NKMNP the vegetation of this plot is typical of the ‘Chiquitano dry forests’ ecoregion that stretches away to the south (Parker *et al.*, 1993; Panfil, 2001). For example, the forest found at AC-2 contains *Caesalpinia* and

Figure 6-12: *Chorisia* sp., a distinctive dry forest tree. The author and Dr. F.E. Mayle next to a specimen with a particularly large ‘belly’ in the Chiquitano forest near Laguna Concepçion, Santa Cruz Province, Bolivia. Photograph R. Gullien.

Anadenanthera, both genera identified as important in the ecoregion (see section 6.1.2).

6.3.3 Cerradão plant community

The floristic structure and composition of the Cerrado (*sensu lato*) found in and around NKMNP has been shown to include different plant communities covering the range of woodland cover associated with this ecoregion (Mostacedo and Killeen,1997; Panfil, 2001) (figure 3-2 and 6-4). Killeen (1998) subdivides these into four groups of plant communities: i) Campo limpo, Campo rupestre, Campo sujo, Campo húmido, ii) Campo cerrado, iii) Cerrado (*sensu stricto*), and iv) Cerradão (figure 3-2). Mostacedo and Killeen (1997) investigated the structure and floristic composition of Cerrado (*sensu stricto*) and Cerradão. They discovered that grasses dominate the lower stratum of both plant communities but that the higher strata differ. The Cerrado (*sensu stricto*) is dominated by shrubs and sub-shrubs and the Cerradão is dominated by trees (figures 6-9 and 6-10). Mostacedo and Killeen (1997) also found that there was relatively little floristic similarity between these two plant communities. Panfil (2001) has shown these *terra firma* savannahs to be floristically distinct from the other types of savannah found in the region. In addition, Panfil (2001) ranked the dominant species of the FC-2 plot by their relative cover within the plot (equation 6-2; table 6-7).

Family	*Genus*	*Species*	Relative cover
Poaceae	*Trachypogon*	*plumosus*	22.6
Guttiferae	*Caraipa*	aff. *densifolia*	19.9
	Indet.	sp. 11	11.8
	Indet.	sp. 5	4.4
Poaceae	*Paspalum*	*pectinatum*	3.0
Poaceae	*Sporobolus*	*cubensis*	2.8
Poaceae	*Thrasya*	*petrosa*	2.6
Melastomataceae	*Miconia*	*albicans*	2.5
Fabaceae (Papilionoideae)	*Ormosia*	sp. 1	2.3
Proteaceae	*Roupala*	*montana*	2.1
Bombacaceae	*Eriotheca*	*gracilipes*	2.1
Icacinaceae	*Emmotum*	*nitens*	2.1

Source: Panfil (2001)

Table 6-7: The twelve most dominant species in Los Fierros, Cerradão.

Calculation of relative cover for a taxon:

Relative cover = $(N_i / N_t)*100$

where, N_i is number of individuals of each life form
N_t is total number of plants

Equation 6-2: Relative cover. Relative cover provides a measure of taxon abundance (Mostacedo and Killeen, 1997).

These data show that grasses (Poaceae) are abundant in this plant community even though it is a part of the woodier component of the Cerrado (*sensu lato*) ecosystem. They also show the importance of short shrubs and trees, including *Roupala montana* which Killeen *et al.* (1993) noted as being common in the savannahs and Cerrado (*sensu lato*) of Bolivia.

The floristic variety and variation in the structure of the different plant communities that comprise the Cerrado (*sensu lato*) mean that the application of any modern pollen signal from one part of the ecoregion to another should be done so with caution. However, the persistence of grass as a major component throughout, given that it is a major pollen producer, and coupled with an understanding of the variations in the floristic diversity should mean that the pollen signature from the Cerradão plant community will aid the understanding of the palaeoenvironmental history of the Cerrado (*sensu lato*) ecoregion. The reasons for selecting samples from the Cerradão rather than other plant communities were discussed in chapters 4 and 5.

6.4 Summary

The three ecosystems that are studied in this project are all shown to be internally diverse to some degree. The extent to which the results of this study can be applied to understanding the wider contexts are as follows:

- The LF-1 plot contains ‘tall *terra firma* evergreen forest’ plant community that is compositionally similar to the other plant communities that are found within the ‘moist *terra firma* evergreen forest’ ecosystem in, and around, NKMNP. In turn, this ecosystem covers much of the ‘Madeira-Tapajós moist evergreen forest’ ecoregion which has broad compositional affinities with other ecoregions within the ‘tropical and subtropical moist forests’ biome. Therefore, the modern pollen rain from this plot is applicable to understanding the palaeoenvironmental history of the ‘Madeira-Tapajós moist evergreen forest’ ecoregion and possibly, with caution, other floristically similar ecoregions of the wider biome.

- The AC-2 plot contains ‘semi-deciduous dry forest’ plant community that is part of the highly diverse ‘deciduous and semi-deciduous dry forest’ ecosystem found in, and around, NKMNP. The forest found in AC-2 is the northernmost extent of the ‘Chiquitano dry forest’ ecoregion. Prado and Gibbs (1993) demonstrated strong floristic similarities with this region and other Neotropical dry forests. Therefore, pollen rain data collected from this plot is probably applicable to understanding the fossil pollen records from many of these regions.

- The FC-2 plot contains vegetation belonging to the Cerradão plant community, one of four floristically distinct types of *terra firma* savannah identified in the vicinity of the NKMNP. This plant community is part of the highly diverse Cerrado (*sensu lato*) ecoregion. Floristic variations between the different types of Cerrado (*sensu lato*), even within the park, mean that any application of results of this study over a wider area must be done so with caution. However, similarities in the woody component and the ubiquitous dominance of grasses should mean some wider understanding could be gained.

In this chapter the wider applicability of modern pollen studies from these three ecosystems has been demonstrated by examining the ecology of the plots and the wider regions associated with them. In the next two chapters the results of the modern pollen study are presented.

Chapter 7

Ecosystem pollen signatures

Chapter 7

Ecosystem pollen signatures

In the previous chapter a detailed ecological background to the ecosystems studied was given. This chapter determines the characteristic pollen signatures of three lowland Neotropical ecosystems and therefore addresses the second aim of this thesis (as defined in chapter 2, section 2.3). In this chapter the statistical methodology used to analyse the pollen trap data is presented (section 7.1). This methodology is described in four sub-sections which explain how the following characteristics of the pollen assemblages of each plot been determined: i) the extent of intra-plot spatial variation, ii) the extent of inter-annual (temporal) variation, iii) the statistically distinctive pollen taxa in the pollen assemblages, and iv) the nature of the pollen-vegetation relationship. The results of these analyses are then presented for each plant community (plot) in turn: the tall *terra firma* evergreen forest in section 7.2, the semi-deciduous dry forest in section 7.3 and the Cerradão in section 7.4. At the end of each of these sections the results of the four stages of analysis are drawn together to determine the characteristic pollen signature for the corresponding plant community and its associated ecosystem.

7.1 Data and statistical techniques used

In this section the statistical methodologies used to investigate the nature of the pollen rain from the individual ecosystems are described. These are explained in the order in which they are used in the analysis.

7.1.1 Intra-plot spatial variability

The question of spatial variability in the pollen data of a particular plot is addressed by the visual analysis of pollen diagrams and Spearman's rank correlation coefficients among traps. The pollen diagrams allow easy visual recognition of the dominant pollen taxa and general similarities, differences and trends in the data. For each plant community two pollen diagrams have been generated, using Psimpol v. 4.10 (Bennett, 2003). They show the percentage and pollen accumulation rate (PAR) data (grains cm^{-2} year^{-1}) of the taxa occurring at ≥3% abundance in the data set. This threshold was chosen on the basis that it is at this point that the pollen assemblages begin to correlate in the Spearman's rank analysis. This improved correlation between traps and suggests that taxa below this threshold are noise in the data created by the presence of odd pollen grains either from low pollen producing taxa or long distance transport. The Spearman's rank correlations were carried out to quantify the statistical similarity of each sample with other samples. This allowed the identification of anomalous traps. The Spearman's rank correlation method was chosen, rather than any other method of bivariate correlation, because it is non-parametric and so the bias caused by the skewed distribution of the pollen data was removed, i.e. pollen assemblages typically contain a few highly abundant taxa and many low abundance taxa (Shaw and Wheeler, 1994; Chatfield, 1995). Spearman's rank analysis was performed on various sections of the data, four of which are presented here: i) all data, and only those taxa occurring at an abundance of ii) ≥3%, iii) ≥5%, and iv) ≥10% in at least one sample. The results of the analysis carried out at these three percentage cut-offs are displayed because they show clearly in which sections of the data variations occur. This means that the heterogeneity of the ecosystem can be demonstrated for taxa occurring at different abundances in the pollen rain. This information was found to be important in identifying differences in the pollen rain caused by high pollen production close to traps and the identification of consistencies in the 'background' pollen rain. The results of these analyses are presented in sections 7.2.1, 7.3.1 and 7.4.1 for each ecosystem respectively.

7.1.2 Inter-annual variability

The issue of inter-annual variability in the pollen assemblages was addressed by applying the same methodology as described above to the data extracted from traps sampled in multiple years. The results of these analyses are presented in sections 7.2.2, 7.3.2 and 7.4.2.

7.1.3 Distinctive pollen taxa

To determine the distinctive pollen taxa found within the complex multivariate pollen assemblages collected from each plant community, a method of analysis was required that both simplified the data set and identified the important components in the original data set. Principal Components Analysis (PCA) was found to perform this function well. PCA is a multivariate data reduction technique that summarises data sets by explaining the variance in terms of a few dominant gradients of variation or 'principal components'. It then relates these new variables back to the original data by analysing how well they correlate (Gauch, 1982; McGarigal *et al.*, 2000). The way in which this technique has been applied in this part of the study means it essentially identifies the key taxa (i.e. the variables) from within the spatially and/or temporally distinct pollen assemblages (i.e. the samples) of each plot. The key taxa are identified by looking at how well each taxon correlates with each of the components, i.e. the closer a taxon correlates to a component then the greater the corresponding portion of the variance explained by that component can be attributed to that taxon. Therefore, the taxa that correlate well with the largest variance in the data set can therefore be said to be statistically distinctive of the pollen assemblage. For a detailed description of the workings of this technique see Birks and Gordon (1985), Krzonowski (2000) or McGarigal *et al.* (2000).

To apply this statistical method to the pollen data, two types of modification had to be made to the data to improve agreement between the data and the computational assumptions of the statistical method (McGarigal *et al.*, 2000): i) data was log transformed to improve normality in the distribution (as recommended for pollen data by Ter Braak, 1986), and ii) outliers identified in earlier analyses were removed from the data set where it could be seen that they were biasing the results (as suggested by McGarigal *et al.*, 2000). However, even after these modifications it should be noted that: i) the pollen data were not uni-variate normal and so can be assumed not to be multi-variate normal (McGarigal *et al.*, 2000), although the percentage data were closer to uni-variate normality than the PAR data, and ii) that the ratio of samples (traps) to variables (taxa) was lower than 1:1, which is the level at which the PCA produces strong correlations (McGarigal *et al*., 2000). Despite these problems PCA was deemed a suitable technique to apply to this data set because the problems inherent with the analyses are understood and because it allowed key taxa to be identified from the highly complex pollen data sets (Gauch, 1982; McGarigal *et al.*, 2000).

The data used to derive the principal components are the percentage pollen data of taxa occurring ≥3% abundance in at least one sample. This threshold was used as the cut off for the inclusion of data for the reasons discussed in section 7.1.1 and because it moved the ratio of samples (traps) to variables (taxa) toward that required by the PCA (see above paragraph). Percentage data are presented, rather than PAR data, for three reasons: i) percentage data allowed the inclusion of all the samples (due to higher than expected input of pollen to some traps the ratio of modern pollen to the exotic marker was too low to allow the accurate calculation of PARs (Stockmarr, 1972) (appendix VII)), ii) principal components derived from the accurately calculated PARs alone produced weaker correlations due to the lower sample to variable ratio, and iii) the PAR data were further from a normal distribution than the percentage data and this resulted in a bias towards the more abundant taxa in the PCA.

The principal components were derived from a correlation matrix because this method applies equal weight to all the variables (Gauch, 1982). This is important when identifying key trends within pollen data because taxa may be distinctive to an ecosystem but present only at a low level due to low productivity and/or poor dispersal mechanisms. The principal components retained for analysis after derivation were done so on the basis of the latent root criterion (McGarigal *et al*., 2000), i.e. only those components that explained more variance in the data set than that explained by the original variables were retained. The results of these analyses are presented in sections 7.2.3, 7.3.3 and 7.4.3.

7.1.4 Pollen-vegetation relationships

The ecological assessment carried out by Panfil (2001) and the detailed plot inventories of T.J. Killeen (unpublished data) provided the basis for the pollen-vegetation assessment (see chapter 6). Direct comparisons were made by examining the ratio of percentage abundance of each taxon identified in both the vegetation and the pollen. This allowed the degree to which each taxon was under/over-represented in the pollen rain to be assessed. The vegetation calculations were based upon the percentage of the number of individuals found >10 cm d.b.h. (diameter breast height) within the forest plots; i.e. Los Fierros 1 (LF-1) and Acuario 2 (AC-2) (T.J. Killeen, *pers. comm.*, 2003). For the Los Fierros, Cerradão plot (FC-2) the vegetation data available were for counts of individuals along a ‘branching’ transect (T.J. Killeen, *pers. comm.*, 2003). These data were chosen because they were available for all the plots. In addition, where possible, calculations were also made with respect to estimates of biomass calculated for each taxon by Killeen using the formula and data presented in Brown (1997) and defined as "*…the total amount of above ground living organic matter in trees…*" (Brown, 1997, p. 4). The calculations against biomass allowed the size and form of the trees to be considered relative to the pollen produced. The pollen data used were the maximum percentage occurrence of each taxon. These data were used so that the full potential for over representation in the pollen rain could be assessed and because other measures of abundance in the pollen were found to be misleading, i.e. mean values were not representative of 'real' taxon abundances found in the pollen rain and median and lowest values were often zero making the ratios calculated meaningless. The results of these analyses are presented in sections 7.2.4, 7.3.4 and 7.4.4.

7.2 Tall *terra firma* evergreen forest

Twenty traps were selected and analysed from those collected from the LF-1 plot (see chapter 5, table 5-1). The tall *terra firma* evergreen forest plant community found in this plot is representative of the moist *terra firma* evergreen forest ecosystem characteristic of much of the Madeira-Tapajós ecoregion of southern Amazonia (as discussed in chapter 6). The pollen rain data extracted from these samples allowed the extent of intra-plot spatial (section 7.2.1) and inter-annual (section 7.2.2) variations to be assessed, the distinctive pollen taxa for the plot to be statistically determined (section 7.2.3), and the relationship with the parent vegetation to be analysed (section 7.2.4). The characteristic pollen signature determined by the analyses is then presented in section 7.2.5.

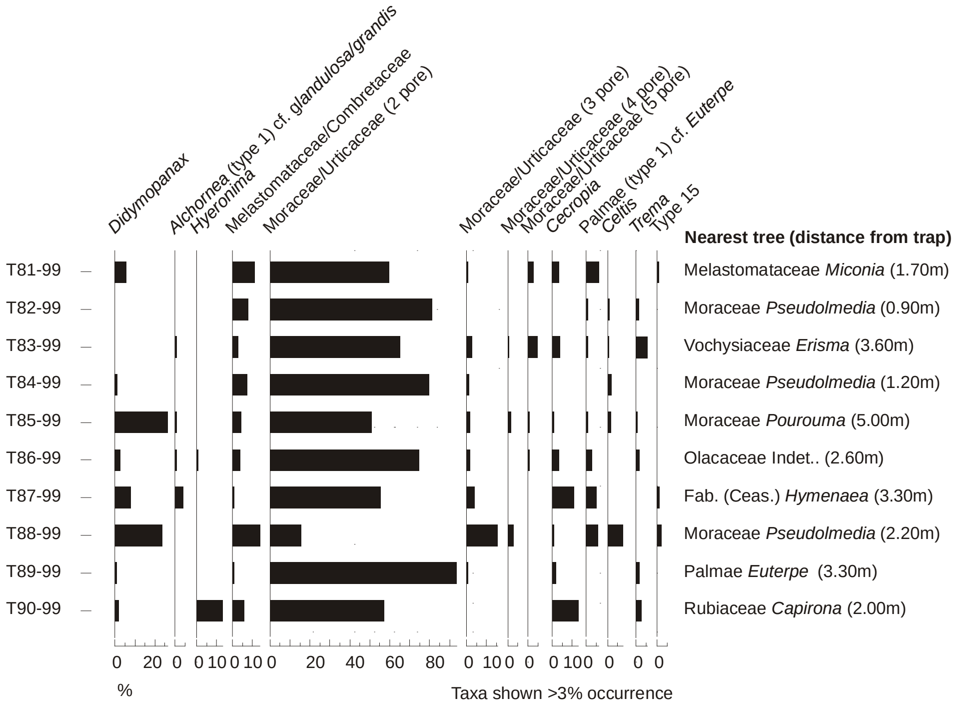
7.2.1 Intra-plot spatial variability

In figures 7-1 and 7-2 the extent of spatial variation within the tall *terra firma* evergreen forest of LF-1 in 1998-1999 is shown.

The Moraceae/Urticaceae pollen type dominates (50-80%) the pollen assemblages in all but one sample, although other taxa do make up a significant proportion (>10%) of the pollen rain at various discrete points within the plot (figure 7-1). This shows the distribution of the pollen rain to be highly locally variable but there is no evidence to suggest that the pollen rain collected is being biased by localised influx from the nearest tree (figure 7-1a). For example, Moraceae/Urticaceae is at its lowest level in T88-99 where a tree of the family Moraceae is nearby and is at its highest in T89-99 where the closest tree is a Palm (figure 7-1). There is also no evidence to suggest that physical damage to the trap is affecting the pollen assemblage collected (figure 7-1b). Figure 7-1b shows similar quantities of damaged grains in samples that were attacked and not attacked by termites, e.g. T86-99 compared to T90-99.

In figure 7-2a the complete pollen assemblages (i.e. all taxa regardless of percentage occurrence) are correlated and this shows that there is little spatial consistency in the pollen rain. However, generally stronger positive correlations are evident once the rarer taxa are removed from the correlation, i.e. more green squares are present in progression from 7-2a to 7-2d (see section 7.1.1 for justification for cut off percentage values). The correlation also picks out two anomalous samples: i) T83-99 is shown to differ markedly from the majority of the other samples when only taxa occurring ≥5% are considered (figure 7-2c) and, ii) T88-99 is different when only taxa ≥10% are considered (figure 7-2d).

a) Pollen percentage data



b) Pollen accumulation rates

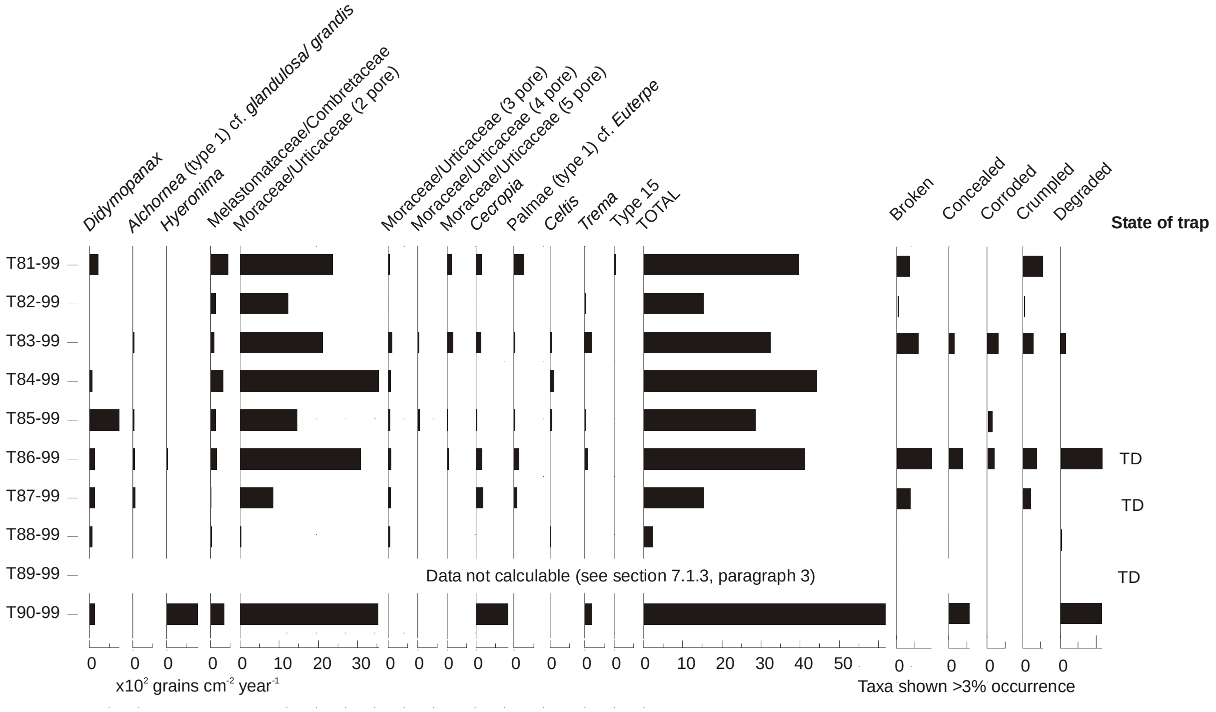
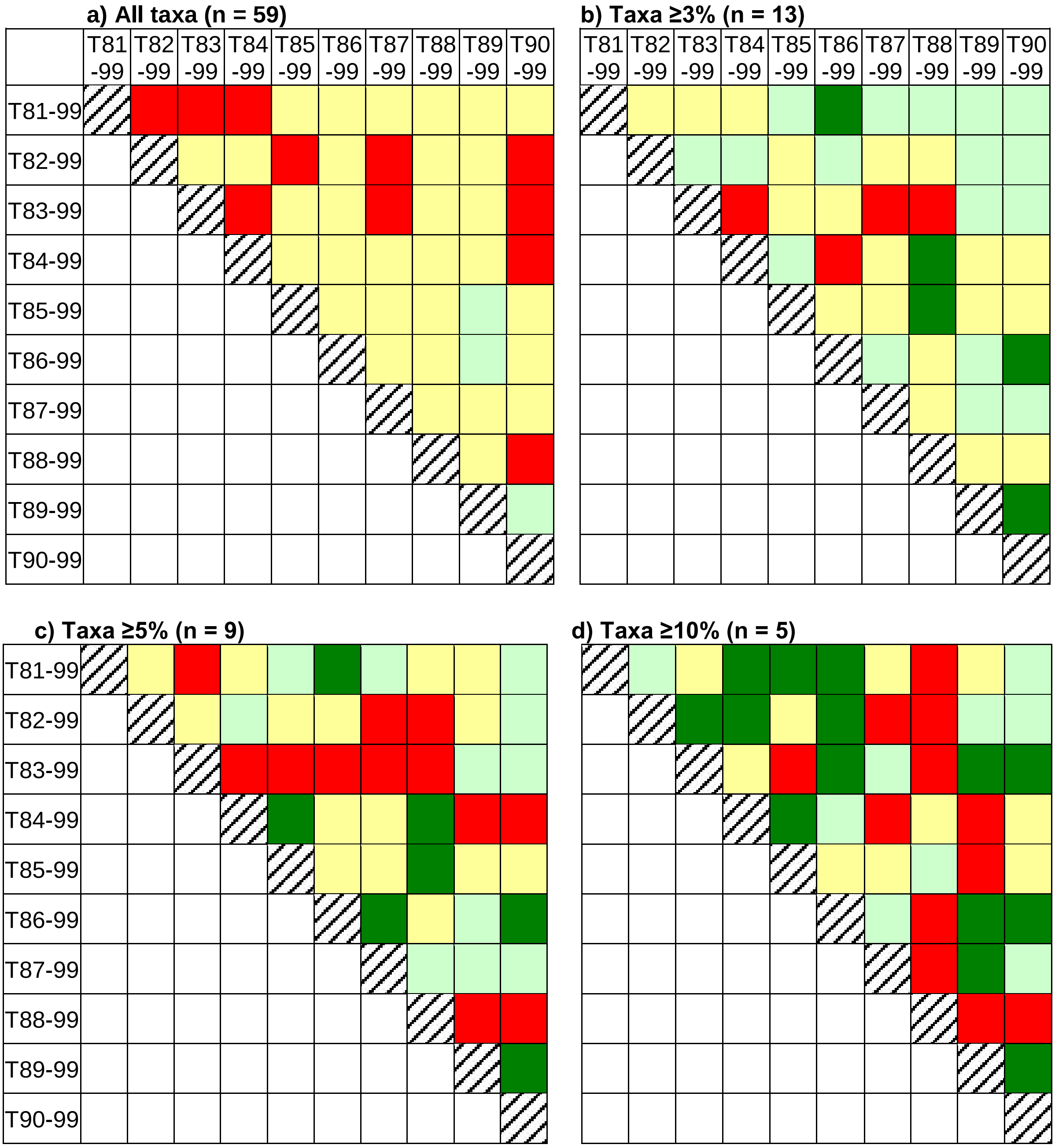


Figure 7-1: Spatial variation of pollen rain in tall *terra firma* evergreen forest. “Nearest tree” indicates the closest tree >10 cm d.b.h. to the trap. “TD” indicates traps that suffered damage from termites. For full data set see appendix VII.



a) All taxa (n = 59)

	T81 -99	T82 -99	T83 -99	T84 -99	T85 -99	T86 -99	T87 -99	T88 -99	T89 -99	T90 -99
T81-99	▨	🟥	🟥	🟥	🟨	🟨	🟨	🟨	🟨	🟨
T82-99		▨	🟨	🟨	🟥	🟨	🟥	🟨	🟨	🟥
T83-99			▨	🟥	🟨	🟨	🟥	🟨	🟨	🟥
T84-99				▨	🟨	🟨	🟨	🟨	🟨	🟥
T85-99					▨	🟨	🟨	🟨	🟢	🟨
T86-99						▨	🟨	🟨	🟢	🟨
T87-99							▨	🟨	🟨	🟨
T88-99								▨	🟨	🟥
T89-99									▨	🟢
T90-99										▨

b) Taxa ≥3% (n = 13)

T81 -99	T82 -99	T83 -99	T84 -99	T85 -99	T86 -99	T87 -99	T88 -99	T89 -99	T90 -99
▨	🟨	🟨	🟨	🟢	🟩	🟢	🟢	🟢	🟢
	▨	🟢	🟢	🟨	🟢	🟨	🟨	🟢	🟢
		▨	🟥	🟨	🟨	🟥	🟥	🟢	🟢
			▨	🟢	🟥	🟨	🟩	🟨	🟨
				▨	🟨	🟨	🟩	🟨	🟨
					▨	🟢	🟨	🟢	🟩
						▨	🟨	🟢	🟢
							▨	🟨	🟨
								▨	🟩
									▨

c) Taxa ≥5% (n = 9)

T81-99	▨	🟨	🟥	🟨	🟢	🟩	🟢	🟨	🟨	🟢
T82-99		▨	🟨	🟢	🟨	🟨	🟥	🟥	🟨	🟢
T83-99			▨	🟥	🟥	🟥	🟥	🟥	🟢	🟢
T84-99				▨	🟩	🟨	🟨	🟩	🟥	🟥
T85-99					▨	🟨	🟨	🟩	🟨	🟨
T86-99						▨	🟩	🟨	🟢	🟩
T87-99							▨	🟢	🟢	🟢
T88-99								▨	🟥	🟥
T89-99									▨	🟩
T90-99										▨

d) Taxa ≥10% (n = 5)

▨	🟢	🟨	🟩	🟩	🟩	🟨	🟥	🟨	🟢
	▨	🟩	🟩	🟨	🟩	🟥	🟥	🟢	🟢
		▨	🟨	🟥	🟩	🟢	🟥	🟩	🟩
			▨	🟩	🟢	🟥	🟨	🟥	🟨
				▨	🟨	🟨	🟢	🟥	🟨
					▨	🟢	🟥	🟩	🟩
						▨	🟥	🟩	🟢
							▨	🟥	🟥
								▨	🟩
									▨

Strength of positive Spearman's rank correlation coefficient indicated by colour:

🟩 = ≥0.750 🟢 = 0.749 - 0.500 🟨 = 0.499 - 0.250 🟥 = <0.250* ⬜ = Blank

* Includes some weak negative correlations.

Figure 7-2: Spatial heterogeneity of pollen rain in tall *terra firma* evergreen forest. Correlations are based upon a Spearman's rank correlation (SPSS v.11.01). For full details of correlation see appendix VIII.

The pollen assemblages collected from the ten different points within the tall *terra firma* evergreen forest demonstrate the full extent of spatial variability within the plot for the 1998-1999 field season. These correlations reveal a generally consistent signal is being extracted from the plot once the noise of low pollen producing taxa and contamination has been removed, i.e. those taxa occurring at <3% abundance (figure 7-2). There are, however, four traps that contain pollen assemblages which differ significantly from the others in at least one respect.

Firstly, T83-99 correlates poorly with six of the other nine traps for the portion of the data set ≥5% abundance (figure 7-2c). The reason for this is a percentage occurrence of *Trema* (figure 7-1a) that in turn alters the rank position of the other taxa occurring ≥5% abundance. This is the reason for the low Spearman's rank correlation co-efficient (figure 7-2c). Values of other taxa found in this sample are similar to those found in a number of other samples (figure 7-1). Therefore, apart from this anomalously high level of *Trema*, T83-99 is shown to contain a fairly typical pollen assemblage from this plot.

Secondly, T88-99 differs from the other samples in that the PAR of Moraceae/Urticaceae (2 pore) is negligible when compared to the other traps (figure 7-1b). The reason for this is unclear because this taxon is the most abundant pollen producer in the ecosystem and a Moraceae tree is located close to this trap (figure 7-1a). One possible explanation is that the trap became covered during the period of flowering of the Moraceae. The low PAR of Moraceae/Urticaceae (2 pore) in this trap has resulted in PARs of other taxa, similar to those found in other traps (figure 7-1b), becoming elevated to relatively higher percentage occurrences, e.g. *Didymopanax* and *Alchornea* (type 1) (figure 7-1a). Therefore, T88-99 can be regarded as having anomalously low Moraceae/Urticaceae (2 pore) PAR but, in terms of the other taxa, PARs are typical (figure 7-1b).

T89-99 contains the highest percentage occurrence of Moraceae/Urticaceae (2 pore) found in this ecosystem, due to an immense input of grains of this type (appendix VII). The huge input of this pollen type resulted in too few exotic marker grains being counted to reliably calculate the exact PAR into the trap (figure 7-1b), although a rough estimate of the influx is around 10x that of the other traps. To reach this high level it is possible that an anther may have fallen into the trap. However, this high percentage occurrence illustrates the ability of this one pollen type to dominate and swamp the other taxa found within this ecosystem. As a result of this dominance the diversity of the taxa found in this sample is below that of the other traps (appendix VII). T89-99 therefore contains an anomalously high proportion of Moraceae/Urticaceae (2 pore) but, with respect to the rank correlation of the taxa in the assemblage, it is not atypical for this ecosystem (figure 7-2).

Finally, T90-99 does not correlate well with four of the other samples when all taxa are considered (figure 7-2a) because, uniquely, it has abundances of >10% *Cecropia* and *Hyeronima*. These are the highest recorded proportions of both these taxa within the plot and it is the only location at which *Hyeronima* reaches a significant proportion of the pollen assemblage. This high percentage occurrence coupled with the absence of these two taxa from all but one other sample (figure 7-1) suggests that their high percentages in T90-99 may be due to nearby plants swamping the background pollen rain.

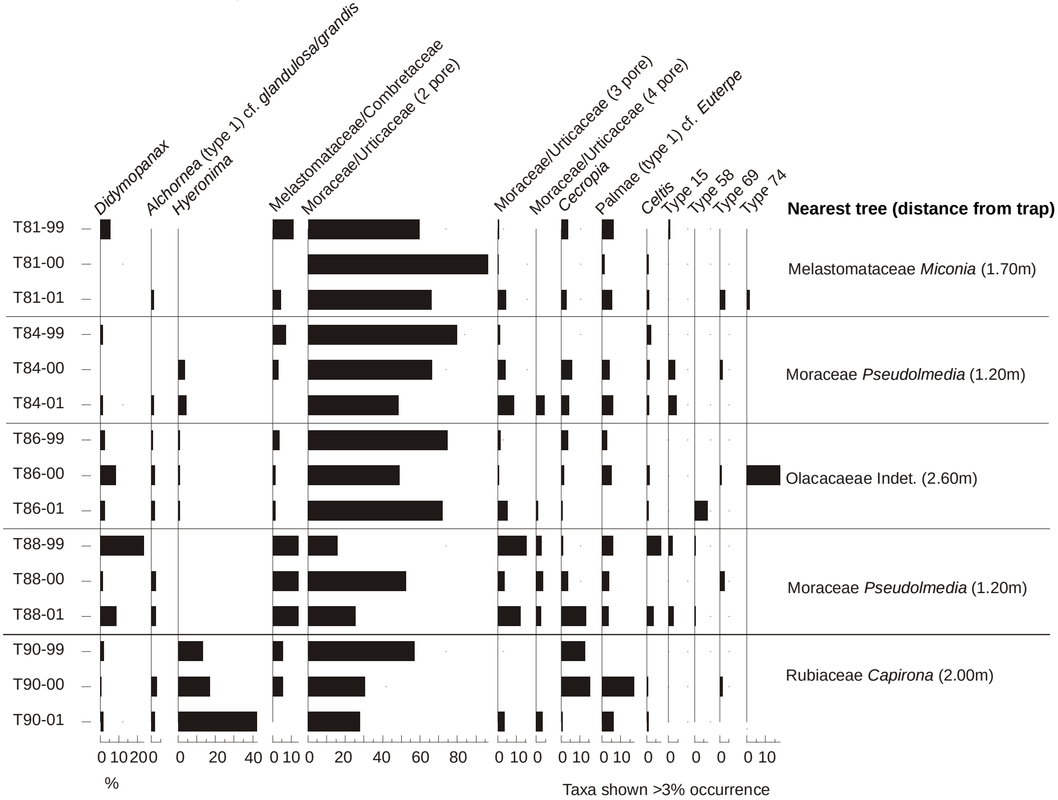
In summary, the Moraceae/Urticaceae pollen type dominates the pollen rain from the tall *terra firma* evergreen forest. The diversity of other taxa occurring at ≥3% abundance is low, but 6 of the taxa that do occur are present in the majority of the samples at reasonably consistent levels (figure 7-1): Melastomataceae/Combretaceae, Palmae (type 1), *Alchornea* (type 1), *Cecropia*, *Didymopanax* and *Trema*. The pollen rain from the plot is spatially variable, especially with respect to the PARs of Moraceae/Urticacae pollen, which therefore affects the percentage occurrence of the other less abundant taxa. However, there is general similarity in the trap spectra once the noise of low abundance taxa (<3%) is removed (figure 7-2b). This suggests that the pollen rain signal from the tall *terra firma* evergreen forest is reasonably spatially consistent.

7.2.2 Inter-annual variability

In figures 7-3 and 7-4 the extent of inter-annual variability in the pollen rain from field seasons 1998-1999 to 2000-2001 for five points within the tall *terra firma* evergreen forest plot is illustrated.

Moraceae/Urticaceae (2 pore) dominates the pollen rain from all three years (figure 7-3) with other taxa accounting for a significant proportion of the pollen rain at distinct spatial locations, e.g. the tree genus *Hyeronima* at location T90. This supports the assertion from the previous section that there are localised inputs of pollen into each of the traps although there is no evidence of this localised input coming from the nearest large tree (figure 7-3a). There is a generally stronger positive correlation between samples collected in 2000 and 2001 compared to those collected in 1999. This is linked to two trends in the data: i) there are higher overall influx rates in 2000 and 2001 compared to 1999, and ii) pollen from some plants is only found in one or two of the three years of study, mostly in 2000 and/or 2001 (figure 7-4). Two trap locations do not follow this pattern exactly. Firstly, at location T86 there is poor correlation between the 2000 and 2001 data. This is attributed to the high percentage of type 74 pollen in the year 2000 (figure 7-3a). The only other trap in which pollen type 74 is present is T81-01. These sporadic occurrences suggest that the plant from which this pollen originates does not flower every year. This is typical of some evergreen

a) Pollen percentage data



b) Pollen accumulation rates

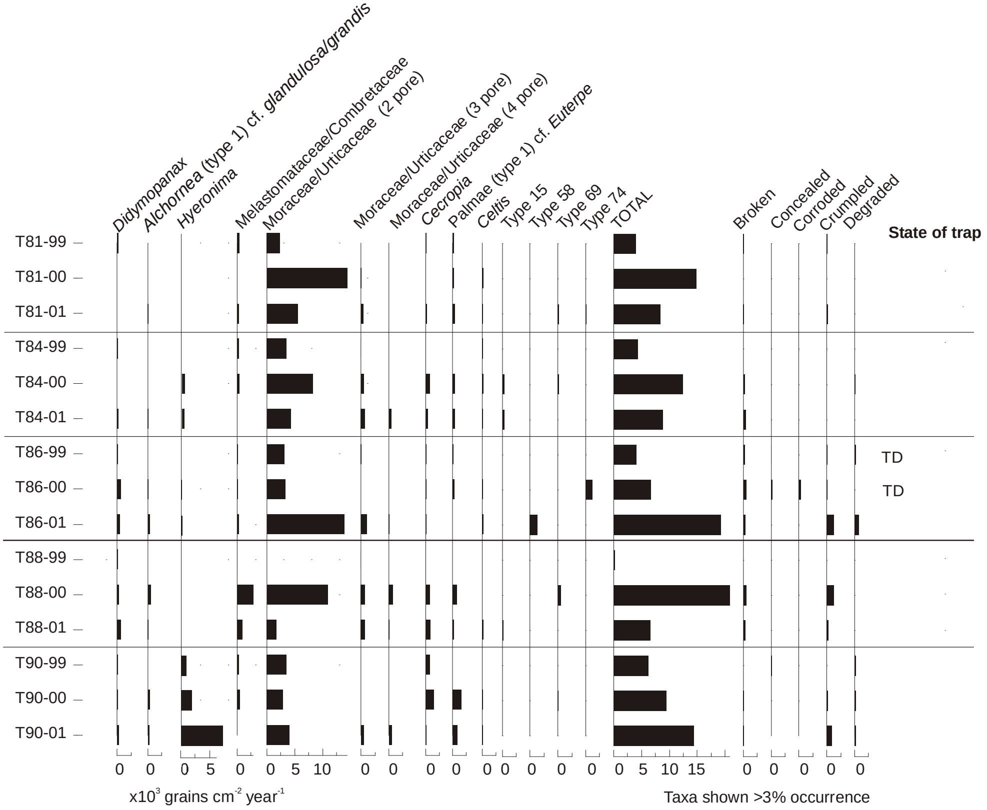
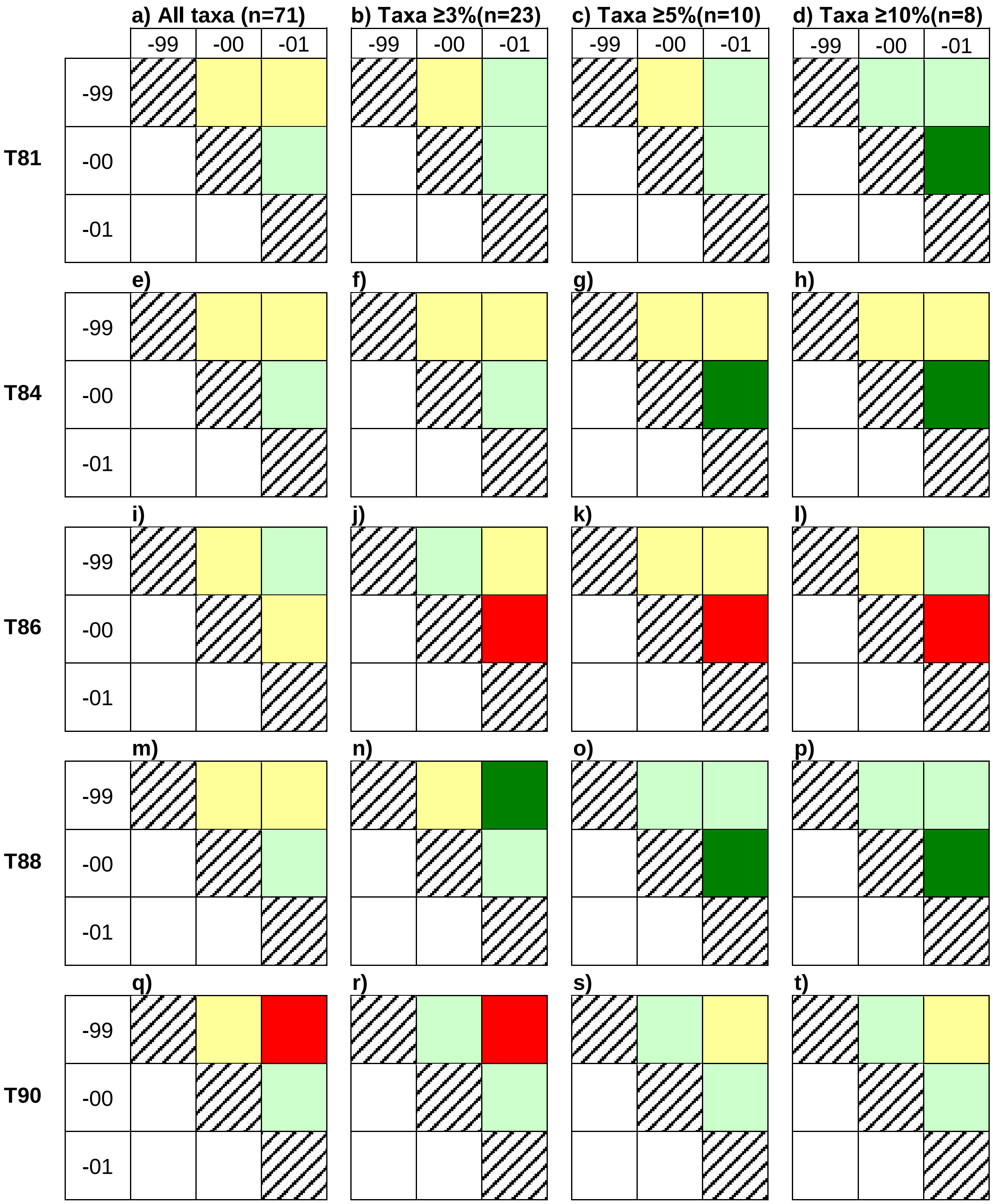


Figure 7-3: Temporal variation of pollen rain in tall *terra* firma evergreen forest. “Nearest tree” indicates the closest tree >10 cm d.b.h. to the trap. “TD” indicates traps that suffered damage from termites. For full data set see appendix VII.



		a) All taxa (n=71)			b) Taxa ≥3%(n=23)			c) Taxa ≥5%(n=10)			d) Taxa ≥10%(n=8)		
		-99	-00	-01	-99	-00	-01	-99	-00	-01	-99	-00	-01
T81	-99	▨	🟨	🟨	▨	🟨	🟢	▨	🟨	🟢	▨	🟢	🟢
	-00		▨	🟢		▨	🟢		▨	🟢		▨	🟩
	-01			▨			▨			▨			▨
		e)			f)			g)			h)		
T84	-99	▨	🟨	🟨	▨	🟨	🟨	▨	🟨	🟨	▨	🟨	🟨
	-00		▨	🟢		▨	🟢		▨	🟩		▨	🟩
	-01			▨			▨			▨			▨
		i)			j)			k)			l)		
T86	-99	▨	🟨	🟢	▨	🟢	🟨	▨	🟨	🟨	▨	🟨	🟢
	-00		▨	🟨		▨	🟥		▨	🟥		▨	🟥
	-01			▨			▨			▨			▨
		m)			n)			o)			p)		
T88	-99	▨	🟨	🟨	▨	🟨	🟩	▨	🟢	🟢	▨	🟢	🟢
	-00		▨	🟢		▨	🟢		▨	🟩		▨	🟩
	-01			▨			▨			▨			▨
		q)			r)			s)			t)		
T90	-99	▨	🟨	🟥	▨	🟢	🟥	▨	🟢	🟨	▨	🟢	🟨
	-00		▨	🟢		▨	🟢		▨	🟢		▨	🟢
	-01			▨			▨			▨			▨

Strength of positive Spearman’s rank correlation coefficient indicated by colour:

🟩 = ≥0.750   🟢 = 0.749 - 0.500   🟨 = 0.499 - 0.250   🟥 = <0.250*   ☐ = Blank

* Includes some weak negative correlations.

Figure 7-4: Annual heterogeneity of pollen rain in tall terra firma evergreen forest. Correlations are based upon a Spearman’s rank correlation (SPSS v.11.01). For full details of correlation see appendix IX.

forest trees (Richards, 1996, p. 250). Aside from this anomaly the pollen assemblage from trap T86-00 agrees well with the other two years' data from this location (figure 7-3). Secondly, at location T90 there is a positive correlation between the 1999 and 2000 data. This is a product of high levels of *Cecropia* being present in the traps from both years (figure 7-3a).

The difference shown between the 1999 assemblages and the following two years is a result of considerably higher pollen productivity in the latter two years and an increase in diversity (of taxa occurring ≥3%) at all but one location (T81) (figure 7-3). This suggests that the amount of pollen produced by the plants found within this ecosystem is responding to regional changes in environmental conditions on an annual basis. Precipitation data from the nearby meteorological station at El Refugio show that the dry season in this region was more pronounced during the 1998-1999 field season than the subsequent two years (L. Emmonds, *pers. comm.*, 2003; appendix X). This suggests that climate and pollen productivity may be related, however the three years of this study is too short to establish a causal link.

In summary, the pollen rain from the tall *terra firma* evergreen forest is dominated every year by Moraceae/Urticaceae, whilst a few other taxa generally appear every year in the pollen rain: Melastomataceae/Combretaceae, Palmae (type 1), *Alchornea* (type 1), *Cecropia*, *Didymopanax* and, where locally present, *Hyeronima*. However, there is also evidence to suggest that sampling from a single year could lead to an inaccurate picture of the true nature of the pollen rain from the plot. This is for two reasons: i) not all plants flower every year (Richards, 1996, p. 250), and ii) some plants have mass flowering events when they do flower, i.e. they produce a large quantity of pollen in a short space of time (Richards, 1996, p. 251). Supporting evidence for inter-annual variation in pollen production is provided by cluster analysis which finds greater similarity between samples from the same year rather than the same location (appendix XI). This emphasises the need to study more than one year's worth of data when trying to establish the nature of the pollen rain from this type of ecosystem.

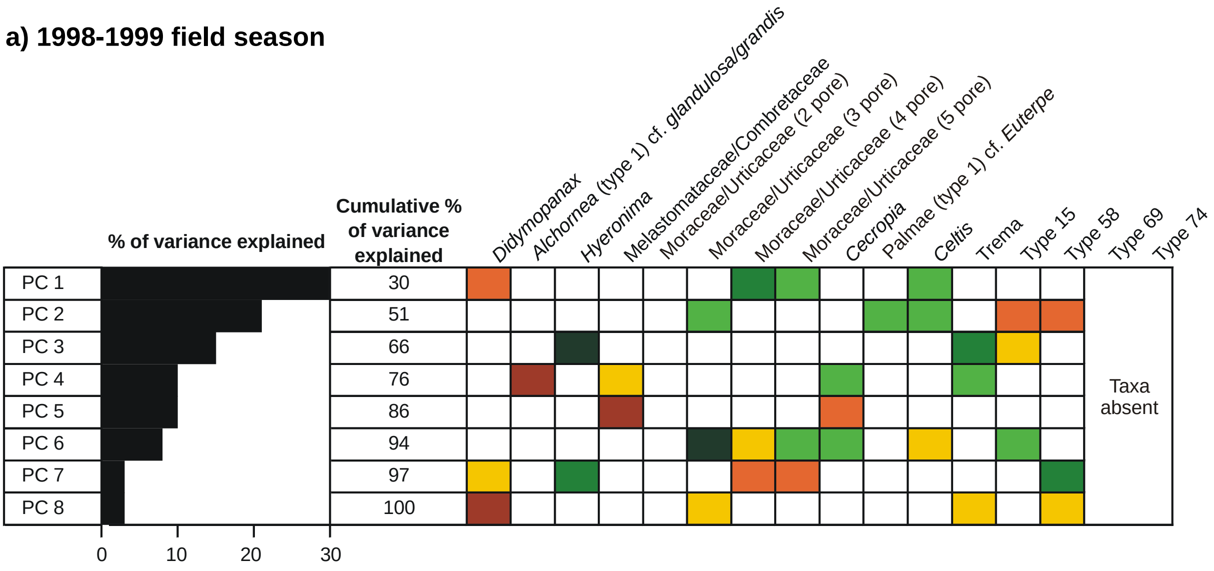
7.2.3 Distinctive pollen taxa

In figure 7-5 the pollen taxa that are important in explaining the variation in the pollen assemblages from the tall *terra firma* evergreen forest are highlighted. The principal components have been derived from each field season's data (figure 7-5a to c) and the whole data set combined (figure 7-5d) following the procedure described in section 7.1.3.

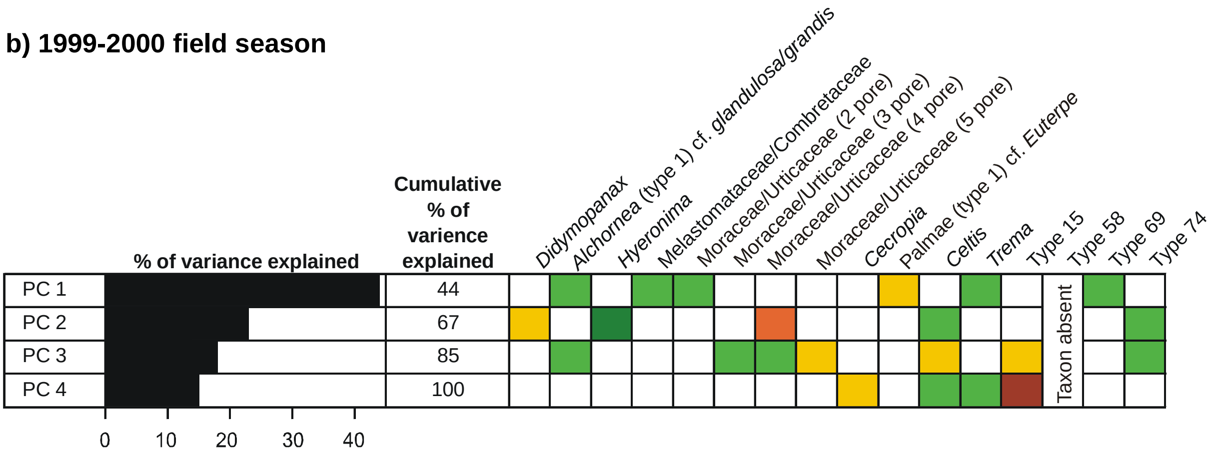
To investigate in detail which components of the pollen assemblage were statistically distinctive and why, PCA was used to examine the pollen data from this plot in three different ways: i) each year's data was examined to identify any consistent patterns occurring year on year, ii) the entire data set was analysed to determine the important taxa for the ecosystem (plot) as a whole, and iii) 'anomalous' samples, identified in the intra-plot spatial and inter-annual variation analyses (sections 7.2.1 and 7.2.2), were removed and the PCA performed again to assess the impact of removing these samples.

Firstly, in the year by year analysis of the pollen assemblages eleven of the sixteen taxa occurring at ≥3% in this plot were significantly correlated in some way to the first two principal components from at least two years (these components alone explain more than half the variance found in the data set) (figure 7-5a to c). These data reveal that there is a small group of statistically determinable taxa within the data set that are consistently important in the pollen rain of the tall *terra firma* evergreen forest. These taxa are: Moraceae/Urticaceae

a) 1998-1999 field season



b) 1999-2000 field season



c) 2000-2001 field season

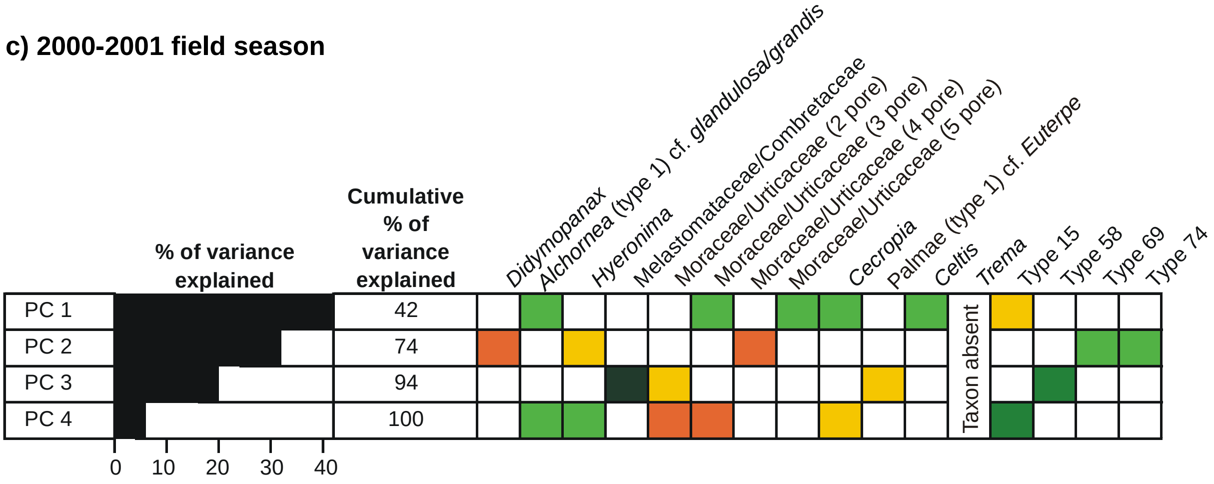


Figure 7-5: Continued over…

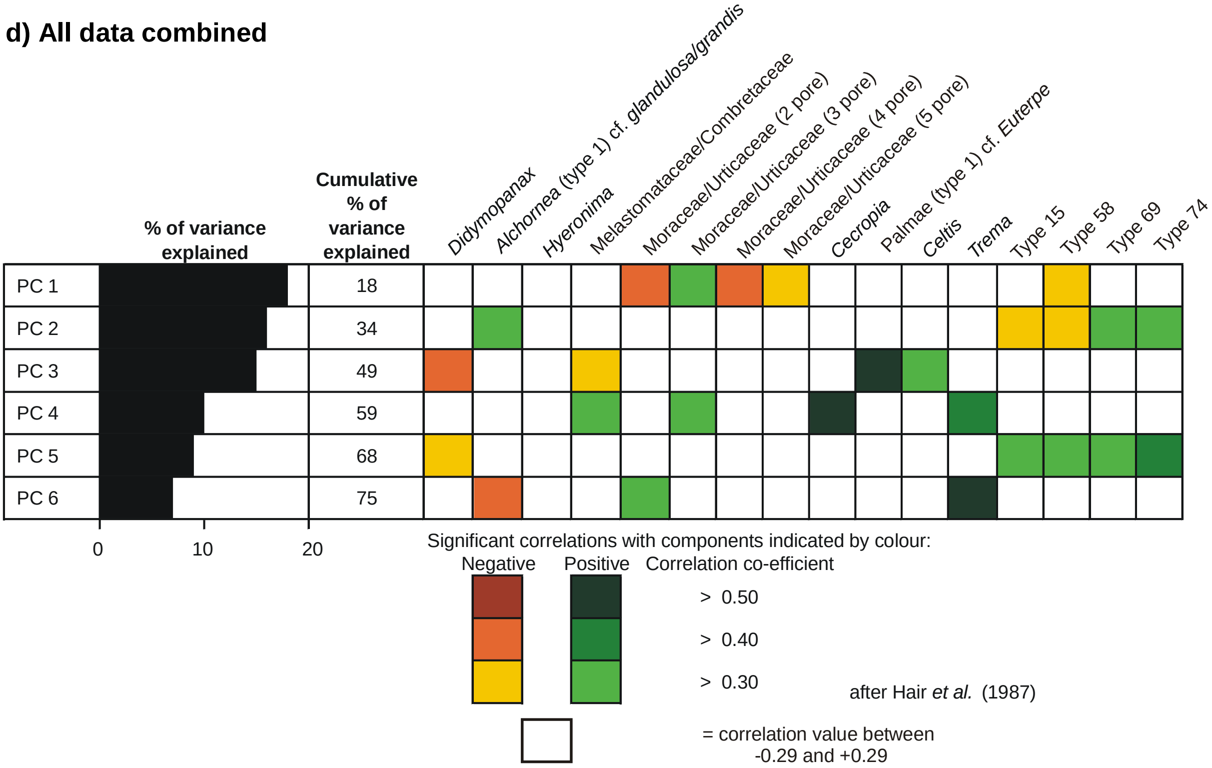


Figure 7-5: Key pollen taxa in tall *terra firma* evergreen forest. Principal components (PC) are listed in descending importance from the top to the bottom of each the diagram. Full data sets can be found in appendix XII.

(3 pore), Moraceae/Urticaceae (4 pore), Moraceae/Urticaceae (5 pore), Palmae (type 1), *Alchornea* (type 1), *Celtis*, *Didymopanax*, *Hyeronima* and unidentified pollen types 15, 69 and 74. The correlations of some of these taxa vary between positive and negative correlation between the years. The reason for the different correlation is the changing level and distribution of occurrence of each taxon between each year (figure 7-3). Positively correlated taxa tend to be those taxa that are present in the majority of the samples, but exhibit a degree of variation through the plot, e.g. this can be seen for Moraceae/Urticaceae (3 pore) in 1998-1999 (figure 7-5a), Moraceae/Urticaceae (2 pore) during 1999-2000 (figure 7-5b) and *Cecropia* in 2000-2001 (figure 7-5c) when related to the corresponding pollen diagrams (figures 7-1a and 7-3a). Negatively correlated taxa tend to be those that are dominant at a distinct location, i.e. when they are present they overwhelm the other pollen types (and when they are not present the other taxa make up a larger portion of the assemblage), e.g.

Didymopanax in all years (figure 7-5a to c), Palmae (type 1) in 1999-2000 (figure 7-5b) and *Hyeronima* in 2000-2001 (figure 7-5c) related to figures 7-1a and 7-3a. This also explains why Moraceae/Urticaceae (2 pore) and Melastomataceae/Combretaceae, which have been shown to be significant in terms of abundance in the pollen rain from this plot (see figures 7-1a and 7-3a), are not picked out by this technique. These taxa are relatively consistently present and therefore are not picked out by the PCA which is looking at explaining the variance in the data set (see section 7.1.3).

The derived components indicate associations between the pollen types and therefore floristic associations within the plot. The most important components derived from each year's data (i.e. principal components 1 and 2) show different associations of taxa (figures 7-5a to c). This supports the inter-annual variations seen in the pollen data from this plot (section 7.2.2). This high variability emphasises the need to consider the whole data set when attempting to characterize the pollen rain from this ecosystem.

Secondly, the PCA for the whole data set (figure 7-5d) picks out ten of the eleven taxa highlighted consistently in each of the years' data in the first four principal components (equating to >50% of the variance in the data set for a direct comparison with the year by year data where the first two principal components represent this portion of the variance). The taxon not picked out when the PCA is run on the whole data set is *Hyeronima* which is spatially restricted in the pollen rain and does not occur in the majority of samples (figure 7-1 and 7-3). Five additional taxa are also picked out in these four principal components: Melastomataceae/Combretaceae, Moraceae/Urticaceae (2 pore), *Cecropia*, *Trema* and unidentified pollen type 58. Each of these taxa correspond to either the first or second principal component for one of the year's data and therefore their occurrence in the overall analysis of the data set can be attributed to the corresponding year's data (figure 7-5a to c).

The negative correlation of Moraceae/Urticaceae 2, 4 and 5 pore types to the first principal component of the whole data set (figure 7-5d) is a function of their dominance in the pollen rain (figure 7-1 and 7-3), i.e. when they go up everything else goes down and vise-versa. This consistent response against the other taxa suggests that these pollen types are probably all produced by the same parent vegetation. The fourth type of Moraceae/Urticaceae, which has 3 pores, however is picked out differently by this PCA. In figure 7-5d Moraceae/Urticaceae (3 pore) correlates positively to the first principal component. The appearance of this pollen type in the pollen rain is different to the other types of Moraceae/Urticaceae in that it is the only type consistently present in 2000-2001 (figure 7-3). This difference between the Moraceae/Urticaceae (3 pore) and the other types of Moraceae/Urticaceae and the fact that distinct types are highlighted in each years data suggests that it may be possible to identify different parent taxa for these pollen types. This observation may be significant because in all previous studies Moraceae/Urticaceae has been considered as one pollen type. If it were possible, in the future, to identify a separate plant species or genus differentiated on the number of pores per grain, then further ecological information may be extractable from the fossil pollen record. It is therefore recommended that pollen counts should record the number of pores present on the Moraceae/Urticaceae grains.

Pollen type 58 is weakly negatively correlated to both the first and second principal components (and is weakly positively correlated to the fifth) of the whole data set (figure 7-5d). Relating the correlation of this pollen type back to the year by year data, it can be seen that it is the low occurrence in 1998-1999 (figures 7-1 and 7-5a) that accounts for the negative values, and the high spike in T86-01 (figure 7-3a) that accounts for the positive correlation in this and the PCA on the 2000-2001 data (figure 7-5c). This indicates that the parent vegetation of pollen type 58 is producing pollen in a pattern that is distinct from the other plants found within the plot, possibly due to a different response to changing ecological thresholds.

Alchornea (type 1) is the only identified pollen taxon that correlates positively with component 2 of the whole data set (figure 7-5d). This is a product of the consistent presence of this taxon through the second and third years of trapping (figure 7-3) and is reflected in the positive correlations with those years' PCA (figures 7-5b and c). The PCA identifies this smaller type of *Alchornea* grain as a statistically distinctive part of the data set even though it only occurs in abundance in two of the three years.

As for *Alchornea* (type 1), unidentified pollen types 69 and 74 are highlighted in the analysis of the whole data set due to their abundances in the latter two years of the study. This pattern supports the findings in section 7.2.2 and the cluster analysis presented in appendix XI that field seasons 1999-2000 and 2000-2001 were more closely correlated in the pollen rain that was produced than either was with the 1998-1999 field season. This may be a product of the harsher dry season and the bimodal distribution of the rain fall during the wet season that occurred in 1998-1999 that is not seen in the subsequent two years (L. Emmonds, *pers. comm.*, 2003; appendix X). However, this data set is too short to establish a causal link between climate and pollen production.

In addition to the taxa discussed above, the PCA of the whole data set reveals strong positive correlations of Palmae (type 1), *Cecropia* and *Trema* with the principal components that represent less of the overall variance in the data set than those already discussed (i.e. components 3 through 6). These three taxa are all highlighted as strongly correlated to at least one of the individual year's first two principal components (figures 7-5a to c). This demonstrates that the PCA of the whole data set is able to pick out taxa that are important in one year alone. Also positively correlated with these components are Melastomataceae/Combretaceae, *Celtis* and type 15. This reflects the consistent levels of occurrence that these taxa exhibit through the majority of the samples (figure 7-1 and 7-3). *Didymopanax* is negatively correlated to components 3 and 6 from the whole data set (figure 7-5d) and the first two components of each of the year's data (figures 7-5a to c), due to the taxon's discontinuous distribution but local dominance in all years.

The third, and final, PCAs were carried out on the whole data set excluding samples T83-99 and/or T88-99, which were identified as correlating badly with the other pollen assemblages in the bivariate analyses carried out in section 7.2.1. The results of these analyses were broadly similar to those presented in figure 7-5d but correlations were generally weaker due to the diminished number of samples relative to variables. The lack of impact in removing these samples is because the anomalous nature of these samples, highlighted by figure 7-2, can be explained by a change in one taxon. The importance and influence of the one 'anomalous' taxon is diminished when the sample is considered as part of a multivariate spectrum in the PCA.

In summary, the statistically distinctive pollen taxa of the tall *terra firma* evergreen forest are Moraceae/Urticaceae undiff., type 58, *Alchornea* (type 1), type 69 and type 74. Other important taxa explaining the underlying nature of the pollen rain from this plant community are Palmae (type 1), *Cecropia* and *Trema*.

7.2.4 Pollen-vegetation relationships

In figure 7-6 the ratio of percentage abundance in the pollen rain for each pollen type is calculated against two different measures of abundance in the vegetation: i) the percentage of the total number of individuals >10 cm d.b.h. (figure 7-6a), and ii) the percentage of the total biomass estimate (figure 7-6b) (as described in section 7.1.4). Almost all the taxa identified in the vegetation of the tall *terra firma* evergreen forest and in the pollen rain are, relatively, over-represented in the pollen compared to either measure of abundance in the vegetation; i.e. the ratio is >1:1, pollen:individuals or biomass.

The dominance of a few taxa within the pollen rain from this plant community is probably a product of the pollination strategies employed by the plants found within this ecosystem. The majority of broadleaf evergreen plants found within this ecosystem employ some form of animal or insect pollination method and therefore they produce low quantities of pollen per individual (Janzen, 1975; Richards, 1996, p. 103). As a consequence of this, the few taxa that employ a wind pollination strategy, e.g. Moraceae, which requires the production of vast quantities of pollen, are heavily over-represented in the pollen rain and those that do not are largely absent, e.g. *Cassia*. The high levels of pollen production by plants found within the ecosystem and the dense canopy (chapter 6, figure 6-3) suggests intuitively that the pollen types found within this plant community are likely to be derived from the vegetation within the plot, rather than by long distance transport from vegetation elsewhere.

In terms of identifying taxa that are useful for the characterization of the associated ecosystem in the fossil pollen record, it is those taxa that are important in the vegetation and well-represented in the pollen rain that are most likely to be present in fossil pollen records. Panfil

(2001) identified the twelve most important species occurring within the plot (chapter 6, section 6.3.1), five of which are represented in the pollen rain. These five taxa in descending order of importance are: Moraceae/Urticaceae, Palmae (type 1), *Sloanea*, *Hyeronima* and Melastomataceae/Combretaceae.

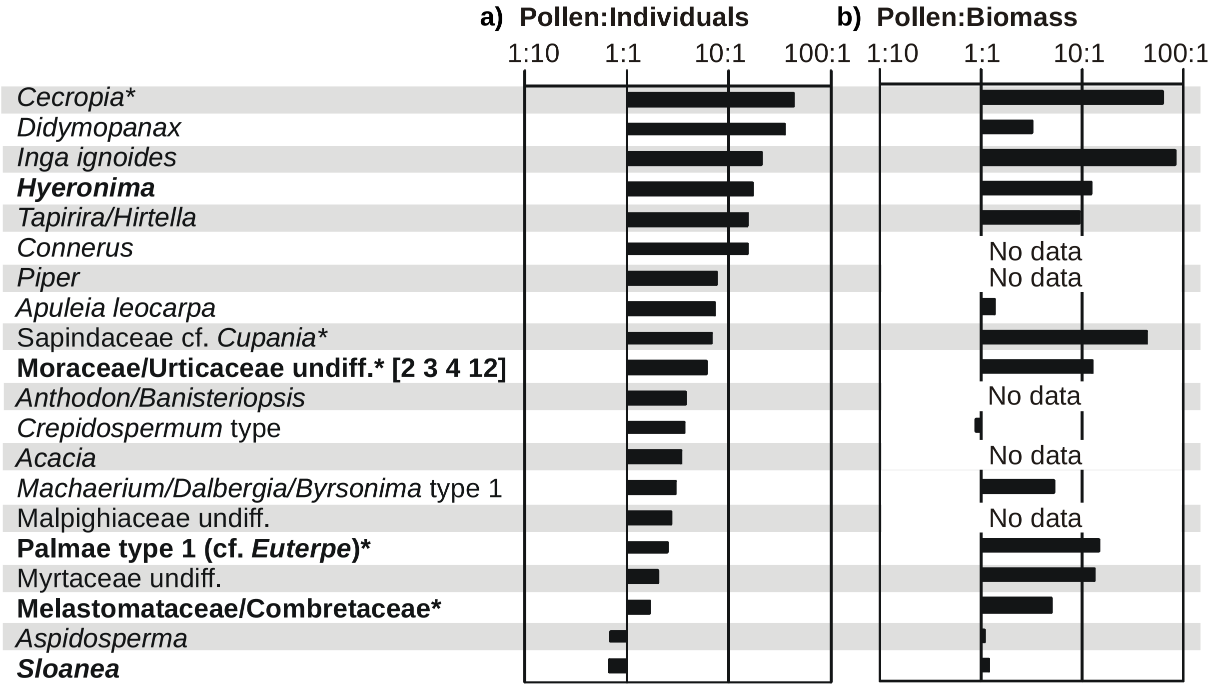


Figure 7-6: Relative abundance of taxa in pollen vs. vegetation. Taxa highlighted in **bold** indicate those shown to be ecologically important to the tall *terra firma* forest found in LF-1 by Panfil (2001) see chapter 6 (section 6.3.2). Taxa marked with an * are those shown to be statistically distinctive in section 7.2.3. Individuals = data derived from plot vegetation lists compiled by T.J. Killeen (unpublished data). Biomass = data derived from estimates of biomass for individual trees calculated by T.J. Killeen (unpublished data). For full data set see appendix XIV.

Moraceae/Urticaceae is the dominant taxon recognised in the pollen rain and produces pollen at over 10x the proportion of its biomass and 8x the proportion of individual trees (figure 7-6). This dominance in the vegetation, coupled with the high pollen productivity of Moraceae (Berg, 1978; J. Ratter, *pers. comm.*, 2003), explains the predominance of this pollen type within the pollen rain from the plot (figures 7-1 and 7-3).

Palmae (type 1) is not present at all the trap locations within the plot (figure 7-1). However, where it is present it can be over-represented by up to 10x the proportion of the biomass. It is possible, though, that this degree of over-representation is an over-estimate because the calculation of biomass for palms is difficult due to the diversity in density of Palm species and a lack of research (Brown, 1997). In the light of this, and given the taxon's discontinuous spatial distribution in the pollen rain, it is more appropriate to use the lower figure of 4x over-representation calculated against the number of individuals found in the plot (figure 7-6a). Therefore, Palmae (type 1) appears to be well represented in the pollen rain from the ecosystem, although prevalence of its pollen is limited by poor dispersal.

Sloanea is the second most abundant tree in the plot, represented by twenty-eight individual plants, although it only occurs at very low levels in the pollen rain. Likewise, *Hyeronima* is a very important plant within the plot (twenty individuals, see appendix XIV) but its representation in the pollen rain is discontinuous; it can be over-represented palynologically by more than 10x the number of individuals but is more often absent from the pollen rain (figure 7-1). These low and discontinuous levels of occurrence in the pollen mean that the presence of the taxon in the pollen rain would probably indicate the presence of the plant in the local vegetation. However, the absence of either taxon in the pollen rain would not rule out the possible presence of the plant in nearby vegetation.

The final pollen type that belongs to species found to be important to the plot by Panfil (2001) is Melastomataceae/Combretaceae. This pollen type contains species and genera that occupy a wide range of habitats in a variety of growth forms (Killeen *et al.*, 1993; Marchant *et al.*, 2002). Melastomataceae/Combretaceae pollen is slightly over-represented in the pollen assemblages (figure 7-6) and is present in all of the sample locations (figure 7-1). It also appears in the pollen rain every year (figure 7-3).

In addition to the taxa discussed above, the ratios of relative abundance of pollen:individuals (figure 7-6) highlights five taxa present within the plot's vegetation that are represented in the pollen, for at least one location, by >10x their abundance in the vegetation. These are, in decreasing order of greatest over-representation compared to the number of individuals: *Cecropia*, *Didymopanax*, *Inga ignoidies*, *Tapirira/Hirtella* and *Connerus*. The high level of over-representation means that if these taxa are present within the vegetation they are highly likely to be recorded in the pollen rain. Other taxa which produce low quantities of pollen relative to their abundance in the vegetation, such as *Crepidospermum* type and *Aspidosperma*, are unlikely to be present in the pollen rain even if they are present in the vegetation, although if they are present in the pollen assemblage they are highly likely to be present in the vegetation.

7.2.5 Tall *terra firma* evergreen forest pollen signature

On the basis of the analysis carried out in the four preceding sections, a characteristic pollen signature has been established for the tall *terra firma* evergreen forest found in LF-1. This was shown to be representative of the wider moist *terra firma* evergreen forest ecosystem because of the affinities discussed in chapter 6. The criteria for the selection of these taxa are detailed in appendix XIII and summarised in table 7-1.

The method adopted here for characterizing the modern pollen rain of a particular ecosystem allows those taxa that are present consistently in space and time to be included alongside those that represent the variability in the pollen rain and the actual vegetation of the plot. The inclusion of taxa occurring consistently through space or time means all abundant or well dispersed taxa will be included. The PCA allows those taxa which vary through the plot to be considered and finally, the correlation with the vegetation ensures that any low pollen producing taxa that are present in the vegetation of the plot are included.

Taxa marked as important for three or more of the criteria (table 7-1) were classified as major taxa and the rest as minor taxa. This threshold was implemented because it meant that taxa had to satisfy the majority of the tests to be considered major taxa. All the four sets of analysis were considered to be of equal importance so that the technique captured the range of different taxa contributing to the pollen rain of the ecosystem. Other taxa found within the pollen rain of the plot but not registering any marks on the criteria were deemed not to be characteristic of the pollen rain of this ecosystem (see appendix XIII). This two tiered system was used to make analysis of the data easier.

The major components of the pollen signature established for this ecosystem are listed in table 7-2. These seven taxa are those likely to be present in a pollen spectrum from this ecosystem within the given range of values. The remaining taxa are mainly a mixture of those that occur in the pollen rain at a low level, but for which the parent plant is present in the plot, and those that are significant in the pollen rain but are not represented in the vegetation. These are considered minor taxa, some of which may be present in any one sample of pollen rain from this ecosystem. The minor taxa are listed in table 7-3 by percentage occurrence in the pollen traps.

The pollen signature of this ecosystem is dominated by the Moraceae/Urticaceae pollen type. The reason for combining the four different pollen types of Moraceae/Urticaceae is twofold: i)

	Highlighted as significant in:			
Pollen taxa	**Spatial**	**Inter-annual**	**Statistical**	**Vegetation**
Moraceae/Urticaeae	✓	✓	✓	✓
Palmae (type 1)	✓	✓	✓	✓
Melastomataceae/Combretaceae	✓	✓	✓	✓
Cecropia	✓	✓	✓	✓
Didymopanax	✓	✓	✓	✓
Celtis	✓	✓	✓	
Alchornea (type 1)	✓	✓	✓	
Trema	✓	✓		
Type 15	✓			
Hyeronima		✓		✓
Type 58			✓	
Type 69			✓	
Type 74			✓	
Acacia				✓
Anthodon/Banisteriopsis				✓
Apuleia leocarpa				✓
Aspidosperma cf. *cruenta*				✓
Connerus				✓
Crepidospermum type				✓
Cupania				✓
Inga ignoides				✓
Machaerium/Dalbergia/Byrsonima (type 1)				✓
Malpighiaceae undiff.				✓
Myrtaceae undiff.				✓
Piper				✓
Sloanea				✓
Tapirira/Hirtella				✓

Table 7-1: Pollen signature selection criteria. ✓ indicates identified as important in the corresponding section. Marks were given on the following basis: i) intra-plot = present in the majority of samples, ii) inter-annual = consistent presence year on year at any one location, iii) statistical = highlighted in PCA of whole data set, and iv) vegetation = presence in the trees >10 cm d.b.h. of the plot (T.J. Killeen, unpublished data). For full details see appendix XIII.

it was shown in section 7.2.3 that this division of the Moraceae/Urticaceae is probably artificial, possibly with the exception of Moraceae/Urticaceae (3 pore), and ii) none of the divisions can currently be assigned to a different genus or species and consequently these divisions do not have any discernible taxonomic meaning. Melastomataceae/Combretaceae, Palmae (type 1), *Alchornea* (type 1), *Cecropia*, *Celtis* and *Didymopanax* pollen types appear consistently at ≥ 1% in the majority of the tall *terra firma* evergreen forest samples (sections 7.2.1 and 7.2.2). A pollen signal from this ecosystem (as defined in chapter 6) should therefore be expected to have these high pollen producing taxa present within it at the levels indicated in table 7-2.

MAJOR	**Percentage occurrence**		
pollen taxa	**Minimum**	**Median**	**Maximum**
Moraceae/Urticaeae	31	64	97
Palmae (type 1)	0	4	17
Melastomataceae/Combretaceae	0	4	14
Cecropia	0	3	16
Didymopanax	0	2	26
Celtis	0	1	8
Alchornea (type 1)	0	1	4

Table 7-2: Tall *terra firma* evergreen forest pollen signature, major components. For full details of percentage occurrence levels see appendix VII.

MINOR pollen taxa	**Frequency of occurrence (% samples)**
Type 74	45
Sloanea	40
Malpighiaceae undiff.	30
Aspidosperma cf. *cruenta*	30
Type 58	30
Acacia	25
Myrtaceae undiff.	20
Inga ignoides	20
Cupania	15
Trema	15
Anthodon/Banisteriopsis	10
Hyeronima	10
Piper	10
Tapirira/Hirtella	10
Type 15	10
Apuleia leocarpa	5
Connerus	5
Crepidospermum type	5
Machaerium/Dalbergia/Byrsonima (type 1)	5
Type 69	5

Table 7-3: Tall *terra firma* evergreen forest pollen signature, minor components. For full details of occurrence levels see appendix VII.

The other taxa, listed in table 7-3, have been shown to be representative of the pollen rain found within this ecosystem but occur either at low levels or within a limited dispersal area from the plant. Even though they occur at low levels, finding sub-sets of this minor taxa list within a pollen sample could be a useful tool in identifying the ecosystems from which it is derived. Some of these taxa therefore may be present within a tall *terra firma* evergreen forest pollen rain signal. It should be expected to find some, but not all, of these taxa within a sample derived from this plant community, however the number of taxa found will depend on the extent to which the main taxa, listed in table 7-2, dominate.

Moraceae/Urticaceae clearly dominates the pollen rain collected from this ecosystem. It is the only continuously present taxon and its consistently high levels often swamp other less abundant taxa. This finding is unsurprising as it has been used as the major identifier of this ecosystem by previous authors (e.g. Colinvaux *et al.*, 1996; Mayle *et al.*, 2000) because it has long been identified as a large pollen producer and dominant component of ‘evergreen forest’ ecosystems (Berg, 1978; Killeen, 1998; J. Ratter, *pers. comm.*, 2003). The range of abundance values found for Moraceae/Urticaceae pollen within this ecosystem is perhaps more surprising. This taxon varies markedly, both spatially and temporally. For example, in T88-99 the Moraceae/Urticaceae (2 pore) is at 16% with a PAR of 39 grains cm^{-2} year^{-1} while only 50 meters away in T89-99 the same pollen type constitute 94% of the pollen rain and the influx rates is approximately 50,000 grains cm^{-2} year^{-1} (figure 7-1, appendix VII). This is the most extreme example but it highlights the variability of the taxa and emphasises the need for caution when interpreting it in the fossil pollen record. Although this highly spatially variable representation is likely to be smoothed in lake sediments by time, bioturbation and catchment area, these data demonstrate that it is possible to have, and identify, pollen rain from tall *terra firma* evergreen forest that has low levels of Moraceae/Urticaceae.

Given this potential variability of Moraceae/Urticaceae, the other major components of the tall *terra firma* evergreen forest (table 7-2) along with the presence of some of the minor taxa (table 7-3) are therefore required to fully characterize the pollen rain. The swamping by the Moraceae/Urticaceae means that all of the other taxa found in this plant community can be absent at any one given point (at these count sizes). However, the taxa listed in table 7-2 have median percentage values that do reflect their ‘typical’ proportion of the pollen rain (figures 7-1a and 7-3a). The presence of these taxa should therefore be expected, within the range of values given in table 7-2, if a pollen assemblage is derived from tall *terra firma* evergreen forest.

The taxa listed in table 7-3 have been highlighted in at least one of the forms of analyses performed on the tall *terra firma* evergreen forest data (table 7-1). These taxa are split into two general categories: i) those that occur at high levels but are limited in their distribution through the ecosystem in either space or time, and ii) those that represent a plant taxon that is present within the ecosystem (table 7-3). The former may occur at high levels in the pollen rain signal from this plot if the parent vegetation is locally present, otherwise they are likely to be absent. If the latter types are present in the pollen then the parent plants are almost certainly present in the vegetation. In the pollen assemblages from LF-1 each has an average of three of these taxa present within them. This number can be used as a rule of thumb for the number of minor taxa that should be expected in a pollen signal from this ecosystem.

7.3 Semi-deciduous dry forest

Twenty traps were selected and analysed from those collected from the semi-deciduous dry forest of AC-2 (see chapter 5, table 5-1 for sampling strategy and chapter 6, section 6.3.2 for vegetation classification). In order to characterise the pollen rain from this plant community, the same approach was used as for the tall *terra firma* evergreen forest in the previous section, i.e. i) the extent of intra-plot spatial variability (section 7.3.1), ii) the inter-annual variability (section 7.3.2), iii) the statistically distinctive pollen taxa (section 7.3.3), and iv) the pollen-vegetation relationship (section 7.3.4) were determined. Following this analysis, the characteristic pollen signature for the semi-deciduous dry forest is presented in section 7.3.5.

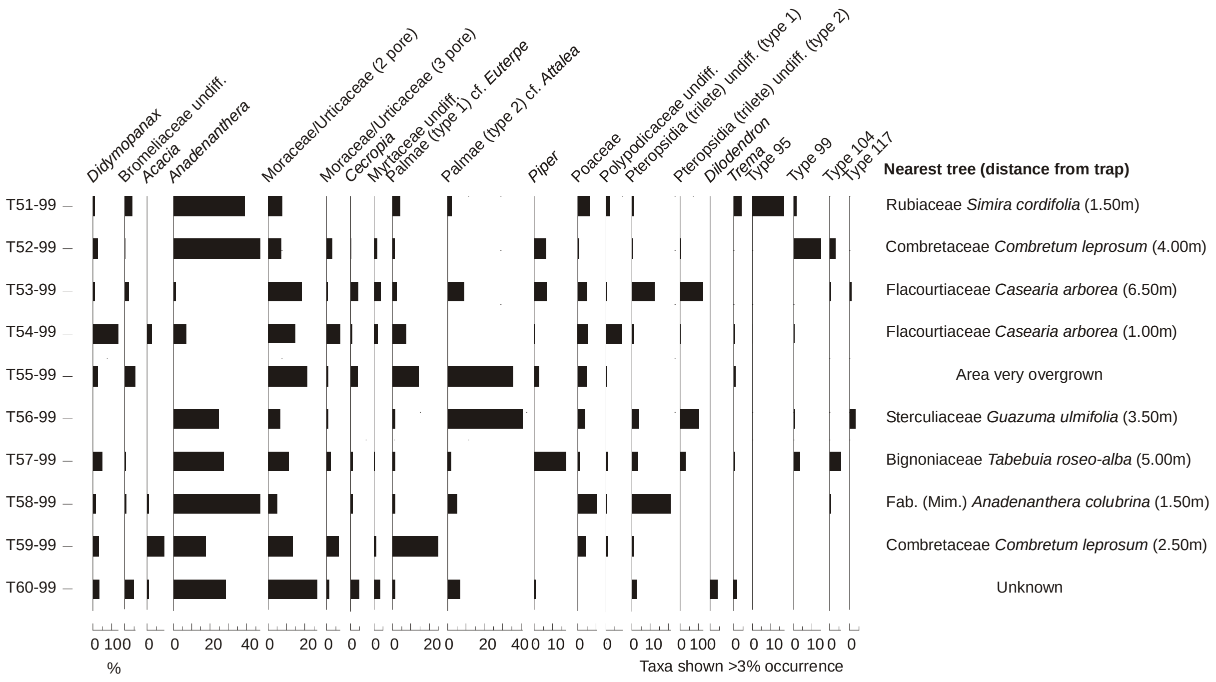
7.3.1 Intra-plot spatial variability

In figures 7-7 and 7-8 the extent of the spatial variation in the pollen rain of semi-deciduous dry forest during 1998-1999 is revealed.

No one taxon dominates the pollen assemblages from the semi-deciduous dry forest. Instead, three taxa, Moraceae/Urticaceae (2 pore), *Anadenanthera* and Palmae (type 2), are dominant in different samples (figure 7-7). This spatial variability can also be seen in taxa that occur at lower abundances. Many of these taxa have high PARs in two or three adjacent samples but are largely absent from the others, e.g. Pteropsidia (trilete) undiff. (type 1) (figure 7-7b). The poor rank correlation found between the samples in figure 7-8 highlights the lack of spatial consistency in the pollen rain of this plot. There is no consistent evidence for the biasing of the pollen assemblages by either the largest nearby tree (figure 7-7a) or by damage to the trap (figure 7-7b).

The spatial variability in the pollen assemblages collected through the semi-deciduous forest is a reflection of the high diversity of the vegetation (as discussed in chapter 6, section 6.3.2; Panfil, 2001). The high spatial variability occurs in the more abundant taxa (figure 7-8c and d). This suggests that there is a reasonably consistent low-level pollen signature from the plot. Therefore, to identify the pollen signature is first necessary to look at each of the dominant taxa in turn to understand how and why they are occurring at different abundances throughout the plot.

a) Pollen percentage data



b) Pollen accumulation rates

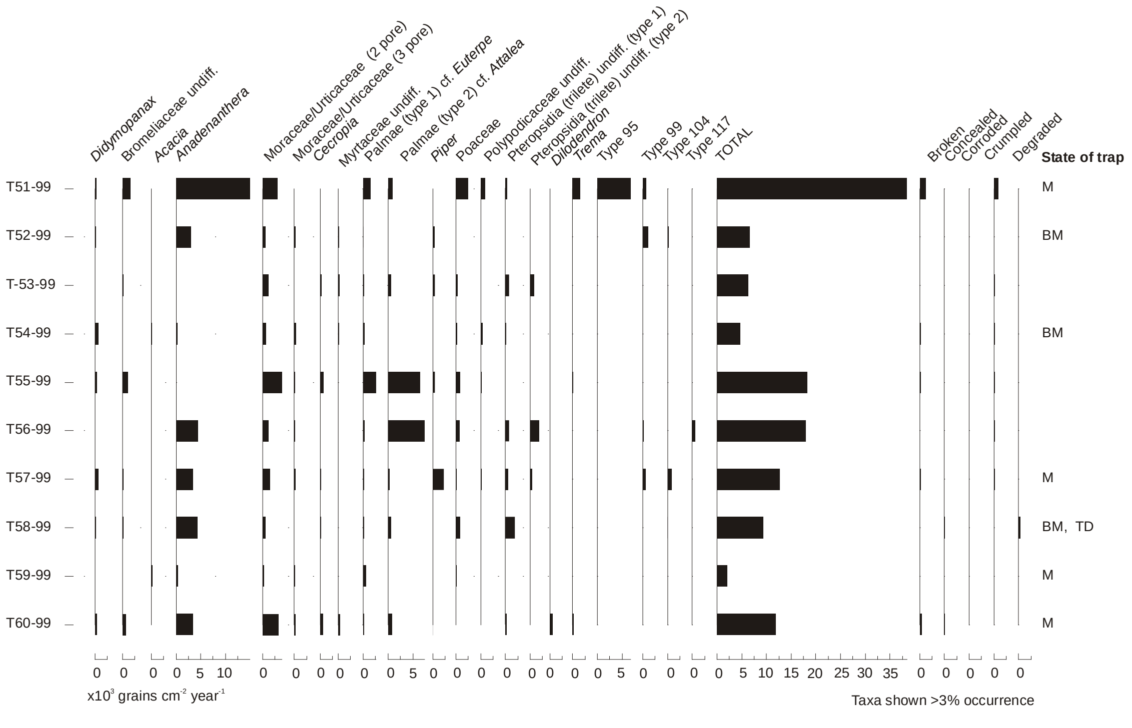
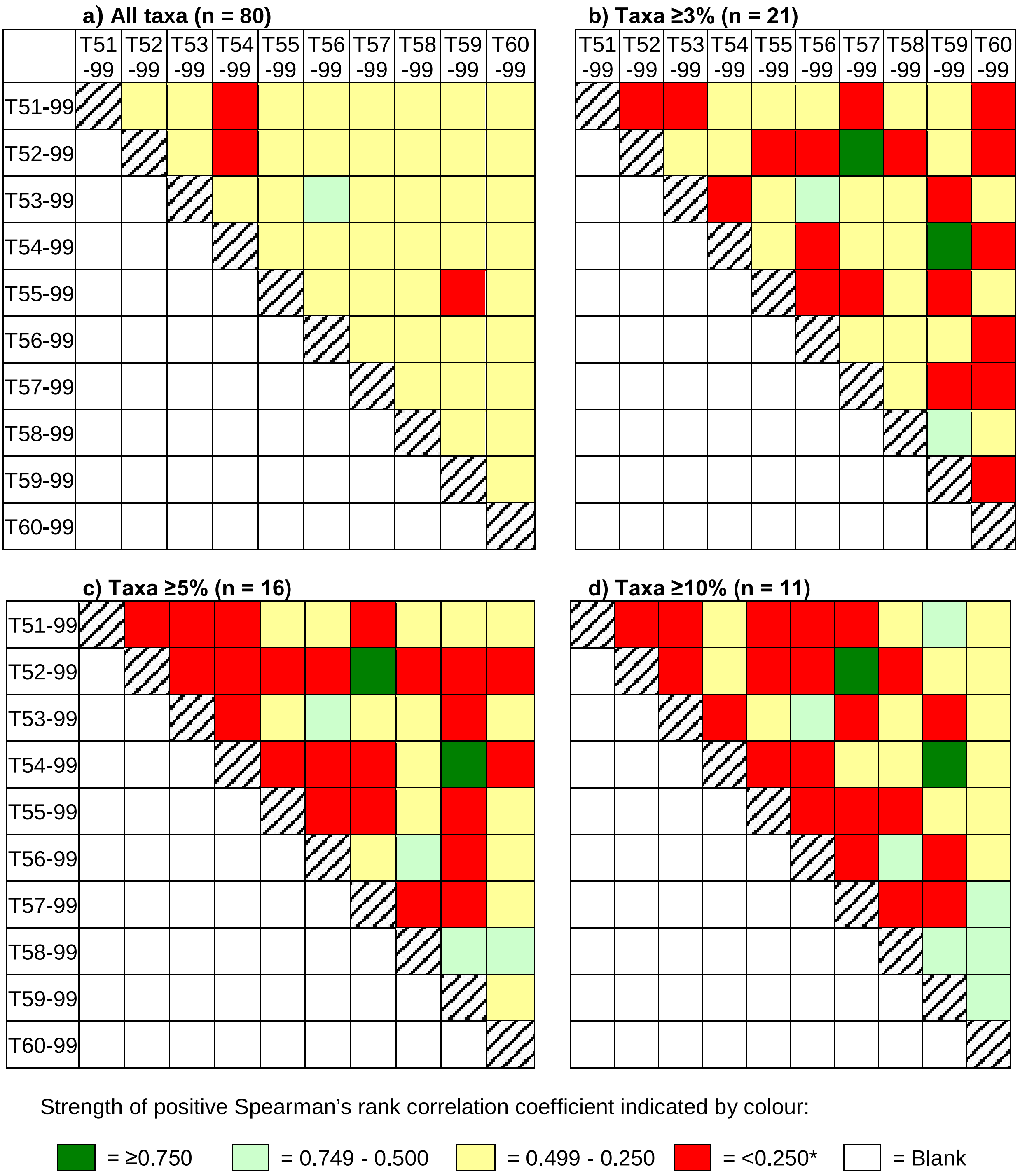


Figure 7-7: Spatial variation of pollen rain in semi-deciduous dry forest. “Nearest tree” indicates the closest tree >10 cm d.b.h. to the trap. “M” indicates traps that suffered melting, “BM” indicates badly melted traps and “TD” indicates termite damage. For full details see appendix VII.



* Includes some weak negative correlations.

Figure 7-8: Spatial heterogeneity of pollen rain in semi-deciduous dry forest. Correlations are based upon a Spearman's rank correlation (SPSS v.11.01). For full details of correlation see appendix VIII.

The locations at which Moraceae/Urticaceae (2 pore) is shown to have the highest pollen percentage occurrence (figure 7-7a) are not the same as those where its PAR is at its highest (figure 7-7b). The high percentages of Moraceae/Urticaceae (2 pore) occur where total PAR of pollen in the trap is low (figure 7-7b). This, coupled with reasonably consistent pollen PARs for all the Moraceae/Urticaceae types through the plot, suggests that the level of input is likely to be a product of general background Moraceae/Urticaceae pollen rain into the trap. The dominance of this pollen type in the percentage diagram (figure 7-7a) is consequently a by-product of a low input from other pollen types.

Palmae (type 2) is locally dominant in T55-99 and T56-99 and is present in low levels at five other locations a pattern which is consistent in both the percentage (figure 7-7a) and PAR data (figure 7-7b). This localised abundance suggests that these large palm grains (see CD enclosed) are not dispersing very far from the source plant and are probably related to the position of palm stands within the plot. This discovery of the very restricted local dominance of palm pollen highlights the importance of high spatial sampling resolution to ensure a sample of the pollen rain that is representative of the variability within the ecosystem has been taken.

Anadenanthera is the most abundant pollen taxon both in terms of percentages and PARs, and dominates the majority of samples, occurring in all but one (figure 7-7). This abundance clearly indicates it is important in the pollen rain of this plot. However, there is some evidence that it is being over-represented in the pollen at certain points, e.g. the *Anadenanthera* tree near to T58-99 is possibly exaggerating the proportional abundance of this taxon by excluding other pollen types (figure 7-7a). This conclusion is drawn because whilst there is not an unusually high PAR for *Anadenanthera* at this location, there is a decrease in the total PAR (figure 7-7b). Despite its presence in most of the samples, the abundance of this pollen type is highly spatially variable. This phenomenon, as with the Palmae (type 2) grains, is possibly due to poor dispersal of these polyads and so the points of high abundance in the pollen rain probably reflect points for local dominance in the vegetation. There is also evidence of a discontinuous distribution of pollen types that are less abundant. *Acacia*, *Trema* and five unknown pollen types occur at c. 4% at a few locations within the plot but are completely absent in the majority of samples (figure 7-7).

In contrast to this pattern of discontinuous or uneven distribution of pollen, ten other taxa occur at low levels in the majority of the samples (figure 7-7): Bromeliaceae undiff., Moraceae/Urticaceae (3 pore), Myrtaceae undiff., Palmae types 1 and 2, Polypodiaceae undiff., Pteropsidia (trilete) undiff. (type 1), *Cecropia*, *Didymopanax* and *Piper*. It is these taxa that explain the improved correlation between the pollen assemblages where taxa ≥3% are considered (figure 7-8b) compared to the weaker correlations shown when they are excluded (figures 7-8c and d).

In summary, the pollen assemblages from the semi-deciduous dry forest are highly spatially variable in terms of the relative dominance of different taxa. It is also clear that there is a background input of Moraceae/Urticaceae grains that can become elevated to a significant proportion of the assemblage if productivity from other taxa is low. Despite the high variability in the abundance of various pollen types, it is evident that a large number of taxa are consistently present throughout most of the plot. This indicates that a reliable pollen signal distinctive to the ecosystem should be achievable.

7.3.2 Inter-annual variability

In figures 7-10 and 7-11 the extent of inter-annual variation in the pollen rain from the semi-deciduous dry forest is shown.

The pollen assemblages collected in 1999 and 2001 show a dominance of *Anadenathera* while 2000 shows a dominance of Moraceae/Urticaceae (2 pore). These fluctuations are borne out in both the percentage and PAR data. Some taxa, such as *Didymopanax* and type 104, are shown to make significant contributions to the pollen assemblages at particular locations (figure 7-10). Other taxa are only recorded for one or two of the years, e.g. *Ferdinandusa elliptica* in 1999-2000. The high variability in the pollen abundances coupled with the presence of most taxa through two or three years means that the samples are neither particularly strongly nor particularly weakly positively correlated (figure 7-11).

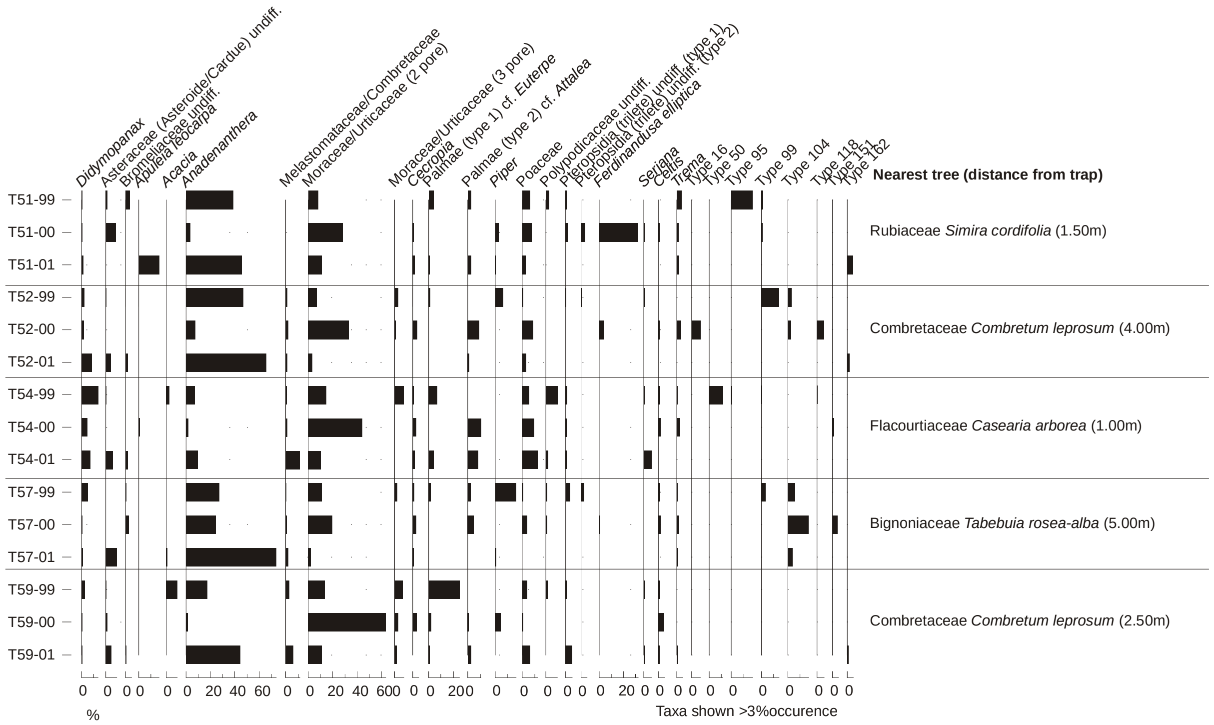
Figure 7-9: M. Siles and J. Sarubi collecting traps in the Acuario 2 plot after 1998-1999 fire. Photograph F.E. Mayle.

The assemblages appear not to be biased towards the pollen produced by the nearest tree (figure 7-10a). None of the traps analysed from the 1999-2000 and 2000-2001 field seasons were subjected to any physical damage in the field. The traps from these two field seasons yielded higher PARs than those collected in 1999. However, it is not suspected that the 1999 traps lost any of the pollen collected through physical damage. This is because the 1999 traps contained comparable numbers of damaged grains to those collected in 2000 and 2001 (figure 7-10b). Eighty percent of the traps from this and the adjacent plot were either melted or subject to fire damage during the 1998-1999 field season (figure 7-9; F.E. Mayle, *pers. comm.*, 2000). This fire damage, which occurred only 2-4 weeks before collection of the traps, possibly contributed to the absence of some pollen types from the trap if they were flowering at, or should have flowered after, the time of burning. The occurrence of this event late on in the field season should mean that it did not have a huge impact on the pollen collected in the traps for the 1998-1999 field season. A more likely reason for the lower PARs in 1998-1999 is that the dry season was drier in this year than the subsequent two years (appendix X) this may have inhibited the flowering of certain plants. The three year time period of this study is, however, too short to establish a causal link between climate and pollen productivity.

A reasonably consistent pattern occurs in the three years sampled from the semi-deciduous dry forest (figure 7-11). In those samples collected in 1999 *Anadenanthera* dominates, in 2000 Moraceae/Urticaceae (2 pore) dominates and in the final year *Anadenanthera* dominates once again. This is borne out in both the percentage and PAR data (figure 7-10a and b).

There is also a general trend in the total PAR of pollen grains through the three years, bucked only by *Anadenanthera*: 1999 consistently records the lowest pollen PARs, probably as a result of a drier dry season (appendix X) and fire damage to plants, 2000 (excluding *Anadenanthera*) records the highest PAR while 2001 (again excluding *Anadenanthera*) records intermediate values. The high PARs in the traps collected in 2000 are primarily due to elevated Moraceae/Urticaceae (2 pore) pollen indicating either that plants producing pollen of this pollen type either: i) were damaged by the 1999 fire but recovered quickly, ii) were not damaged as much as other plants by the fire, or iii) the parent vegetation is located in an area that was not affected by the fire. It appears that the *Anadenanthera* either has taken two years to recover from the fire or that the conditions of 2001 were particularly favourable.

a) Pollen percentage data



b) Pollen accumulation rates

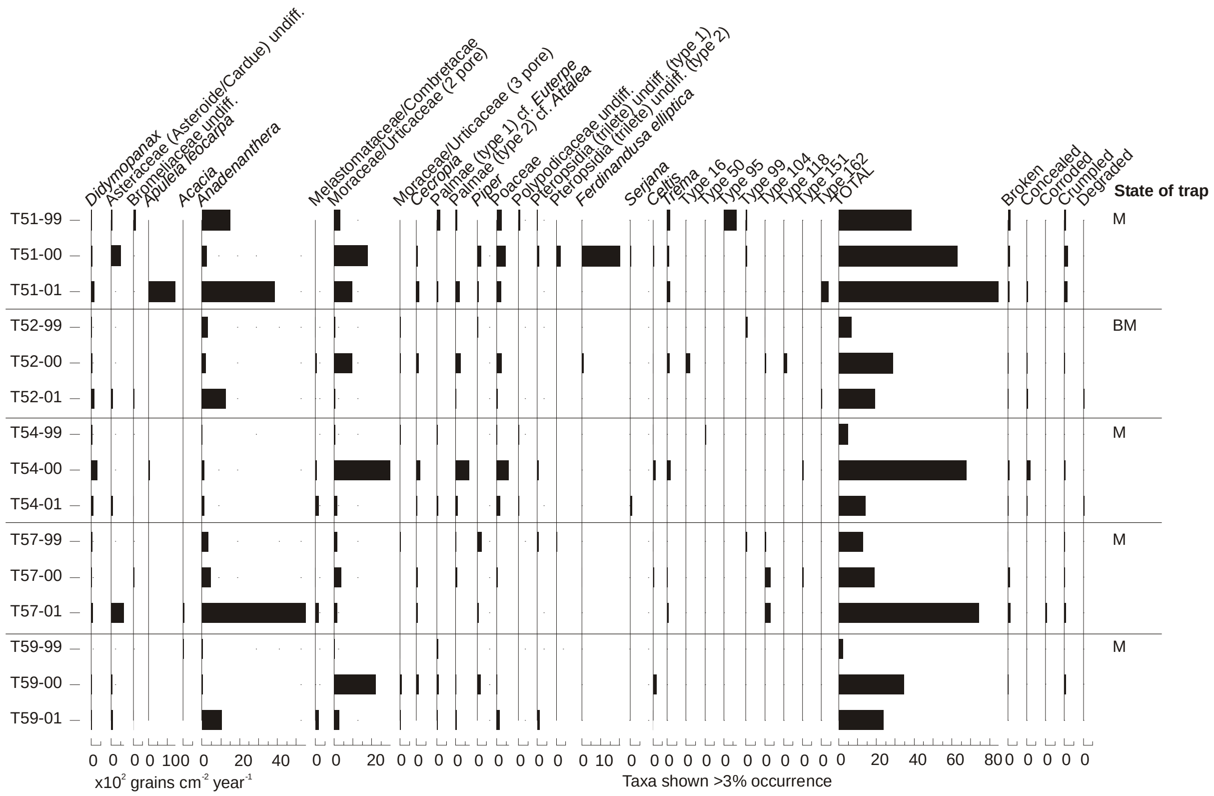
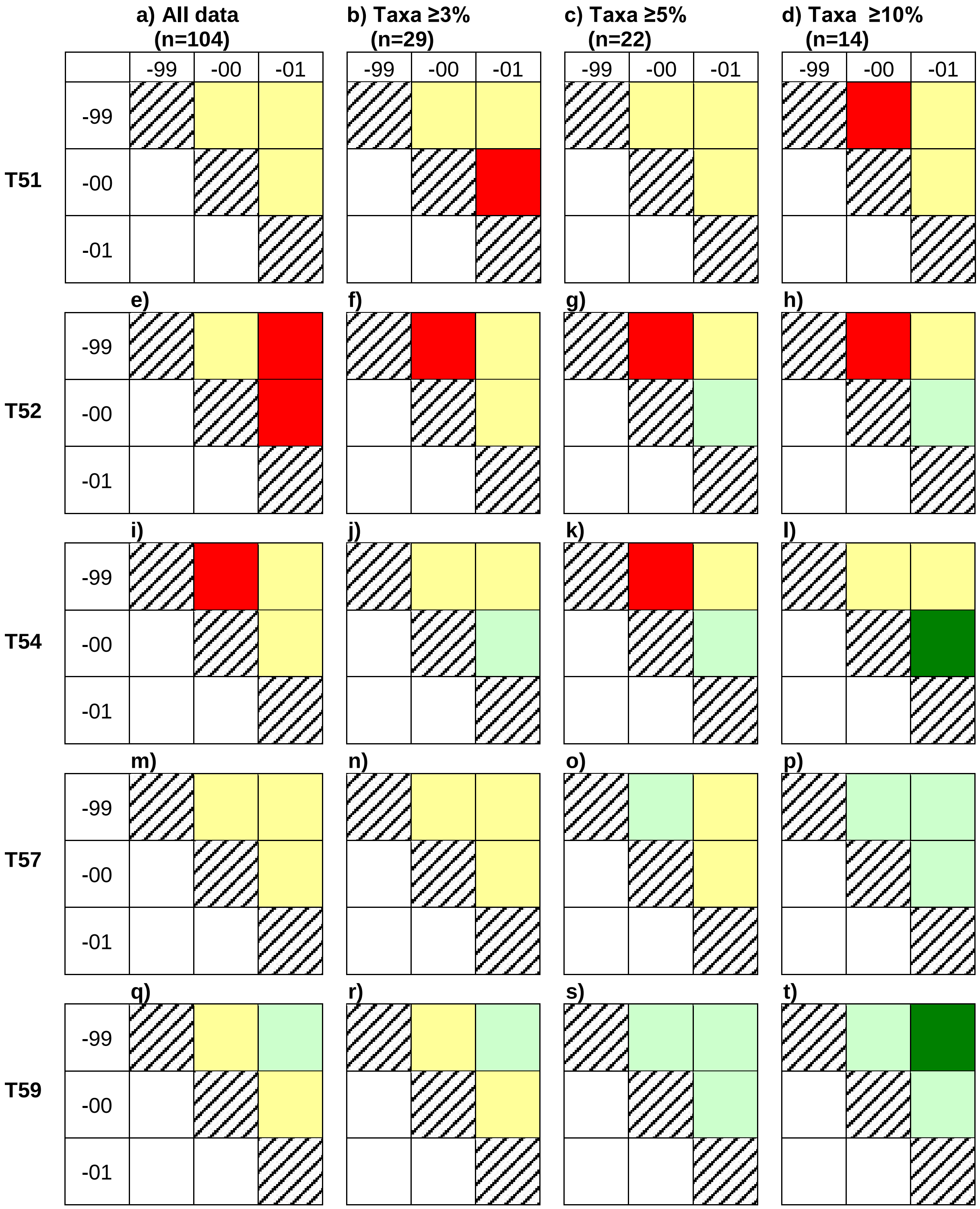


Figure 7-10: Temporal variation in pollen rain in semi-deciduous dry forest. "Nearest tree" indicates the closest tree >10 cm d.b.h. to the trap. "M" indicates traps that suffered melting, "BM" indicates badly melted traps and "TD" indicates termite damage. For full details see appendix VII.



Strength of positive Spearman's rank correlation coefficient indicated by colour:

🟩 = ≥0.750 🟩 = 0.749 - 0.500 🟨 = 0.499 - 0.250 🟥 = <0.250* ☐ = Blank

* Includes some weak negative correlations.

Figure 7-11: Annual heterogeneity of pollen rain in semi-deciduous dry forest. Correlations are based upon a Spearman's rank correlation (SPSS v.11.01). For full details of correlation see appendix IX.

Of the less abundant taxa (occurring at ≥3%) all but six are present in the 1999 data at some point within the plot. This suggests that the fire damage, while having a discernible impact on the vegetation of the plot, either did not wipe out plant types completely or they had flowered prior to the fire (figure 7-10). The presence of pollen from certain taxa within only one year suggests that certain plant types are not flowering every year, e.g. *Ferdinandusa elliptica*, which appears to have responded well to the fire occurring in high quantities during the 1999-2000 field season (figure 7-10b).

In summary, the semi-deciduous dry forest is shown to have a changing pollen signal through the three years sampled. This is probably in part a response to the fire damage to the plot that occurred during 1998-1999 although it must be remembered that harsh dry seasons and fires are part of the environmental conditions which typify this ecosystem (chapter 6, section 6.1.2). Therefore, these differences in the pollen rain can be seen as part of the natural variability of this plant community. However, the pollen signal that has been extracted from each year does show the same major pollen types present (figure 7-10), indicating that there is reasonable correlation between the assemblages once the low abundance taxa have been removed (figure 7-11). In the light of this understanding, and given that these semi-deciduous dry forests are subject to a natural burning regime (Middleton *et al*., 1997), the pollen assemblages extracted from this plot can be regarded as typical for this plant community and the associated ecosystem. This also highlights the need to sample multiple years to gain a full insight into the pollen rain of the semi-deciduous dry forest.

7.3.3 Distinctive pollen taxa

In figure 7-12 the pollen taxa that correspond strongly with the main gradients of variation measured in the data set by the PCA are picked out. The PCA (as described in section 7.1.3) was used to examine the pollen data from this plot in three ways: i) to identify the significant pollen taxa from each year, ii) to identify the distinctive pollen from the whole data set, and iii) to see if excluding any samples identified as ‘anomalous’ in section 7.3.1 or 7.3.2 would affect the analysis.

Firstly, the PCA carried out on the individual year’s data derived components that were only weakly correlated to the original variables (the taxa). This is because the ratio of samples (traps) to variables (taxa) was extremely low and consequently the statistical test was unable to identify strong links (as discussed in section 7.1.3). Therefore, the results of these analyses are not presented here, but are included in appendix XII. The weak correlations that were derived follow the pattern of explanation demonstrated in section 7.2.3 for the tall *terra firma* evergreen forest, i.e. negative correlations pick out locally dominant taxa and positive correlations pick out consistently present but varying taxa. For example: i) *Trema* and type 95 are negatively correlated to principal component 1 derived from the 1998-1999 data set and these taxa peak in one sample (see figure 7-7a), and ii) Melastomataceae/Combretaceae only occurs consistently in 2000-2001 (figure 7-10) and this is the only year when it is positively correlated in the PCA. However, these correlations are weak and it is difficult to identify clear trends in the data. As a consequence of this the PCA of the whole data set was used to identify the statistically distinctive components of the semi-deciduous dry forest.

The PCA for the whole data set also struggles to relate variables (taxa) to the derived components (figure 7-12) due to the low ratio of samples (traps) to variables (taxa). However, some strong correlations that relate to the original data set suggest the technique is working sufficiently well to be identifying the key trends. In the first two components two groups of taxa are highlighted: i) *Cecropia*, Moraceae/Urticatceae (2 pore) and *Trema* in the first component, and ii) *Celtis* and Pterposidia (trilete) undiff. (type 2) in the second (figure 7-12). Both these groups are shown to correlate negatively with the rest of the data. All these taxa are unevenly distributed in the pollen rain of the plot (figures 7-7 and 7-10). *Serjania*, type 151 and type 50 are strongly negatively correlated with components 6, 8 and 9 respectively. This is because of local and limited occurrence of these taxa: *Serjania* appears only in 2000-2001, while type 151 and 50 appear only in 1999-2000. The lack of positive correlation of taxa with components is also in part due to no one taxon varying in a consistent way through the data set and reflects the highly discontinuous nature of the pollen rain (figures 7-7 and 7-10).

Principal components 3 to 10 show few strong positive correlations with the original variables (figure 7-12). This is because of the highly complex spatial and temporal variation in the pollen rain (figures 7-7 and 7-10). In spite of this, eleven pollen types are shown to correlate positively with the components retained for analysis: Asteraceae (Asteroide/Cardue) undiff, Bromeliaceae undiff., Palmae (type 1), *Anadenanthera*, *Dilodendron*, *Piper*, *Serjania* and unidentified pollen types 16, 95, 117 and 151. These taxa are the most consistently occurring and varying taxa in the plot and are therefore statistically distinctive of the pollen rain from this semi-deciduous dry forest.

The final stage of this analysis, in which certain samples identified as badly correlated with one another were removed from the PCA, proved difficult. This was because the highly heterogeneous nature of the pollen rain (figures 7-7 and 7-10) resulted in poor bivariate correlations in all parts of the data set and between the majority of the samples (figures 7-8 and 7-11). As a consequence of the discontinuous nature of the pollen rain throughout the plot, removing one or two samples could result in the exclusion of one taxon almost

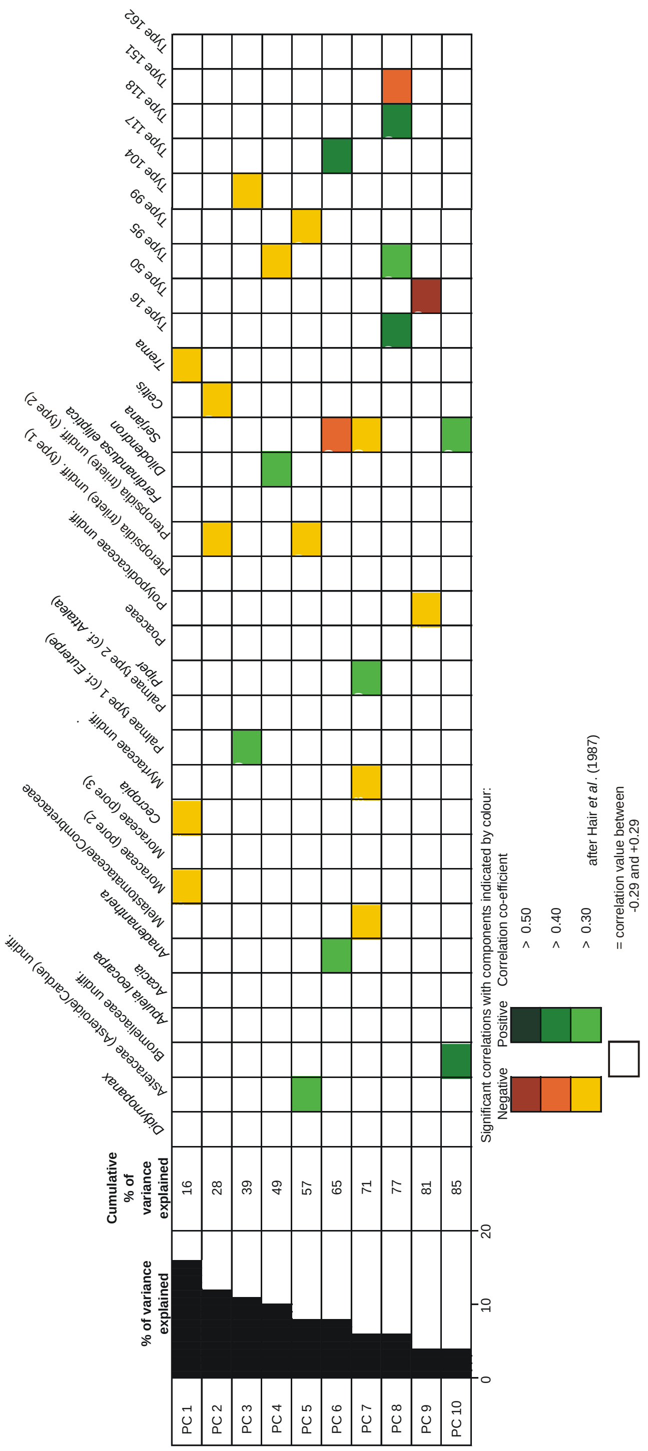


Figure 7-12: Key pollen taxa from the semi-deciduous dry forest. Colours highlight the correlation of the pollen types with the first ten axes derived from the PCA of all the percentage pollen data from the plot. Component importance descends from the top to the bottom of the diagram. For full details see appendix XII.

completely, i.e. excluding samples T55-99 and T56-99 would almost totally exclude Palmae (type 2) from the analyses (figure 7-7). As there is no way of differentiating the bad correlations from one another, and given that the flora of the ecosystem is extremely heterogeneous (chapter 6, section 6.3.2; Panfil, 2001), it was decided that the most accurate way of characterizing this ecosystem by its modern pollen spectra was by being as inclusive a possible and using the PCA of the whole data set to identify the statistically distinctive taxa.

In summary, the PCA of the whole data set identified eleven taxa that explain a number of small sections of the variance found within the semi-deciduous dry forest pollen rain: *Anadenanthera*, Asteraceae (Asteroide/Cardue) undiff., Bromeliaceae, *Dilodendron*, Palmae (type 1), *Piper*, *Serjania*, type 16, type 95, type 117 and type 118 (figure 7-12). The complex nature of the PCA result and the lack of positive correlations with the first two principal components is a product of the highly variable nature of the pollen rain shown in figures 7-7 and 7-10.

7.3.4 Pollen-vegetation relationship

Figure 7-13 illustrates the relationship between the relative abundance of taxa identified in the pollen and the abundance of those taxa in the vegetation (trees >10 cm d.b.h.) by depicting the ratio of: i) the highest percentage occurrence in the pollen vs. the percentage of individuals (figure 7-13a), and ii) the highest percentage occurence in the pollen vs. the percentage of the estimated biomass of the plot (figure 7-13b).

The presence of *Anadenanthera* and *Caesalpinia* in the pollen rain (figure 7-13) is particularly significant as they are the major vegetation components of the ‘soto/carapaú’ type of dry forest that this plot represents (chapter 6, section 6.3.2). Also of note is the c. 100x over-representation of Moraceae/Urticaceae and *Didymopanax*.

The pollen rain from the semi-deciduous dry forest contains taxa that are both under and over represented proportional to their occurrence in the vegetation (figure 7-13). Those taxa which include species identified by Panfil (2001) (chapter 6, section 6.3.2) as ecologically important to the vegetation of the plot are split in to two groups. The first of these, containing *Caesalpinia* undiff., *Tabebuia*, *Chorisia*, and *Sterculia*, are under represented in the pollen rain (figure 7-13). This suggests that the presence of these taxa in the pollen rain is a strong indication of the plants' presence nearby but that their absence does not mean they are necessarily absent from the local vegetation. The second group, made up of *Cordia*, Melastomataceae/Combretaceae, Palmae undiff. and *Anadenanthera*, appear to be slightly over represented in the pollen rain. This demonstrates that their presence in the landscape is likely to be manifested as a significant proportion of the pollen rain.

There are five other taxa that are over represented in the pollen rain by up to 10x their abundance in the vegetation (figure 7-13a): *Amburana*, *Didymopanax*, *Hymenaea*, cf. *Samanea* and *Serjania*. With the exception of *Didymopanax*, all these taxa occur at low abundances in the vegetation and the pollen, but due to their relative over representation in the pollen they are likely to be recorded in the pollen rain even if only present as one or two individuals in the plot. *Didymopanax* is the second most over represented pollen type found in this plot and it is frequently found to make up >5% of the pollen rain (figure 7-7 and 7-10). There is only one individual (>10 cm d.b.h.) of this genus recorded in the plot (Killeen, unpublished data; appendix XIV), demonstrating that *Didymopanax* is either an extremely high pollen producer or that there are plants below this size range producing the pollen in abundance in this plot or that there is long-distance transport from outside the plot. The occurrence of *Amburana* is also particularly important because it is typical of what Panfil (2001) classifies as edaphically controlled dry forests, its occurrence here suggests that it may be very useful in identifying this similar ecosystem if it is found there in greater abundance (further work would be required to clarify this).

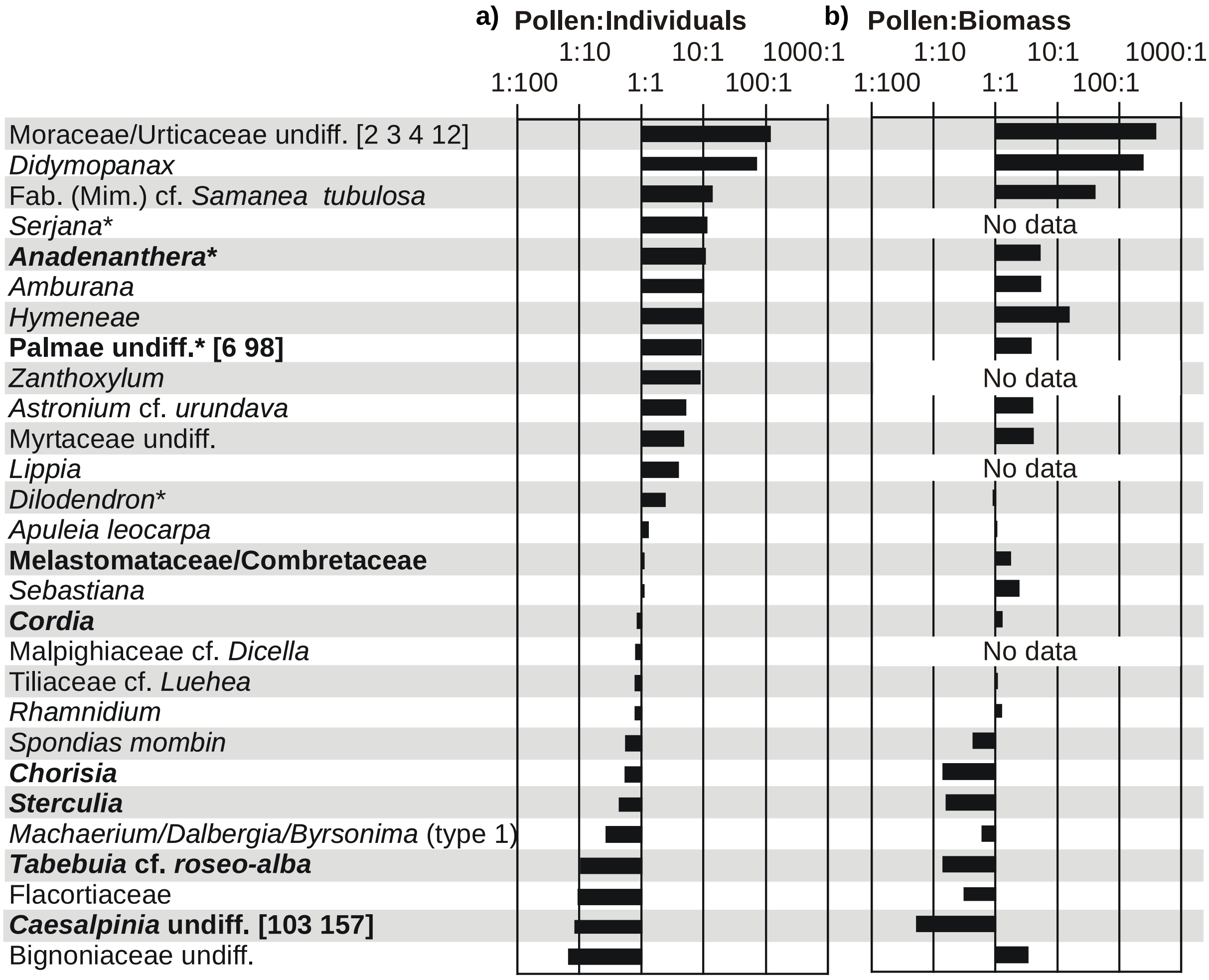


Figure 7-13: Relative abundance of taxa in the pollen vs. vegetation in the semi-deciduous dry forest. Taxa highlighted in **bold** indicate those shown to be ecologically important to the AC-2 plot by Panfil (2001) (chapter 6, section 6.3.2). Taxa marked with an * are those shown to be statistically distinctive in section 7.3.3. Individuals = data derived from plot vegetation lists compiled by T.J. Killeen (unpublished data). Biomass = data derived from estimates of biomass for individual trees calculated by T.J. Killeen (unpublished data). For full details see appendix XIV.

Interestingly, the most over-represented taxon found in the semi-deciduous dry forest is Moraceae/Urticaceae undiff., which is over represented by more than 100x its occurrence in the vegetation (figure 7-13). This massive over-representation suggests either of two possibilities: i) that the few individuals producing this type of pollen within the plot are generating massive amounts of pollen, or ii) that much of this pollen is being blown into the plot by long-distance transport from parent vegetation in the moist evergreen forests 20 kilometres to the north (chapter 6, figure 6-11). The former possibility is unlikely because this taxon is over-represented by a factor of 10x in the tall *terra firma* evergreen forest (section 7.2.4). Therefore, long-distance transport is a more likely explanation; supporting this theory is the opinion of J. Ratter (*pers. comm.*, 2003) who stated that Moraceae species found in the semi-deciduous dry forest are not known to be higher pollen producers than those found in the evergreen forest.

In summary, there are two key groups of characteristic taxa from the semi-deciduous dry forest: i) *Cordia*, Melastomataceae/Combretaceae, Palmae undiff. and *Anadenanthera* are all well represented in the pollen rain, and ii) *Caesalpinia* undiff., *Tabebuia, Chorisia,* and *Sterculia* are all present in the pollen rain at low levels and are important in the vegetation. In addition to this Moraceae/Urticaceae undiff. is massively over-represented in the pollen rain (>100:1, figure 7-13) suggesting that part of the pollen rain may be coming from outside the plot. The input of airborne pollen being transported long distances into the traps here is possible due to the open canopy and is supported by the presence of *Podocarpus* and *Alnus* at low levels, but at frequencies suggesting against laboratory contamination (appendix VII), which must have been transported from the Andean flank to the east or it is possible that the *Podocarpus* was blown northwards from a small population >600 km to the south (T.J. Killeen, *pers. comm.*, 2003).

7.3.5 Semi-deciduous dry forest pollen signature

The analysis carried out in the four preceding sub-sections has allowed a characteristic pollen signature to be established for the semi-deciduous dry forest found in AC-2. The basis on which these taxa were selected is summarised in table 7-4 and detailed in appendix XIII.

	Highlighted as significant in:			
Pollen taxa	**Spatial**	**Inter-annual**	**Statistical**	**Vegetation**
Anadenanthera	✓	✓	✓	✓
Moraceae/Urticaceae type	✓	✓	✓	✓
Palmae type 1	✓	✓	✓	✓
Cecropia	✓	✓	✓	
Poaceae	✓	✓	✓	
Pteropsidia (trilete) undiff.	✓	✓	✓	
Palmae type 2	✓	✓		✓
Didymopanax	✓	✓		✓
Myrtaceae undiff.	✓		✓	✓
Bromeliaceae undiff.	✓			
Piper	✓			
Polypodicaceae undiff.	✓			
Celtis		✓	✓	
Trema		✓	✓	
Asteraceae (Asteroide/Cardue) undiff.		✓		
Melastomataceae/Combretaceae		✓		✓
Acacia		✓		
Ferdinandusa elliptica		✓		
Type 104		✓		
Type 16		✓		
Amburana				✓
Apuleia leocarpa				✓
Astronium cf. *urundava*				✓
Bignoniaceae undiff. type 1				✓
Caesalpinia type 1				✓
Caesalpinia type 2				✓
Chorisia				✓
Cordia				✓
Dilodendron				✓
Fab. (Mim.) cf. *Samanea tubulosa*				✓
Flacortiaceae				✓
Hymeneae				✓
Lippia				✓
Machaerium/Dalbergia/Byrsonima type 1				✓
Malpighiaceae cf. *Dicella*				✓
Rhamnidium				✓
Sebastiana				✓
Serjana				✓
Spondias mombin				✓
Sterculia				✓
Tabebuia cf. *roseo-alba*				✓
Tiliaceae cf. *Luehea*				✓
Zanthoxylum				✓

Table 7-4: Pollen signature selection criteria, semi-deciduous dry forest. ✓ indicates identified as important in the corresponding section. Marks were given on the following basis: i) intra-plot spatial = present in at least half the samples, ii) inter-annual = consistent presence year on year at any one location, iii) statistical = highlighted in PCA of whole data set, and iv) vegetation = presence in the trees >10 cm d.b.h. of the plot (T.J. Killeen, unpublished data).

In table 7-4 the taxa that score three or more marks have been classified as major components of the pollen rain of the plot (table 7-5) (for the same reasons as discussed in section 7.2.5). In addition *Celtis* and *Trema* score twice but are not present within the plot. These two taxa have also been included as major taxa because of their significance in the pollen, but they were classified as part of a regional signal rather than a local signal because they are absent from the local vegetation. Moraceae/Urticaceae undiff. and *Cecropia* were also classified as part of the regional signal because of over-representation in the pollen compared to the vegetation of the plot, indicating that the pollen is coming mainly from parent vegetation in other ecosystems (section 7.2.4). Therefore, the semi-deciduous dry forest pollen signature is comprised of eleven major taxa that are likely to be present. The local and regional pollen taxa and their ranges of occurrence are detailed in table 7-5a and b respectively.

Seven taxa related to the local vegetation were identified as being present in the pollen rain from the semi-deciduous dry forest at consistently detectable levels (table 7-5a). On average six of these taxa were found in any one sample from AC-2. Of these *Anadenathera* is dominant, with the others consistently present at lower levels. Other pollen found here probably originates mainly from outside the dry forest ecosystem (figure 7-5b). Among these regionally derived pollen

a) Local pollen

MAJOR	Percentage occurrence		
pollen taxa	**Minimum**	**Median**	**Maximum**
Anadenanthera	0	25	74
Poaceae	0	4	12
Palmae type 2	0	3	41
Palmae type 1	0	2	25
Didymopanax	0	2	14
Pteropsidia (trilete) undiff.	0	1	13
Myrtaceae undiff.	0	1	4

b) Regional pollen

MAJOR	Percentage occurrence		
pollen taxa	**Minimum**	**Median**	**Maximum**
Moraceae/Urticaceae undiff.	2	19	69
Cecropia	0	1	5
Celtis	0	1	5
Trema	0	1	4

Table 7-5: Semi-deciduous dry forest pollen signature, major components.

types are the only ever present pollen type, Moraceae/Urticaceae, and three other taxa, *Cecropia*, *Celtis* and *Trema,* are consistently present at low levels.

The dominant local taxon is *Anadenanthera* and, despite its uneven distribution in the pollen rain (section 7.3.1), is present in significant quantities throughout most of the plot (figures 7-7 and 7-10). The dominance of this genus is important because it is ecologically distinctive of the disjunct dry forest distributions that boarder southern Amazonia (Prado and Gibbs, 1993). As it is also prominent in the pollen rain, it can be used as a marker for the presence of this ecosystem in the fossil pollen record. The other taxa listed in table 7-5a are not, individually distinctive of the semi-deciduous dry forest but if found occurring together and in sufficient abundance, they provide a pollen signature typical of this ecosystem.

The pollen rain signal collected from the semi-deciduous dry forest is further complicated by the presence of pollen types that are likely to have been blown into the plot from other nearby ecosystems and beyond. The open canopy structure of the semi-deciduous dry forest means that pollen is easily able to penetrate the canopy if present in the air (chapter 6, figure 6-3). There are four taxa that are likely to have been blown into the AC-2 plot, namely Moraceae/Urticaceae undiff., *Cecropia*, *Celtis* and *Trema* (table 7-5b). The reasons these taxa can be identified as originating from the regional pollen rain are: i) they are not present in the floristic inventory of trees >10 d.b.h. for the plot (figure 7-13), and ii) they are all found, in abundance, in the moist evergreen forest c. 15 kilometres away (section 7.2). These four taxa are all disturbance indicators or pioneer taxa (Marchant *et al*., 2002) and are therefore likely to be located at the fringes of the evergreen forest were this ecosystems may still be expanding (Mayle *et al.*, 2000). Their presence close to the AC-2 plot (see chapter 6, figure 6-11) and high rates of pollen production (e.g. *Cecropia*, figure 7-6), coupled with prevailing winds from the north for much of the year (chapter 3, figure 3-3), make it likely that pollen from thse four taxa would be dispersed into the dry forest region. The level at which these taxa are present within a pollen rain signal from a semi-deciduous dry forest is therefore strongly dependant on the proximity of evergreen forest. However, it should not be forgotten that Moraceae/Urticaceae and *Cecropia* should be expected in the dry forest even if no evergreen forest is nearby, as plants contributing to these taxa can be present within the ecosystem (Killeen and Schulenberg, 1998).

MINOR pollen taxa	Frequency of occurrence (% samples)
Asteraceae (Asteroide/Cardue) undiff.	57
Bromeliaceae undiff.	52
Melastomataceae/Combretaceae	52
Piper	48
Polypodicaceae undiff.	43
Serjana	43
Zanthoxylum	33
Type 104	33
Type 99	29
Acacia	24
Apuleia leocarpa	24
Fab. (Mim.) cf. *Samanea tubulosa*	19
Malpighiaceae cf. *Dicella*	19
Astronium cf. *urundava*	14
Caesalpinia type 1	14
Cordia	14
Ferdinandusa elliptica	14
Rhamnidium	14
Sebastiana	14
Sterculia	14
Flacortiaceae	10
Dilodendron	10
Hymeneae	10
Lippia	10
Machaerium/Dalbergia/Byrsonima type 1	10
Type 16	10
Bignoniaceae undiff. type 1	5
Tiliaceae cf. *Luehea*	5
Amburana	5
Caesalpinia type 2	5
Chorisia	5
Spondias mombin	5
Tabebuia cf. *roseo-alba*	5

Table 7-6: Semi-deciduous dry forest pollen signature, minor components

In addition to these major taxa there are thirty-three minor taxa that have been identified as occurring either at a low level throughout the ecosystem or being dominant in the pollen rain at one particular point in space or time (table 7-6). Typically eight of these are present within any one sample from AC-2.

The large number of taxa included in table 7-6 reflects the high diversity found within the semi-deciduous dry forest (Panfil, 2001). There are two groups of taxa present in the list that are more likely to be represented in the pollen rain than the others. The first group comprises Asteraceae (Asteroide/Cardue) undiff., Bromeliaceae undiff., Melastomataceae/Combretaceae and *Piper*, all occurring in at least half of the samples taken from AC-2 and all present within the dry forest of NKMNP (Killeen and Schulenberg, 1998). (Asteraceae (Asteroide/Cardue) undiff., Bromeliaceae undiff. and *Piper* are not trees so are therefore not listed in the inventory of arboreal taxa used in table 7-6). The second group contains *Serjania*, *Apuleia leocarpa*, *Astronium* cf. *urundueva* and *Caesalpinia* (type 1), all of which occur in the vegetation and are significant in the pollen rain indicating they are likely to be present in this ecosystem as well as represented in the pollen rain from it.

In summary, the identification of the pollen signature from the semi-deciduous dry forest is complicated by the diverse nature of this plant community and the input of pollen rain from external sources. However, it is possible to characterise this plant community as one dominated by *Anadenanthera*, with the likely presence of grass, palm, fern spores, *Didymopanax* and Myrtaceae. There are also likely to be some minor taxa present, most commonly Asteraceae (Asteroide/Cardue) undiff., Bromeliaceae undiff., Melastomataceae/Combretaceae, *Apuleia leocarpa*, *Astronium* cf. *urundueva*, *Caesalpinia* (type 1), *Piper* and *Serjania*. Given the similarities of this plant community and other plant communities in the deciduous and semi-deciduous dry forest ecosystem (chapter 6) and in particular the importance of *Anadenanthera,* this pollen signal can be regarded as characteristic of the wider ecosystem.

7.4 Cerradão

Twenty-two traps were selected and analysed from those collected from the FC-2 plot with varying degrees of success (see chapter 5, table 5-2). These data allow the extent of intra-plot spatial (section 7.4.1) and inter-annual (section 7.4.2) variations to be assessed, the statistically distinctive pollen taxa to be determined (section 7.4.3) and the pollen-vegetation relationship analysed (section 7.4.4) for the Cerradão plant community and the associated Cerrado (*sensu* lato) ecosystem which was described in chapter 6. Then, in section 7.4.5 the results of these analyses are collated and the characteristic pollen signature of the Cerradão is presented.

7.4.1 Intra-plot spatial variability

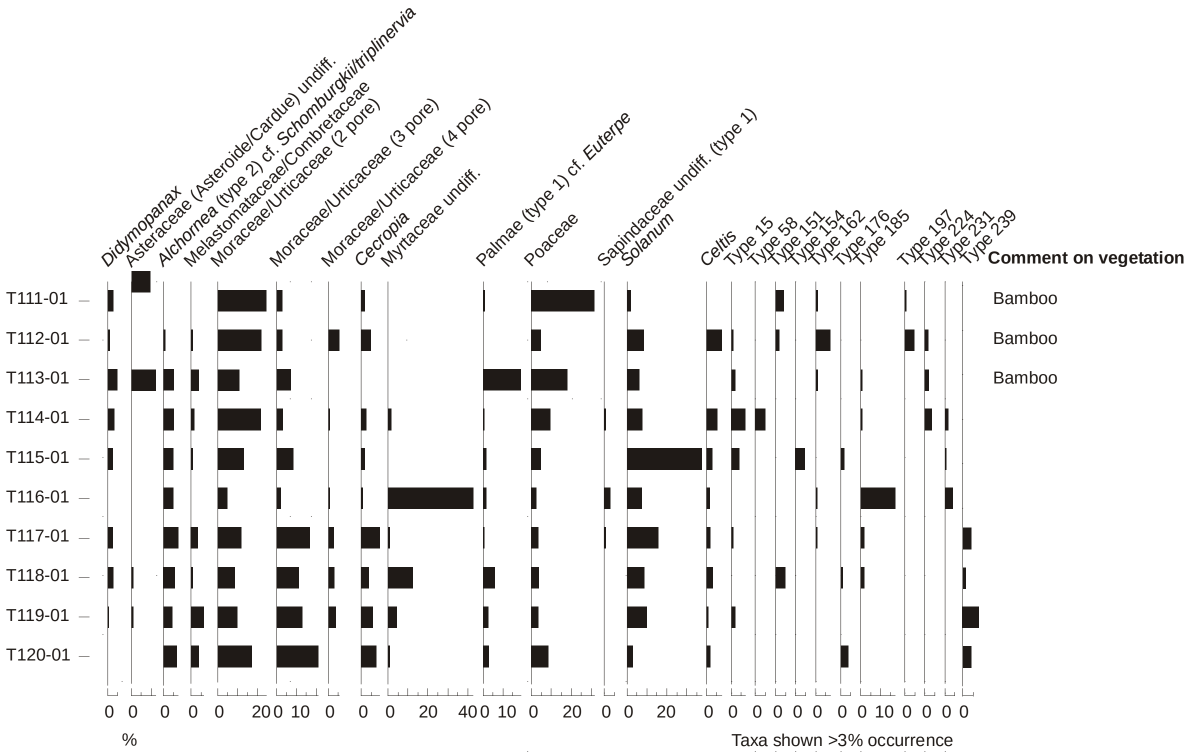
In figures 7-14 and 7-15 the extent of spatial variation within the Cerradão is illustrated for the 2000-2001 field season.

The pollen assemblages from this plot have nine or ten taxa, each contributing c. 5% abundance (figure 7-14). There is no clear dominant taxon but Moraceae/Urticaceae (2 and 3 pore) do contribute heavily throughout. Percentage and PAR data both show spatially restricted peaks in the distribution of Myrtaceae undiff., Palmae (type 1), Poaceae and *Solanum* pollen types, suggesting that the traps were probably located close to plants of these species (figure 7-14b).

There is some evidence to suggest that the local vegetation is biasing the pollen rain collected from the traps. The only vegetation data spatially related to the traps is from observations made during the collection of the traps in 2001 (figure 7-14a). From these observations a general link can be seen between the grass (Poaceae) pollen and the bamboo that dominates the northern end of the plot; i.e. trap locations T111 to T113 (figure 7-14a). There was damage to only one trap so this is thought not to be effecting the pollen assemblages examined (figure 7-14b).

In figure 7-15 the strength of correlation between the spatially distinct pollen assemblages is highlighted. There is a general improvement in correlation as the lower abundance taxa are progressively excluded from the data set (figure 7-15a to d). The correlation also identifies three traps that differ significantly from all the others: i) T111-01 is only weakly correlated with the other assemblages when all the taxa are considered (figure 7-15a) but the strength of the correlation improves gradually through the analysis (figures 7-15b to d), ii) T113-01 shows a stronger negative correlation with the other samples as the smaller taxa are removed (figure 7-14d), and iii) T116-01 is weakly correlated with the other samples for all portions of the data set ≥3% (figures 7-15b to d) and is strongly negatively correlated with both T111-01 and T113-01 when only taxa of ≥10% abundance are considered. Also of interest is the strong positive correlation between the spatially contiguous samples T117-01, T118-01, T119-01 and T120-01, which show a good correlation with each other that increases in strength as the lower abundance taxa are removed.

a) Pollen percentage data



b) Pollen accumulation rate

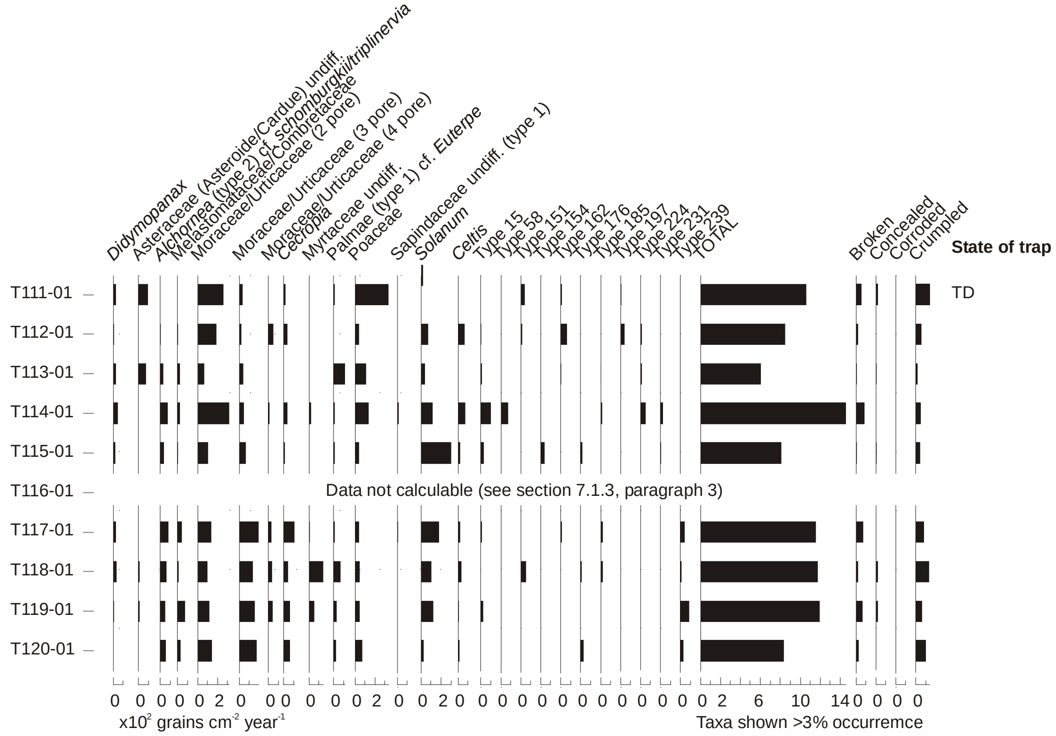
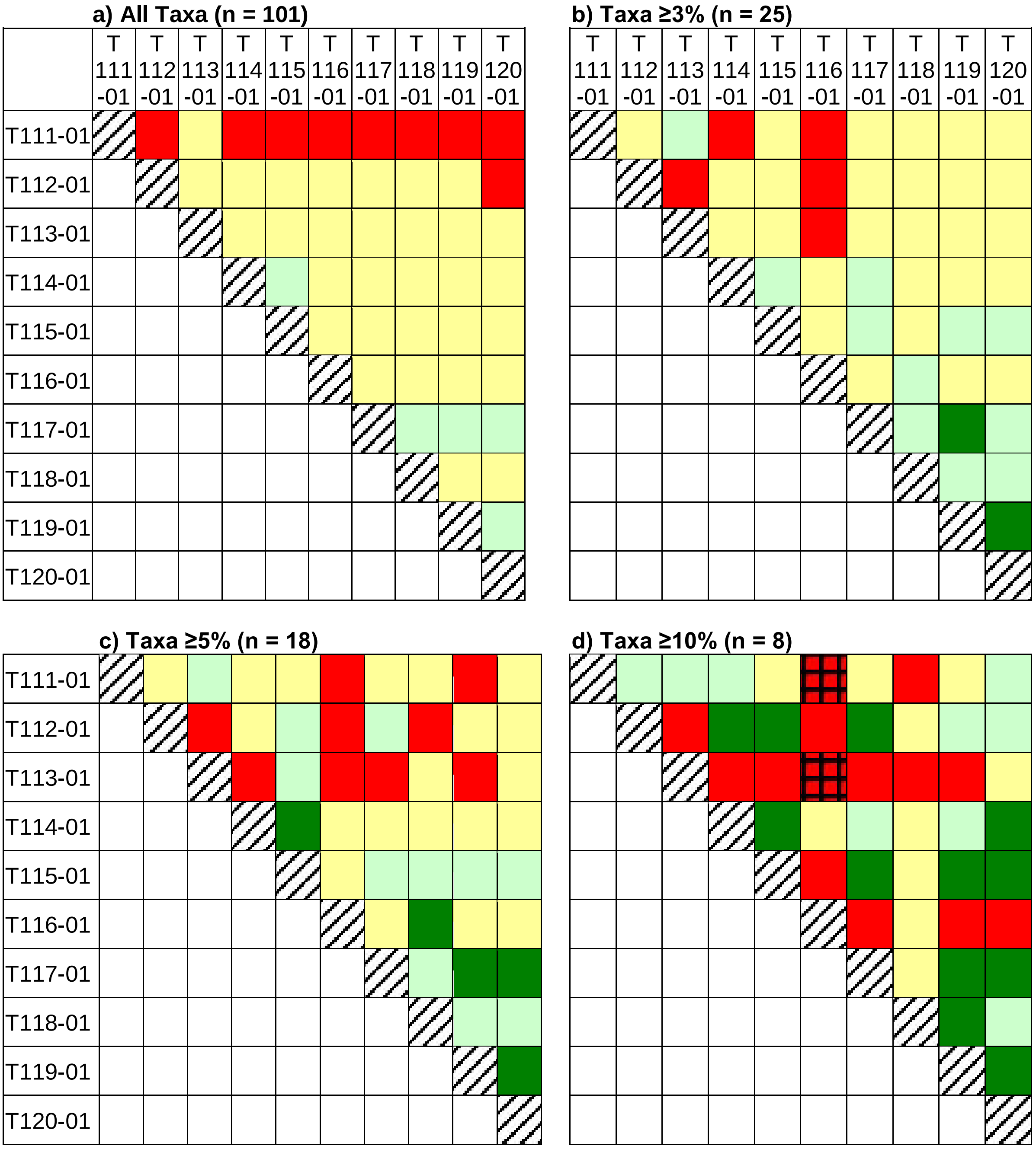


Figure 7-14: Spatial variation in the pollen rain in Cerradão. “Comment on vegetation” indicates field notes on trap or location. “TD” indicates the trap has suffered from termite damage.



Strength of positive Spearman's rank correlation coefficient indicated by colour:

🟩 = ≥0.750 ▩ = 0.749 - 0.500 🟨 = 0.499 - 0.250

🟥 = <0.250* ▦ Strong negative (<-0.750) ☐ = Blank

* Includes some weak negative correlations.

Figure 7-15: Spatial heterogeneity of pollen rain in Cerradão. Correlations are based upon a Spearman's rank correlation (SPSS v.11.01). For full details of correlation see appendix VIII.

The ten pollen assemblages collected from the Cerradão show a generally consistent signal with fifteen taxa occurring at over half of the locations (figure 7-14). However, traps T111-01, T113-01 and T116-01 yielded pollen assemblages markedly different from the others.

T111-01 exhibits strong differences from the rest of the traps when all the taxa are correlated (figure 7-15a) but, has a weak positive correlation with all but one of the other traps when the taxa <3% abundance have been excluded (figure 7-15b). Except for the higher abundance of Poaceae, taxa ≥3% abundance in the pollen assemblage collected from T111-01 show a broad agreement with the other pollen assemblages collected from within the plot (figure 7-14). Poaceae is at its highest abundance in T111-01 (c. 25%) this is probably due to a high localised input of pollen from the bamboo that dominates this part of the plot (figure 7-14a). Therefore, apart from the elevated grass signal it is shown that T111-01 collected a pollen assemblage similar to those found in the rest of the plot.

T113-01 is also within the bamboo-dominated area of the plot and also has a high percentage of Poaceae relative to most other traps (figure 7-14a). This, coupled with the high percentage of Palmae (type 1) found at this trap (figure 7-14a), explains the samples lack of correlation at the ≥5% and ≥10% slices of the data set (figure 7-15c and d). The peak in palm PAR suggests that a palm tree was close by (figure 7-14b). However, the total PAR for this trap is lower than all the other traps, possibly due to the trap being sheltered from pollen rain by the dense bamboo at this location. The sample collected from T113-01 is therefore compositionally similar to the others from this plot, although pollen abundance was lower for all taxa except Poaceae and Palmae.

T116-01 recorded the highest pollen percentages of Myrtaceae undiff. It is because of the extremely high input of this pollen type that the PARs for the trap could not be calculated (figure 7-14b). The input of Myrtaceae undiff. into this trap was roughly 100x greater than that found in other traps (appendix VII) and explains why this pollen assemblage is poorly correlated with the others (figure 7-15). The extreme difference between this sample and the others is also evident by the degree to which it is split from the other samples in the divisive cluster analysis performed on the data (appendix XI). This high abundance, coupled with low abundances throughout the rest of the plot, suggests that this value may be the product of highly localised production. It is possible that an anther from a plant of the Myrtaceae family fell into the trap or perhaps one flowered particularly close by. Amazonian Myrtaceae are known to have ‘mass flowering’ events (Richards, 1996, p. 251). It is possible that one of these events occurred close to trap 116 during the 2000-2001 field season. This high input of Myrtaceae suppressed the percentage abundance of Poaceae, resulting in the strong negative Speraman’s rank correlations with T111-01 and T113-01 (figure 7-15). However, aside from the high influx of Myrtaceae and its suppression of the pollen percentages of the other taxa it is still clear that the pollen assemblage from T116-01 is typical of those from other traps within the plot because it contains the majority of the same taxa (figure 7-14).

The pollen signal collected from all traps throughout the Cerradão plot show consistent PARs of c. 1,000 grains cm^{-2} year^{-1} (figure 7-14b) with the exception of T116-01, which reaches approximately 10,000 grains cm^{-2} year^{-1} (appendix VII). It has been demonstrated that Poaceae, Palmae (type 1) and Myrtaceae undiff. pollen grains are unevenly distributed in the pollen rain of the plot, which is probably spatial heterogeneity of the vegetation within the plot. Only two of the identified pollen types >3% abundance occur in less than half the samples: Asteraceae (Asteroide/Cardue) undiff. and Sapindaceae undiff. (type 1). The other twelve identified pollen types are all present in the majority of the samples at roughly similar abundances of 3-5 % (figure 7-14). It is therefore clear that a consistent pollen signal is being extracted from throughout the Cerradão plot.

7.4.2 Inter-annual variability

Figures 7-16 and 7-17 show the extent of year to year variability in the pollen rain collected from the Cerrodão plot. Due to the poor recovery rate of traps and poor pollen preservation from this plant community (only 53% of the traps were recovered in pristine condition) it was not always possible to sample from the same point for three consecutive years (chapter 5, table 5-2c). This makes the pattern of change between the years more difficult to discern, although with at least two traps analysed from eight of the ten locations within the plot, a picture of the temporal variability in the pollen rain has been gained.

No one pollen type dominates the Cerradão pollen assemblages (figure 7-16) and there are only weak correlations between the temporally distinct samples (figure 7-17). However, samples from all years and all locations do have c. 10% Moraceae/Urticaceae (2 pore) pollen (figure 7-16) and Poaceae is the only other continuously present taxon, although its PAR fluctuates greatly between years (figure 7-16b). Total PARs show no consistent pattern between the years and high influxes from of *Solanum*, Poaceae and Myrtaceae undiff. meant that PARs were incalculable for T112-00, T115-00 and T116-01 respectively (figure 7-16b). In spite of these variations in production, many taxa do occur in most samples at any given location, even if the level of abundance changes (figure 7-16). There are, however, two identified taxa, Fabaceae (Mimosoideae) undiff. and *Piper*, and four unknown pollen types (numbers 58, 154, 178 and 187) which occur in only one year at any one location (figure 7-16).

The link between abundance of bamboo in the vegetation of the plot and the abundance of grass pollen is less clear than when the spatial data for 2001 were considered in isolation (section 7.4.1), with higher Poaceae PARs being recorded in other locations at different times (figure 7-16b). This possibly suggests that the pollen productivity of bamboo varied from year to year.

Although there is no strong correlation between physical damage to traps and the amount of degraded pollen present (figure 7-16b), five out of the seven traps found on the ground had lower total PARs than others present at the same location in different years. This suggests that the collection of pollen in these traps might have been impeded by the dislodgement of the trap from its stake. The extent of the impact of this on the ability of the trap to collect the pollen rain is dependent on the time at which the trap was dislodged (this information is however unavailable). It should be noted that the improved recovery of traps from the 2001 field season is attributed to the modified trap design described in chapter 4, section 4.2 (Gosling *et al.*, 2003); the old style traps with the bottle present were damaged by animals which were trying to drink the water that they contained.

There are no strong positive correlations between pollen trap assemblages for any of the sample locations through the three years (figure 7-17). In general the pollen assemblages from 1999 correlate better with those from 2001 than those from 2000 and there is little correlation between the 2000 and 2001 data (figure 7-17). There is also only a slight improvement in the correlations when only the more dominant taxa are considered, i.e. those with abundances of ≥5% or ≥10%.

a) Pollen percentage data

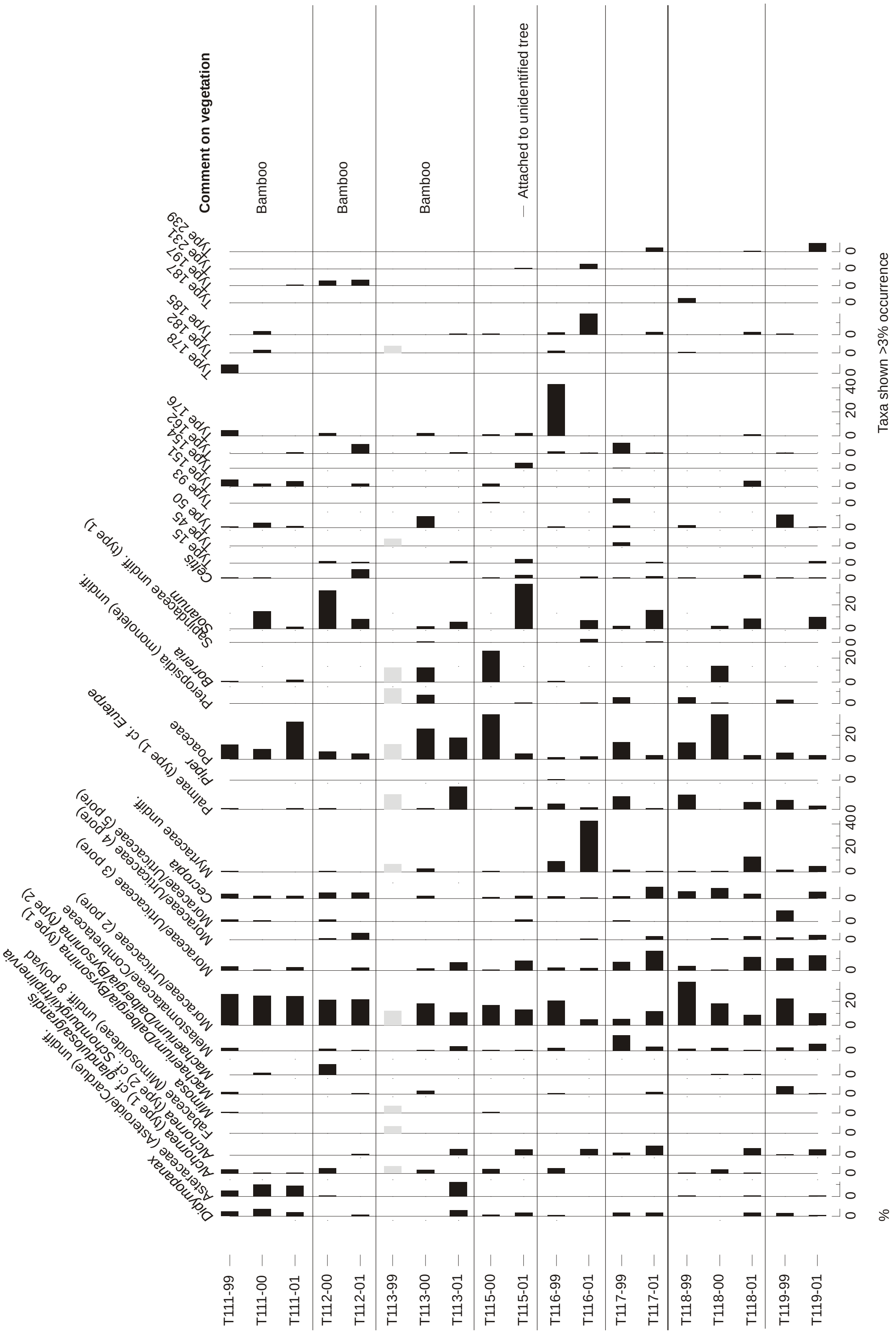


Figure 7-16: Continued over…

b) Pollen accumulation rates

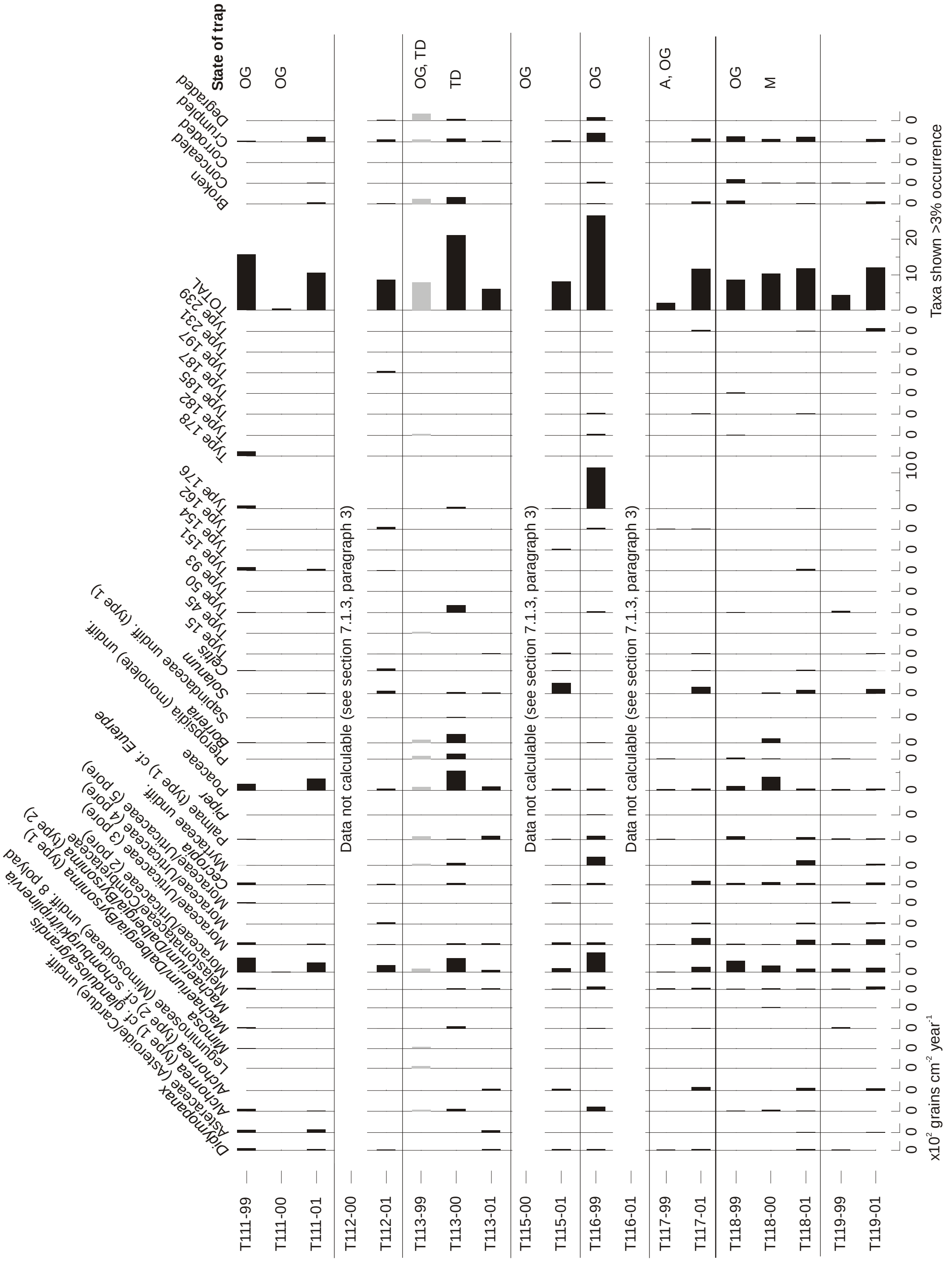


Figure 7-16: Temporal variation of pollen rain in Cerradão. “Comment on vegetation” indicates field notes on trap or location. “TD” indicates the trap has suffered from termite damage. T113-99 is grey because the pollen count for this trap was only 16 grains therefore the data should be viewed with extreme caution. The following letters indicate the following “A” animal damage, “M” melting and “OG” on ground.

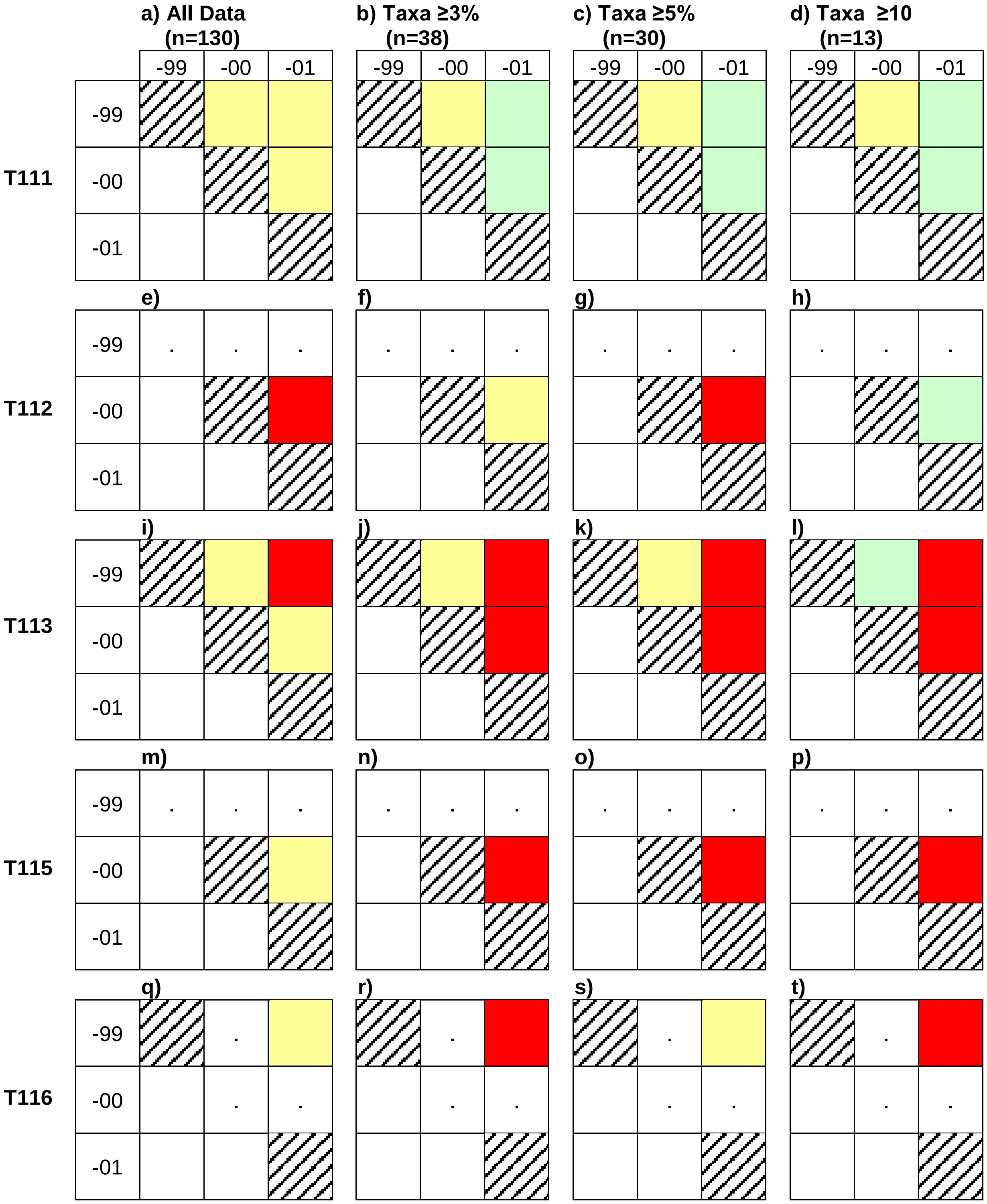


Figure 7-17: Continued over…

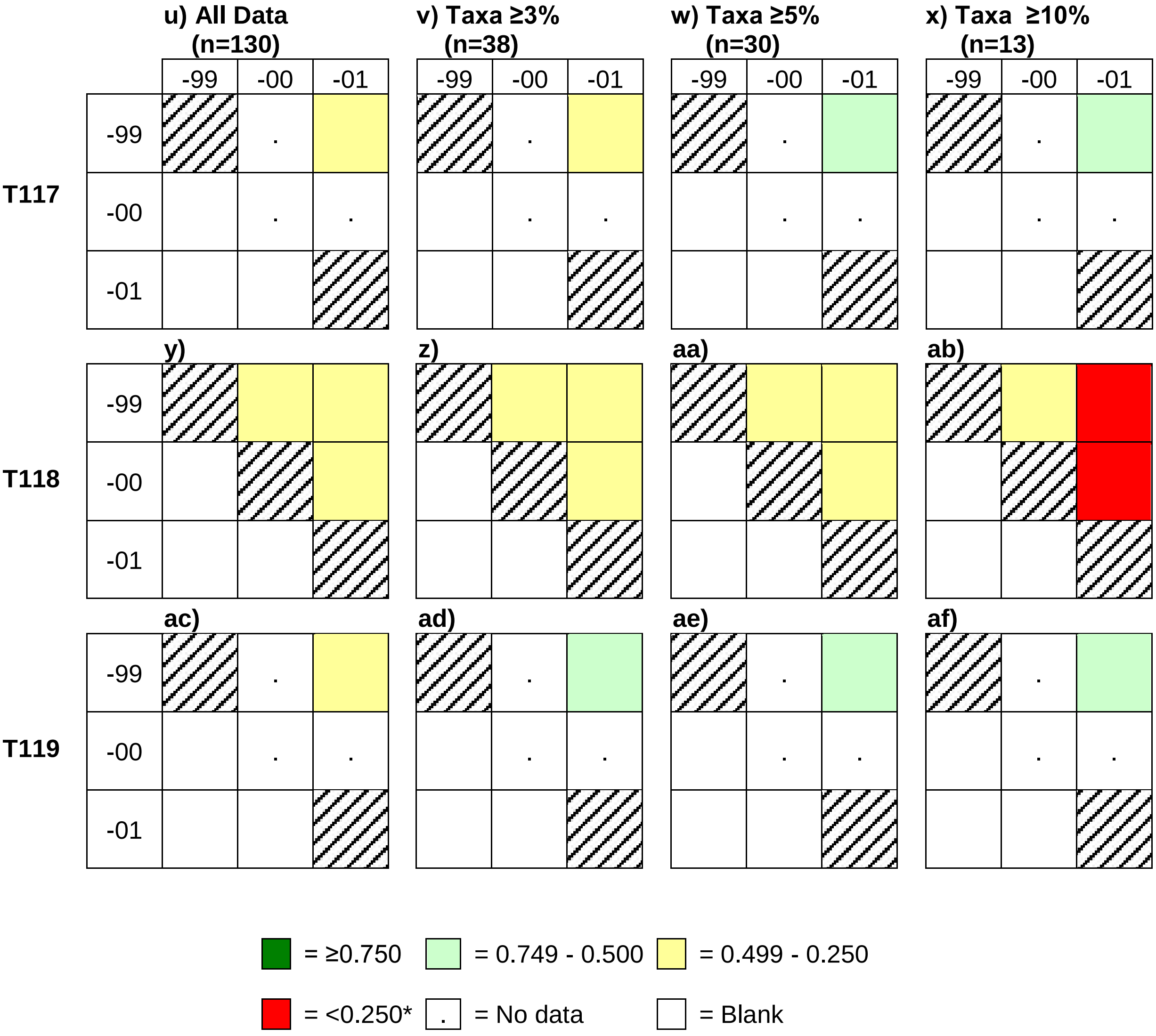


Figure 7-17: Annual heterogeneity of pollen rain in Cerradão. Correlations are based upon a Spearman's rank correlation (SPSS v.11.01). For full details of correlation see appendix IX. Note, the sample size obtained from T113-99 was only 16 grains, these data are included because of the lack of other locations with samples from all three years. However, in the light of this tiny sample size these results should be interpreted with caution.

At the three locations where it was possible to sample the pollen rain from all three years, i.e. T111, T113 and T118, there is no consistent pattern of variability (figure 7-16). These locations all show different patterns of fluctuation in total PAR (figure 7-16b). At T111 and T113 the pattern follows the PARs of Moraceae/Urticaceae (2 pore) and Poaceae which do the same thing. In contrast the total PAR recorded at T118 relatively consistent because when influx from Moraceae/Urticaceae (2 pore) drops then the input from Poaceae rises and visa versa (figure 7-16b). This demonstrates a spatial variability in the inter-annual variability of the pollen rain from this plot.

The inconsistent response of taxa between the years at different locations is also apparent in the rest of the locations where pollen rain was sampled for only two of the three years (figure 7-16). This is well illustrated by the over-representation of three different taxa in samples T112-00 (*Solanum*), T115-00 (*Borreria*) and T116-01 (Myrtaceae undiff.) to the point where calculations of PARs became statistically unreliable (figure 7-16b). This is supported by divisive cluster analysis, which splits these samples from the rest (appendix XI). The massive localised input of these pollen types to the traps suggest that they may be the product of individual pollen dispersal events occurring in close proximity to the respective traps. The only other pollen type that shows an equivalent pattern is type 176, which has an isolated peak in T116-99, again suggesting high local input from a plant that does not flower every year.

The less abundant pollen types, i.e. those typically making up 3-5% of the pollen assemblage, can be split into two groups: i) those which are consistently present at particular trap locations over the three years, and ii) those that are not present every year. The first group, containing the consistently occurring taxa, comprises Asteraceae (Asteroide/Cardue) undiff., Moraceae/Urticaceae (3 pore), Myrtaceae undiff., Palmae (type 1), *Alchornea* (type 1), *Ceropia*, *Celtis*, *Didymopanax* and unidentified types 151 and 197. These taxa, while not dispersing their pollen throughout the plot, are represented in the pollen every year. The second group contains many taxa which only occur in one or two of the samples (figure 7-16). These taxa are either not flowering every year or are not producing sufficient pollen to be recognised in the pollen rain.

In summary, the only components of the pollen rain from the Cerradão plot that are consistently present at all locations over the three years are Moraceae/Urticaceae (2 pore) and Poaceae, although the values of Poaceae fluctuate widely. Other taxa, especially *Solanum*, *Borreria* and Myrtaceae undiff., occasionally exhibit massive influxes of pollen at certain localities, although they are absent from the majority of the samples. There are, however, a suite of less abundant taxa that do occur consistently from year to year at the same location. These taxa, coupled with the presence of Moraceae/Urticaceae (2 pore) and grass, are representative of a consistent signal from the Cerradão every year.

7.4.3 Distinctive pollen taxa

PCA (as described in section 7.1.3) was used to explore the pollen data from FC-2 in three different ways in an attempt to identify the statistically distinctive taxa from this plant community and therefore the associated ecosystem (as discussed in chapter 6): i) the data from each field season, ii) the whole data set, and iii) the whole data set excluding certain samples identified as ‘anomalous’ in the previous analysis (sections 7.4.1 and 7.4.2).

Firstly, the principal components derived from the pollen data from the individual field seasons produced only weak correlations because, like the semi-deciduous dry forest data, the ratio of samples (traps) to variables (taxa) was low (as discussed in section 7.1.3). The weak correlations that were derived do not appear to make ecological sense when related to the pollen diagrams (figures 7-14 and 7-16). These results are therefore only included for reference in appendix XII and are not discussed further here.

Secondly, the PCA carried out on the whole data set produced stronger correlations that can be related to trends in the original data (figure 7-17a). For example, the negative and positive correlations of *Alchornea* type 1 and 2 with the first component suggest that these pollen types belong to are different taxa, rather than the same taxon, because they are present at different locations in the data set. This observation is borne out in the inter-annual pollen data (figure 7-16) where the presence of one is usually coupled with the absence of the other. However, the PCA of the whole data set is not able to correlate many of the original taxa with the first few components derived (figure 7-18a). This is due to the high variability in the data set. Therefore, to improve the correlations and identify the underlying trends that detect the characteristic taxa of this ecosystem, some of the taxa identified as ‘anomalous’ in the analysis of intra-plot spatial and inter-annual variability were removed.

PCA was therefore performed on the data with a variety of combinations of different samples excluded. The best correlations with the most important components were found when T113-99, T113-01 and T116-01 were removed (figure 7-18b). T113-99 was excluded because the extremely low pollen count of only 16 grains meant that the statistical reliability of the data derived from this sample was low. T113-01 was excluded on the basis of poor correlation with other samples caused by an anomalous level of Palmae (type 1) and high Poaceae (as discussed in section 7.4.1, figure 7-16). T116-01 was excluded because, compared with the other traps, this trap contained a 100x over-representation of Myrtaceae undiff. (as discussed in section 7.4.1, figure 7-15).

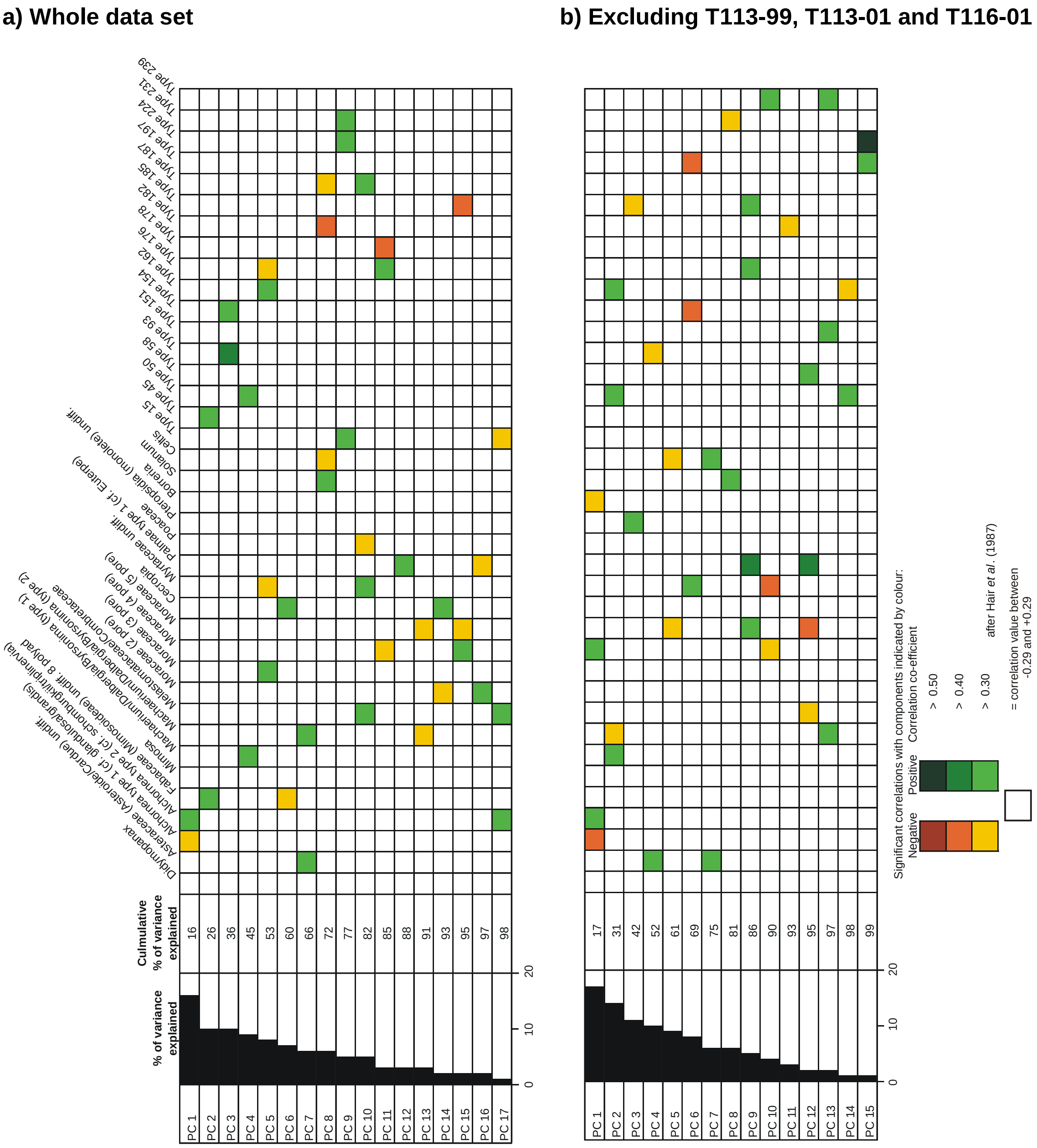


Figure 7-18: Key pollen taxa from the Cerradão. Component importance descends from the top to the bottom of the diagram.

This third PCA picks out the statistically distinctive taxa from the FC-2 plot. However, even after removing some of the samples, the high diversity of the taxa found at ≥3% abundance within the plot means that the data reduction achieved by the PCA is still poor, i.e. many components containing correlations to numerous variables are retained for analysis (figure 7-17b). Using the latent root criterion for retaining components for analysis (as discussed in section 7.1.3) means that fifteen components must be considered (figure 7-18b). These fifteen components correlate with the majority of the original variables (taxa). Therefore the PCA is not working effectively as a data reduction technique. To circumvent this problem, the cruder, ‘broken stick’ method of retaining components can be applied. This method looks at the “% of variance explained” section of figure 7-18 and retains only those components above the first point at which this graph flattens out. In figure 7-18b the first six components are retained because both component 7 and 8 explain the same portion of variance in the data (6%) so at this point the graph is ‘flat’ (for details see McGarigal *et al.,* 2000). In the light of this, only the first six components are discussed in detail in this section, the other components are presented in figure 7-18b to allow direct comparison with the analyses carried out on the other plots.

The two types of *Alchornea* pollen and the two types of *Machaerium/Dalbergia/Byrsonima* pollen correlate differently with the first and second components respectively (figure 7-18b). The opposite correlation of pollen types suggests they belong to distinct species. If they simply encompassed intra-specific pollen variability of a single taxon then they should behave in the same way in the data set because they would be subsets of the same variations in pollen rain distribution through the plot.

Over half the variance found in the Cerradão data set is explained by the first four components, which correlate positively with seven taxa: *Alchornea* (type 2), Asteraceae (Asteroide/Cardue) undiff., *Machaerium/Dalbergia/Byrsonima* (type 1), Moraceae/Urticaceae (4 pore), Pteropsidia (monolete) undiff., type 50 and type 162 (figure 7-18b). These taxa are therefore highlighted as being distinctive to the pollen assemblages of this ecosystem. The other five taxa highlighted in these first few components are those that are negatively correlated (figure 7-18b). The negative correlation of *Alchornea* (type 1), *Borreria*, *Machaerium/Dalbergia/Byrsonima* (type 2) and type 185 to the main variance in the data set marks them out as distinctive in the variation of this data set. This correlation is a product of each taxon’s dominance at specific points in the data (figures 7-14 and 7-16).

The remaining two components, that are discussed here, highlight four other taxa that are negatively correlated with the main variance in the data set: *Celtis*, Moraceae (5 pore) and types 151 and 224. Of these, *Celtis* occurs in the majority of the pollen assemblages while the other three have a more discontinuous distribution in the pollen rain (either spatially or temporally). These three taxa are highly variable because they produce a significant amount of pollen but have only a limited range of dispersal through either space or time.

It is also worth noting that neither Moraceae/Urticaeae (2 pore) nor Poaceae are highlighted in figure 7-18b, even though they are the two most abundant taxa found in the plot (figures 7-14 and 7-16). This absence is because, compared to the less abundant taxa, the variation in occurrence of these pollen types are low, i.e. they are continuously present within the samples.

In summary, the statistically distinct pollen taxa of the Cerradão are Asteraceae (Asteroide/Cardue) undiff., Moraceae/Urticaceae 4 and 5 pore, Pteropsidia (monolete) undiff., *Alchornea* types, *Machaerium/Dalbergia/Byrsonima* types, *Celtis* and type numbers 50, 93, 151, 162, 185 and 197. The pollen rain is also shown to be highly diverse and this means that the PCA is not able to summarise the variance in the data set very effectively.

7.4.4 Pollen-vegetation relationships

In figure 7-19 relative abundance of the taxa in the pollen rain from the Cerradão are compared to their percentage occurrence as individuals in the total vegetation (details of the pollen-vegetation relationship are presented in appendix XIV). All but two of the taxa that have been identified as occurring in both the vegetation and the pollen are over represented in the pollen. The under represented taxa are *Ormosia* and, perhaps surprisingly, Poaceae.

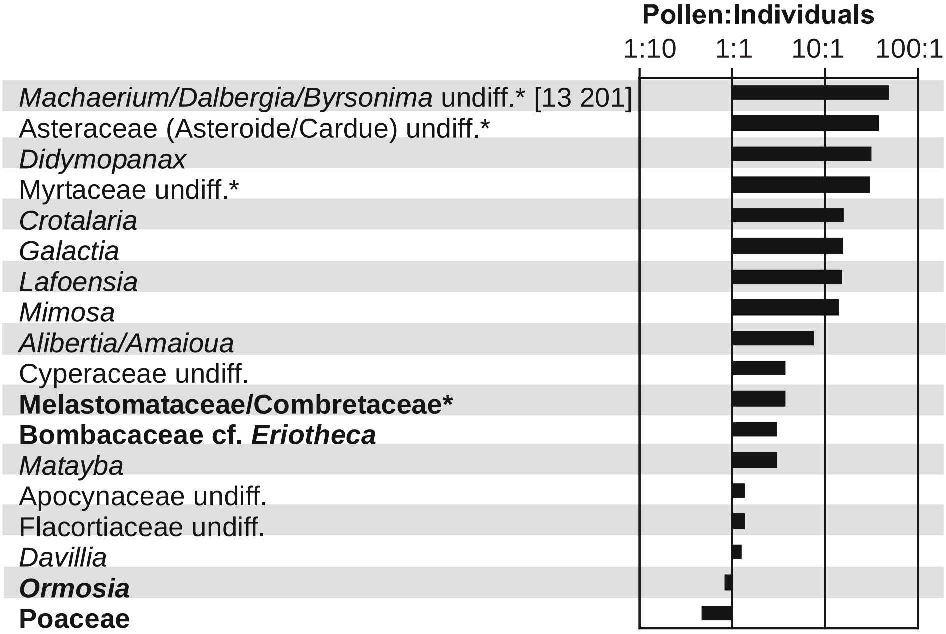


Figure 7-19: Relative abundance of taxa in pollen vs. vegetation in Cerradão. Taxa highlighted in **bold** indicate those shown to be ecologically important to the FC-2 plot by Panfil (2001). Taxa marked with an * are those shown to be statistically distinctive in section 7.4.3. Data derived from plot vegetation lists compiled by T.J. Killeen (unpublished data). For details see appendix XIV.

The under representation of grasses (Poaceae) in the pollen rain is surprising given the high pollen productivity of this taxon (Janzen, 1975). The reasons for this under-representation are unclear. Grass dominates this ecosystem (chapter 6, section 6.3.3) making up 79% of the number of individual plants recorded in the FC-2 plot (T.J. Killeen, unpublished data; appendix XIV). This overwhelming dominance of Poaceae in the vegetation is dwarfing the slight dominance of this taxon in the pollen (figure 7-19). The reason for the under representation may be due to one or more of the following reasons: i) only a small portion of the grasses flower every year, ii) very effective dispersal of the pollen grains away from the plot, or iii) an external factor, such as fire or drought, restricted or prevented flowering. However, it must also be remembered that the Cerradão sampled in this plot is at the woodier end of the Cerrado (*sensu lato*) ecosystem (chapter 6, figure 6-4). Therefore, it is likely that pollen rain from the more open forms of Cerrado (*sensu lato*) would have a relatively higher proportion of grass pollen present. These findings lend support to the caution placed upon the interpretation of Poaceae in the fossil pollen record by Bush (2002) and suggest that it is an unreliable indicator of this grass dominated ecosystem even though it is, in comparison to other pollen types found in the plot, the highest pollen producer in percentage terms.

There are three other taxa found in the pollen rain from the plot that include species identified by Panfil (2001) as important (figure 7-19). One, *Ormosia*, is under-represented in the pollen and the other two, cf. *Eriotheca* and Melastomataceae/Combretaceae, are both slightly over-represented (figure 7-19). *Ormosia* and cf. *Eriotheca* occur at very low abundances, relative to other taxa, in both the pollen and the vegetation, although their over-representation shows that if present in the vegetation they are likely to be present in the pollen rain also. Melastomataceae/Combretaceae pollen occurs consistently in the pollen rain from the Cerradão at c. 3% (figure 7-14 and 7-16), although its percentage occurrence in the pollen rain is slightly above the total percentage occurrence of the four Melastomataceae species found within the plot (T.J. Killeen, unpublished data; appendix XIV). This reveals that this taxon is only slightly over-represented in the pollen rain.

Two taxa highlighted as distinctive in the pollen rain of the plot are reported in the vegetation list from the plot (figure 7-19). Both the Asteraceae (Asteroide/Cardue) undiff. and *Machaerium/Dalbergia/Byrsonima* undiff. are shown to be over-represented in the pollen by greater than 10x the number of individuals of these taxa present within the plot. These taxa are only of low abundance in the vegetation of the plot (T.J. Killeen, unpublished data) indicating that they are high pollen producing taxa that are likely to be recorded in the pollen rain even if only a few individuals are present in the vegetation. Also, Myrtaceae undiff., *Didymopanax*, *Crotalaria*, *Galactia*, *Lafoensia* and *Mimosa* are significantly over-represented in the pollen rain, indicating that they are likely to be present in the pollen rain if they are present in the vegetation of a region.

In summary, taxa demonstrated to be important components of the vegetation of the plot by Panfil (2001) that are identifiable in the pollen rain are Melastomataceae/Combretaceae and cf. *Eriotheca*, which are over-represented in the pollen, and *Ormosia* and Poaceae, which are under-represented in the pollen. In addition three taxa, Asteraceae (Asteroide/Cardue) undiff., *Machaerium/Dalbergia/Byrsonima* undiff. and Myrtaceae undiff., are over-represented in the pollen rain relative to their proportion of the vegetation.

7.4.5 Cerradão pollen signature

Based upon the four stages of analysis discussed above (sections 7.4.1 to 7.4.4) a characteristic pollen signature has been established for the Cerradão (table 7-7) (for full details see appendix XIII).

Pollen taxa	Intra-plot	Inter-annual	Statistical	Vegetation
Alchornea (type 2)	✓	✓	✓	
Celtis	✓	✓	✓	
Moraceae/Urticaceae	✓	✓	✓	
Didymopanax	✓	✓		✓
Melastomataceae/Combretaceae	✓	✓		✓
Myrtaceae undiff.	✓	✓		✓
Poaceae	✓	✓		✓
Cecropia	✓	✓		
Palmae (type 1)	✓	✓		
Solanum	✓	✓		
Type 162	✓		✓	
Type 15	✓			
Alchornea (type 1)		✓	✓	
Type 176		✓		
Asteraceae (Asteroide/Cardue) undiff.			✓	✓
Machaerium/Dalbergia/Byrsonima (type 1)			✓	✓
Machaerium/Dalbergia/Byrsonima (type 2)			✓	✓
Borreria			✓	
Lafoensia			✓	
Pteropsidia (monolete) undiff.			✓	
Type 50			✓	
Type 93			✓	
Type 151			✓	
Type 185			✓	
Type 197			✓	
Alibertia/Amaioua				✓
Apocynaceae undiff.				✓
Bombacaceae cf. *Eriotheca*				✓
Crotalaria				✓
Cyperaceae				✓
Davillia				✓
Flacortiaceae				✓
Galactia				✓
Matayba				✓
Mimosa				✓
Ormosia				✓

Table 7-7: Pollen signature selection criteria for FC-2. ✓ indicates identified as important in the corresponding section. Marks were given on the following basis: i) intra-plot = present in at least half the samples, ii) inter-annual = consistent presence year on year at any one location, iii) statistical = highlighted in PCA of whole data set excluding samples T113-99, T113-01 and T116-01, and iv) vegetation = presence in the trees >10 cm d.b.h. of the plot (T.J. Killeen, unpublished data).

Based upon the scores in table 7-7 taxa were identified as major or minor components of the pollen rain characteristic of this ecosystem. Firstly, those taxa scoring three or more marks were considered major taxa (for the same reasons as discussed in section 7.2.5). These were divided into local (table 7-8a) and regional (table 7-8b) taxa on the basis of the presence of the taxon in the local vegetation. Two more taxa were added to each category: i) Palmae (type 1) and *Solanum* were classified as major local taxa because both are important in the vegetation of this ecosystem (Panfil, 2001) even though they are not recorded as present as trees >10 cm d.b.h. in FC-2 plot (T.J. Killeen, unpublished data), and ii) *Cecropia* and *Alchornea* (type 1) were upgraded to major regional taxa because of their consistent presence in the pollen rain and given their absence from the vegetation in the plot (Panfil, 2001) and the plant community (Killeen and Schuleberg, 1998).

The Cerradão pollen signature is composed of eleven major components, six of which are derived from the local pollen rain and the remainder are probably from other ecosystems nearby (table 7-5a and b). There are also twenty-five minor taxa that occur either at low levels or are distributed unevenly in space and/or time through the plot which have been identified as characteristic of this plant community (table 7-6).

a) Local pollen

MAJOR	**Percentage occurrence**		
pollen taxa	**Minimum**	**Median**	**Maximum**
Poaceae	2	9	38
Solanum	0	3	38
Palmae (type 1)	0	2	19
Melastomataceae/Combretaceae	0	2	13
Myrtaceae undiff.	0	1	43
Didymopanax	0	1	6

b) Regional pollen

MAJOR	**Percentage occurrence**		
pollen taxa	**Minimum**	**Median**	**Maximum**
Moraceae/Urticaceae	8	24	44
Cecropia	0	2	8
Celtis	0	1	8
Alchornea (type 2)	0	1	7
Alchornea (type 1)	0	1	6

Table 7-8: Cerradão pollen signature, major components.

The low median values and high maximum percentages for the major components reflect the discontinuous nature of the pollen rain from the Cerradão (table 7-8a) (as discussed in sections 7.4.1 and 7.4.2). Of the major taxa, Poaceae is dominant and is always present in the pollen rain, most likely because grass overwhelmingly dominates the vegetation of the ecosystem (Panfil, 2001) even though it is rather under-represented in the pollen rain (section 7.4.4). This consistent, but relatively low-level, occurrence of grass pollen means that other plants producing pollen in high quantities at discrete locations in the plot can become locally dominant (e.g. *Solanum* or Myrtaceae undiff., figure 7-13). Therefore the pollen rain signal from this ecosystem is highly variable as discussed in section 7.4.3. Even given this uneven distribution of the pollen rain, on average five out of the six major taxa occur in each of the FC-2 samples indicating that pollen rain from this ecosystem can be expected to contain the majority of the major components.

The signal is further complicated by the input from the evergreen forest c.10 kilometres away (chapter 6, figure 6-11). As discussed for the dry forest (section 7.3.5) Moraceae/Urticaceae, *Cecropia* and *Celtis* pollen are likely to be originating predominantly from the moist evergreen forest ecosystems nearby. In addition, to this the two types of *Alchornea* pollen must also originate from parent vegetation outside the plot because *Alchornea* does not occur in the vegetation of the plot (Panfill, 2001).

The twenty-five minor taxa shown to be indicative of the Cerradão also reflect the discontinuous distribution of the pollen rain from this plant community. No one taxon is present in over half the samples taken and on average only six of the twenty-five taxa appear in any one sample. To further complicate matters, eight of the pollen types could not be identified.

MINOR pollen taxa	**Frequency of occurrence (% samples)**
Pteropsidia (monolete) undiff.	43
Asteraceae (Asteroide/Cardue) undiff.	38
Lafoensia	38
Type 162	38
Borreria	33
Type 93	29
Machaerium/Dalbergia/Byrsonima (type 1)	24
Cyperaceae	14
Matayba	14
Type 197	14
Flacortiaceae	10
Machaerium/Dalbergia/Byrsonima (type 2)	10
Type 15	10
Type 50	10
Type 151	10
Apocynaceae undiff.	5
Bombacaceae cf. *Eriotheca*	5
Alibertia/Amaioua	5
Crotalaria	5
Davillia	5
Galactia	5
Mimosa	5
Ormosia	5
Type 176	5
Type 185	5

Table 7-9: Cerradão pollen signature, minor components.

Despite the high diversity of the minor taxa, and an inability to identify eight pollen types, a number of the taxa can be highlighted as being particularly useful in characterizing the pollen rain of the Cerradão plot. The identified minor taxa that most frequently occur are fern spores, Asteraceae (Asteroide/Cardue) undiff., *Lafoensia*, *Borreria* and *Piper*, which represent the ground cover and under-story of the Cerradão. This collection of taxa, coupled with the presence of other minor taxa in the pollen rain, reflects the high diversity of pollen types that should be expected in the pollen rain from this ecosystem.

In summary, the pollen signature of the Cerradão is one that is dominated by grass with varying amounts of *Solanum*, Palm, Melastomataceae/Combretaceae, Myrtaceae undiff. and *Didymopanax* pollen. In addition there is a high diversity of pollen types with the occasional presence of fern spores, Asteraceae (Asteroide/Cardue) undiff., *Lafoensia*, *Borreria* and *Piper*. The strong grass signal, in conjunction with floristic similarities (as discussed in chapter 6), indicates that this characteristic pollen signal can be considered as representative of the wider Cerrado (*sensu lato*) ecosystem. The strength of this pollen signal is likely to be affected by the proximity of other ecosystems. In the case of FC-2 there is a strong detectable input from the nearby moist evergreen forests.

7.5 Summary

In this chapter a pollen signature is defined for three ecosystems. This was achieved by determining spatial and temporal variations, identifying statistically distinctive pollen types, and examining the pollen-vegetation relationships. These analyses have identified fifteen taxa that in various proportions are shown to be characteristic of each of the three ecosystems (figure 7-20).

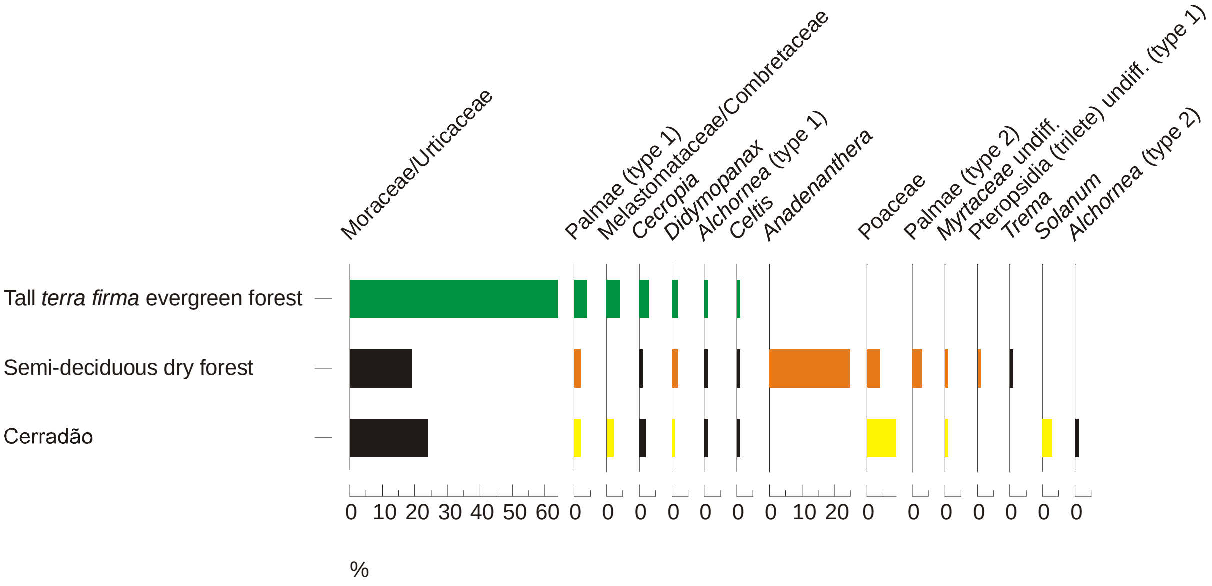


Figure 7-20: Ecosystem pollen signatures, major taxa. Percentage occurrence levels are median values. Taxa that comprise a major local component of the ecosystems local pollen rain signature are coloured. Taxa are ordered left to right by greatest abundance in each ecosystem, first the *terra firma* evergreen forest, then the semi-deciduous dry forest and finally the Cerradão.

From figure 7-20 it can be seen that there are distinct differences between the pollen rain collected from each of the ecosystems. However, figure 7-20 also reveals that most of the taxa are not unique to an ecosystem. Therefore, before these modern pollen data can be applied to the interpretation of the fossil pollen record it is first necessary to establish the degree to which they can be used to separate the ecosystems. In the next chapter these distinctive pollen signatures are analysed to determine the most effective method of distinguishing the ecosystems using the pollen alone.

Chapter 8

Palynological differentiation of ecosystems

Chapter 8

Palynological differentiation of ecosystems

In chapter 7 the distinctive pollen signatures of the three ecosystems were established. The aim of this chapter is to statistically compare and contrast the pollen spectra from each ecosystem to determine whether or not they can be reliably distinguished from one another palynologically. This achieves the third aim of this project, as defined in chapter 2 (section 2.3). Firstly, the main differences between the groups of major taxa that characterize each ecosystem are identified using principal components analysis (PCA) (section 8.1). Then the same analysis is performed on an independent data set comprised of pollen spectra obtained from surface samples of lakes within different ecosystems (section 8.2). This serves two purposes: i) it tests the robustness of the divisions established from the pollen trap data, and ii) it gives an insight into the effect of taphonomic processes on the accumulation of pollen rain in lakes, and so moves a step closer to understanding fossil pollen records that are collected from lake sediments. In section 8.3 three other ways of examining the pollen data are explored to see if any further ecological information can be gleaned. These are: i) the minor taxa, ii) the taxa diversity, and iii) the pollen accumulation rates (PARs). Then, in section 8.4, the palynological differentiations established in this chapter are placed within the ecological context of the ecosystems.

8.1 Major taxa

To establish how effectively the major taxa, defined for each ecosystem in chapter 7 (sections 7.2.5, 7.3.5 and 7.4.5), can be used to differentiate between the ecosystems, a method of multivariate analysis had to be found that allowed any consistent differences between the samples to be identified. A covariance principal components analysis (PCA) was found to perform this job well and had the advantage over other multivariate statistical techniques of relating the derived components back to the original variables (taxa). This allows the reasons for the variation between the samples to be assessed.

8.1.1 Data and statistical techniques used

A covariance PCA identifies the greatest variance within a data set (McGarigal *et al*., 2000). This differs from the correlation PCA used in chapter 7 in the following way. A covariance PCA considers the absolute magnitudes of the variables (taxa), whereas the correlation PCA considers the relative variability of the variables (taxa) (for a detailed explanation see McGarigal *et al.*, 2000). When applied to pollen data the principal components derived from the covariance PCA explain the greatest variability within the data set and therefore determine which taxa are 'most different' between the samples. As the aim of this section is to determine the extent to which the pollen rain from these ecosystems can be differentiated from one another, this covariance PCA was deemed to be a suitable statistical technique to use.

The covariance PCA is applied to the percentage abundance and PAR data of the major taxa identified in chapter 7 (sections 7.2.5, 7.3.5 and 7.4.5). Both these data sets were log transformed to improve normality (for the reasons discussed in chapter 7, section 7.1.3).

8.1.2 Results and discussion

Figures 8-1a and b are bi-plots of the first two principal components derived from the percentage and PAR data. The x-axes show the correlation of the samples (traps) with principal component 1 and the y-axes the correlation with principal component 2. The circles, colour coded by ecosystem, represent the traps and are positioned on the graph according to the strength of the correlation of their major taxa to each of these components. The significance of the locations of the samples (traps) on the graphs is shown by the blue numbers, which identify the original pollen taxa (the variables) (see table 8-1). The length of the associated blue arrows indicates the strength of the correlation of that part of the graph with the occurrence of that particular taxon, e.g. in figure 8-1a pollen type 72 (*Anadenanthera*) is strongly present in those samples grouped towards the left of the graph, i.e. those samples that are negatively correlated with principal component 1. Analyses of further components did not show any meaningful ecological divisions and were therefore not presented.

a) Pollen taxa

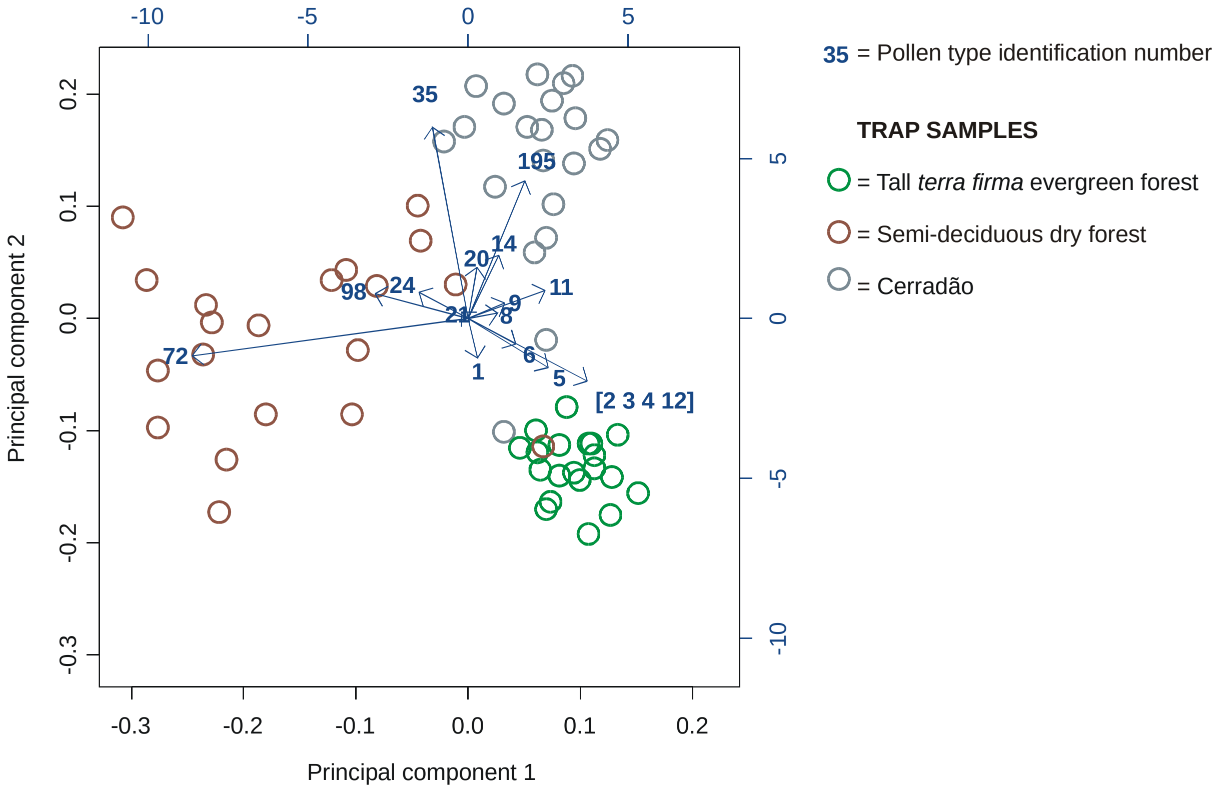
Reference number	Taxa
1	*Didymopanax*
2	Moraceae/Urticaceae (2 pore)
3	Moraceae/Urticaceae (3 pore)
4	Moraceae/Urticaceae (4 pore)
5	Melastomataceae/Combretaceae
6	Palmae (type 1)
8	*Celtis*
9	*Alchornea* (type 1)
11	*Cecropia*
12	Moraceae/Urticaceae (5 pore)
14	*Alchornea* (type 2)
20	Myrtaceae undiff.
21	*Trema*
24	Pteropsidia (trilete) undiff. (type 1)
35	Poaceae
72	*Anadenanthera*
98	Palmae (type 2)
195	*Solanum*

b) Combined taxa

Reference numbers	Taxa
[2 3 4 12]	Moraceae/Urticaceae undiff.
[6 98]	Palmae undiff.
[9 14]	*Alchornea* undiff.

Table 8-1: Major taxa pollen reference numbers. Counts for the different Moraceae/Urticaceae types were combined because there was no way of taxonomically defining these differences. The other taxa were grouped to allow correlation with the lake surface pollen data that had been identified, by Mayle *et al.* (2000), Burbridge *et al.* (in press) and Mayle (unpublished data) (see analyses in section 8.2.2).

a) Percentage data



b) Pollen accumulation rate data

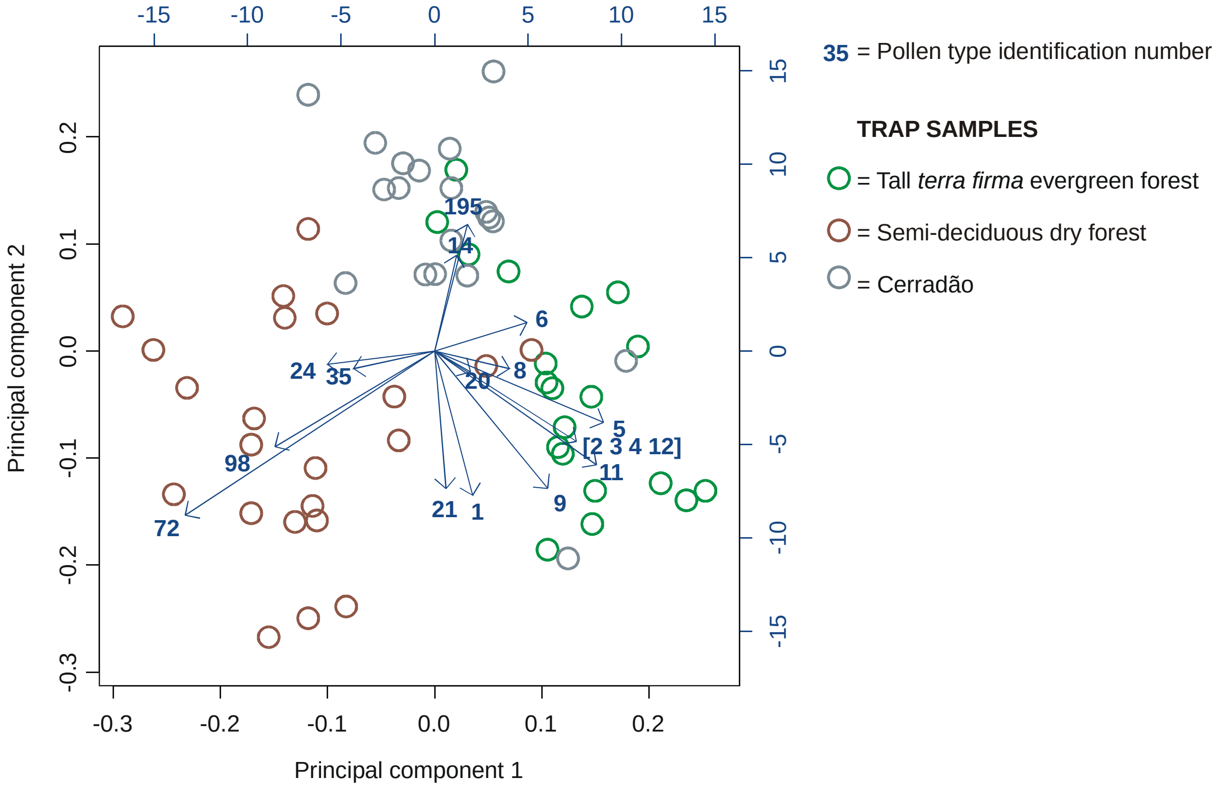


Figure 8-1: Taxa explaining main variance between ecosystems. The bi-plots are derived from covariance PCA of the major taxa. In a) the first two components explain 44% of the variation in the data set and, in b) the first

two components explain 41% of the variation. For pollen reference numbers see table 8-1. See appendix XV for details.

The grouping of the traps from the different ecosystems into distinct sections of the graphs (i.e. similarly coloured circles are clustered together) reveals that the ecosystems are differentiated from one another by differences in the assemblages of the major pollen taxa (figure 8-1). The blue numbers present in the corresponding sections of the graph indicate the taxa that are differentiating that part of the graph from the others.

The use of all the trap samples from all the ecosystems in the PCA allows the range of values found within each ecosystem to be assessed. In this way the spatially and/or temporally discrete trap samples present a 'snap shot' of the pollen rain at various points within the ecosystem. These 'snap shots' are highly variable in space and time within each ecosystem (chapter 7). Comparison between this fine scale variability within the pollen rain collected in the traps and the larger spatial and temporal scale variability found within the lake surface sediments may help to explain variability within the fossil pollen records obtained from lake sediments (figure 8-2).

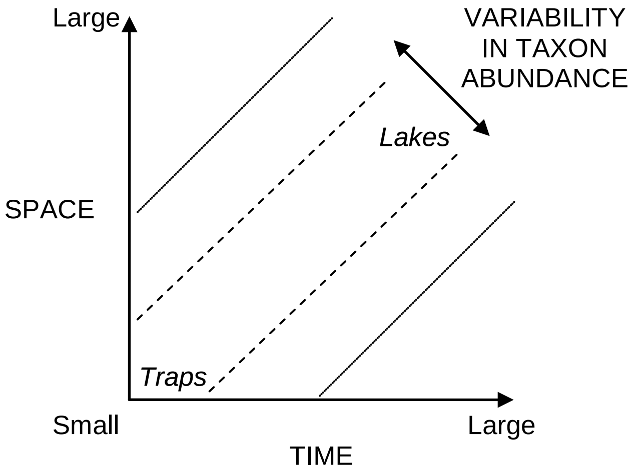


Figure 8-2: Theoretical taxon variability at different spatial and temporal scales.

The PCA of the percentage data, presented in figure 8-1a, shows that: i) the traps from the tall *terra firma* evergreen forest are differentiated from the semi-deciduous dry forest by the first component (x-axis), and ii) the Cerradão is differentiated from both the forest ecosystems by the second component (y-axis). The PCA of the PAR data, presented in figure 8-1b, also splits the three ecosystems on the first two axes, although the divisions are less distinct than in the percentage data because there are large disparities between the ecosystems' PARs, e.g. median values are: 6642 grains cm^{-2} year^{-1} for the tall *terra firma* evergreen forest, 1860 grains cm^{-2} year^{-1} for the semi-deciduous dry forest and 1061 grains cm^{-2} year^{-1} for the Cerradão (appendix VII). These differences in pollen abundance affect the levels of importance attributed to the different taxa by the PCA.

In figure 8-1 each of the ecosystems is shown to be distinguishable from the other ecosystems by a small number of taxa (table 8-2).

Ecosystem	Plant community	Plot	Pollen taxa
Moist *terra firma* evergreen forest	Tall *terra firma* evergreen forest	Los Fierros 1 (LF-1)	Moraceae/Urticaceae undiff. - Melastomataceae/Combretaceae - Palmae (type 1) - *Didymopanax*
Deciduous and semi-deciduous dry forest	Semi-deciduous dry forest	Acuario 2 (AC-2)	*Anadenanthera* - Palmae (type 2) - Pteropsidia (trilete) undiff.
Terra firma savannah	Cerradão	Los Fierros, Cerradão (FC-2)	Poaceae - *Solanum* - *Alchornea* (type 2) - Myrtaceae undiff.

Table 8-2: Ecosystem distinctive taxa.

The divisions shown by the pollen percentage data are generally supported by the PAR data (figure 8-1b) with two notable exceptions. Firstly, in contrast to the percentage data (figure 8-1a) the PAR data suggest that Poaceae is more diagnostic of the semi-deciduous dry forest than the Cerradão (figure 8-1b). This discrepancy is a product of the difference in the total PARs from the two ecosystems (appendix VII). In the Cerradão the total PAR is low and therefore Poaceae, a relatively high pollen producing taxon in comparison to the other taxon in this plot, constitutes an important component of the assemblage. In the semi-deciduous dry forest the total PAR is higher so, even though the actual PAR of Poaceae in the semi-deciduous dry forest is higher than in the Cerradão, the relative (percentage) importance of the taxon is lower. Secondly, the tall *terra firma* evergreen forest trap data are more widely spread by the analysis performed on the PAR data than that performed on the percentage data (compare figure 8-1a with b) due to the relative importance of Moraceae/Urticaceae undiff. In the percentage data the tall *terra firma* evergreen forest trap samples are defined primarily by the overriding relative dominance of this taxon (figure 8-1a), whereas in the PAR data abundances of different pollen types are absolute and independent from one another. Consequently, the importance of the other taxa are not affected by the relative dominance of the Moraceae/Urticaceae undiff. This means that the tall *terra firma* evergreen forest trap samples are positioned in figure 8-1b without the over-riding influence of Moraceae/Urticaceae. This reveals those taxa that are important in distinguishing this ecosystem, although they are less abundant, i.e. *Alchornea* (type 1), *Cecropia*, *Celtis* and Palmae (type 1).

The identification of co-variation of the pollen assemblages extracted from the same ecosystem (i.e. the samples from the same plot are clustered together in figure 8-1) demonstrates that the major taxa identified in chapter 7 not only characterise that ecosystem but also serve to differentiate that ecosystem from the other two.

8.2 Lake surface sample data

To test i) the robustness of the palynological divisions determined in the preceding section, and ii) to gain an insight into the effect of the processes of deposition on the pollen assemblages obtained from lakes, the same analysis was applied to pollen counts from lake surface samples. The samples were taken from a depth of 0-1 centimetres, from roughly central positions in the lakes and were prepared using standard pollen preparation procedures, e.g. Moore *et al.* (1991).

Pollen traps and lakes (from which fossil pollen records are often collected) capture pollen in somewhat different ways. A pollen trap set up within an ecosystem: i) captures only airborne pollen, ii) is of pre-determined dimensions, iii) is placed at a known location, iv) is left in the field for known amount of time, and v) is surrounded by the vegetation type of interest. Lake sediments, on the other hand, *may* contain: i) airborne pollen, ii) river washed pollen, iii) pollen from plants within the lake, iv) pollen mixed in an unknown manner over, v) an unknown amount of time, and vi) from a variety of different vegetation types. To assess the applicability of the divisions established in section 8.1.2 to the pollen rain collected in lakes the same analysis applied to the pollen trap data was applied to pollen spectra extracted from surface samples taken from lakes surrounded by known ecosystems. This comparison between the traps and lake surface sediments allows differences in the taphonomic processes to be assessed (figure 8-3).

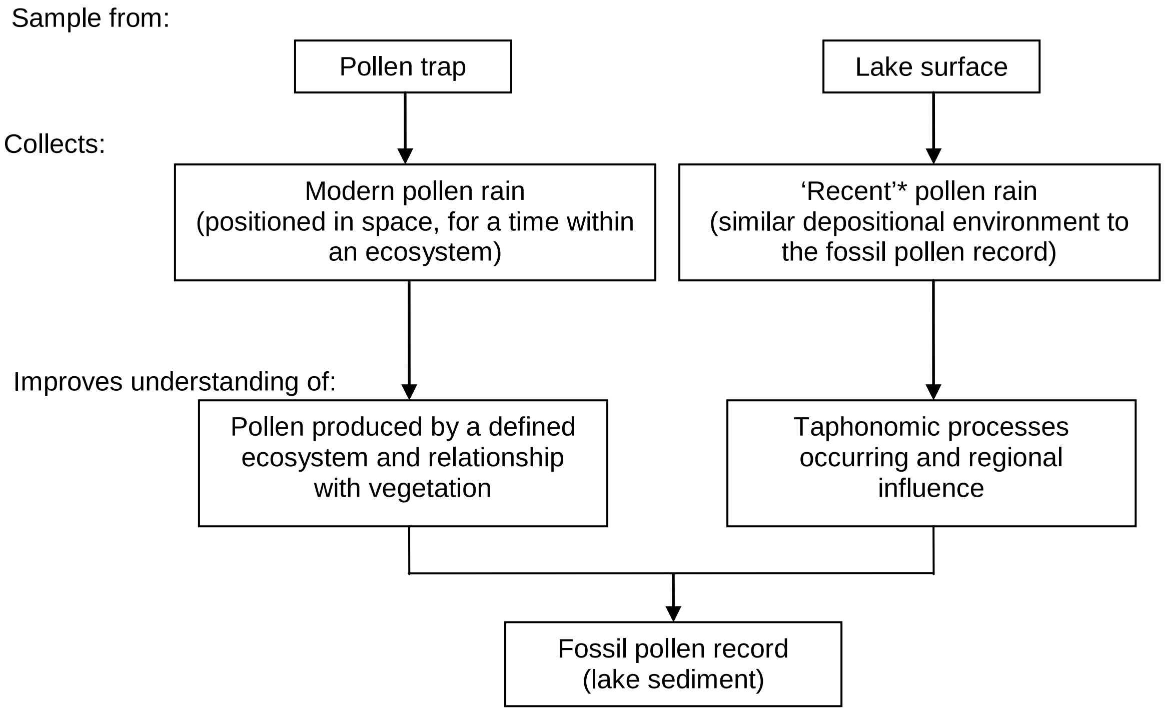


Figure 8-3: Achieving better understanding of the fossil pollen record. By studying and comparing different aspects of modern and 'recent'* pollen rain and their relationships the fossil pollen record can be better understood. * = 'recent' pollen rain is that collected in the first cm of lake sediment (exact duration of accumulation is unknown).

8.2.1 Data and statistical techniques used

Log transformed pollen percentage data from surfaces samples of five lakes were analysed using the same covariance PCA as was applied to the pollen trap data (as described in section 8.1.1) (table 8-3).

The PCA was performed on the lake surface sample data in two stages: i) on the lake data alone to discover if pollen data from the lakes distinguishes between the ecosystems in the same way as the traps (figure 8-2), and ii) on the lake data in conjunction with the trap data to identify any differences between the two methods of collecting modern pollen rain (figure 8-3). These analyses were carried out using the percentage pollen data only, because it is impossible to calculate PARs from the lake samples that are comparable to those calculated from the traps. This is because of the amount of time pollen has been accumulating in the lake surface samples is not known to the same accuracy as it is with pollen traps, i.e. a pollen trap can be placed in the field for a determined amount of time, whereas lake surface samples can only be attributed to rough estimates that can vary from the last 10, 50 or 200 years dependant on sediment accumulation rates.

Laguna	Dominant ecosystem	Analyst	Reference
Bella Vista	Moist *terra firma* evergreen forest	F.E. Mayle	Mayle *et al.* (2000)
Chaplin	Moist *terra firma* evergreen forest	R.E. Burbridge	Mayle *et al.* (2000); Burbridge (2001)
La Gaiba	Deciduous and semi-deciduous dry forest	W.D. Gosling	Unpublished data
Mandioré	Deciduous and semi-deciduous dry forest	W.D. Gosling	Unpublished data
Socórros	Deciduous and semi-deciduous dry forest	F.E. Mayle	Unpublished data

Table 8-3: Lake surface sample data provenance. For full location details and pollen count data see appendix XVI.

The ecosystems that surround these lakes represent two of the three ecosystems for which characteristic modern pollen spectra have been established (table 8-3). The ecological classifications for the plots and their relationship with the ecosystems that surround the lakes were discussed in chapter 6 (section 6.3; table 6-4). To recap: i) the tall *terra firma* evergreen forest found in LF-1 is typical of the moist *terra firma* evergreen forest ecosystem, ii) the semi-deciduous dry forest of AC-2 is representative of the deciduous and semi-deciduous dry forest ecosystem, and iii) the Cerradão of the FC-2 plot is part of the *terra firma* savannah ecosystem. Despite these ecosystems being dominant around the lakes, the input of pollen into the lakes is likely to be also derived from the other ecosystems that are present in the surrounding landscape. The following ecosystems are in close proximity to these lakes: i) Bella Vista - inundated savannah (Mayle *et al.*, 2000; Burbridge *et al.*, in press), ii) La Gaiba - the Pantanal wetlands, iii) Mandioré - the Pantanal wetlands and *terra firma* savannah, and iv) Socórros - pasture.

8.2.2 Results and discussion

In figure 8-4 the lake surface samples, represented by the colour coded letters, are divided in a similar way to the trap samples from the same ecosystems (figure 8-1a). Principal component 1 (x-axis) splits the samples from lakes surrounded predominantly by deciduous and semi-deciduous dry forest from those surrounded predominantly by moist *terra firma* evergreen forest. Principal component 2 (y-axis) does not distinguish the two forest types but does split the dry forest samples. This is possibly indicative of regional differences in the composition of the dry forests or varying input from the other ecosystems in the vicinity of the lakes, e.g. Laguna Soccóros differs from the other two dry forest lake on the second principal components axis by a greater proportion of Myrtaceae undiff. (number 20) and less palm ([9

98]) (figure 8-4). The bi-plots of the first two principal components only are shown because other components were found not to have any clear ecological meaning.

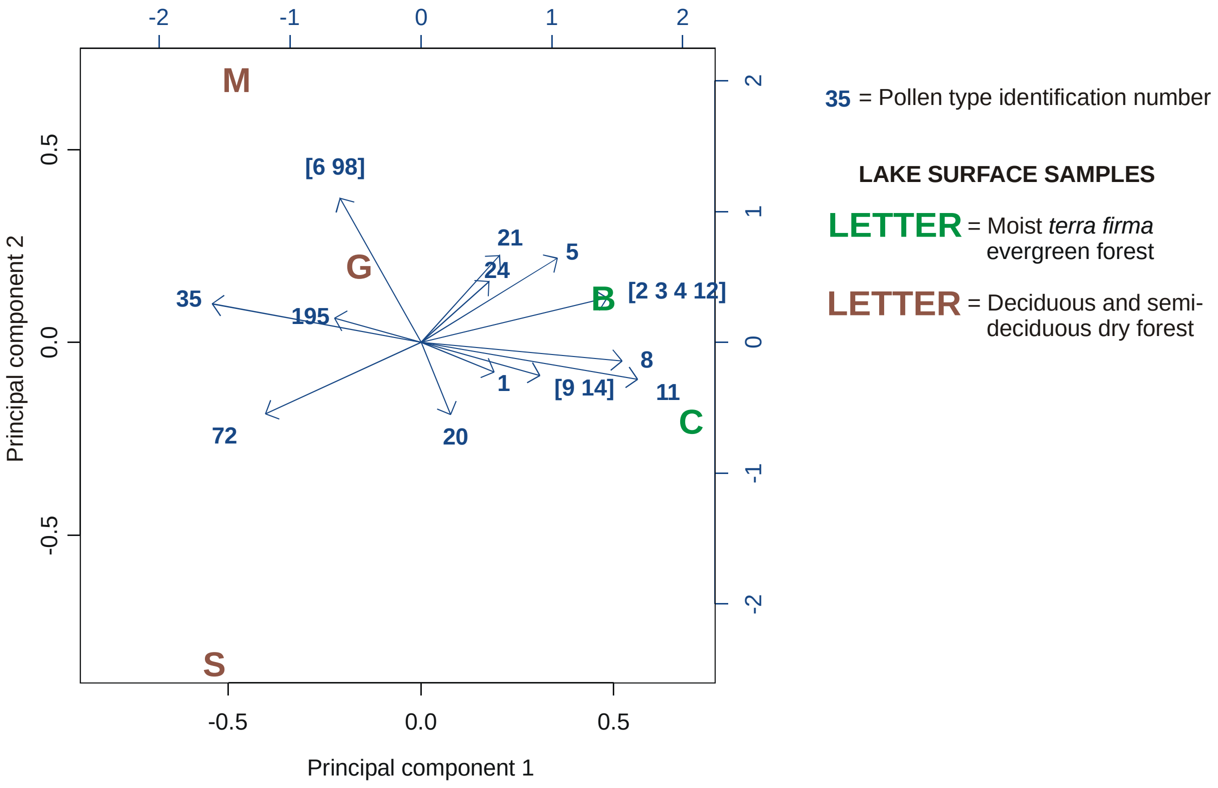


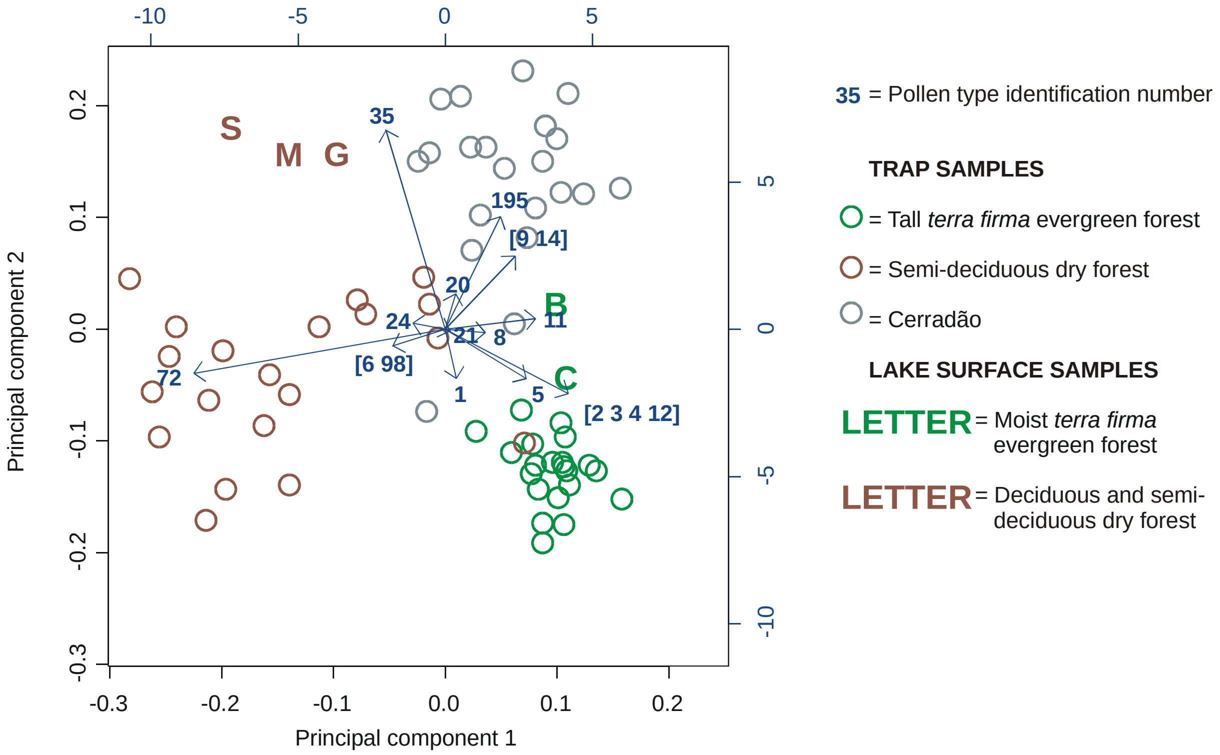
Figure 8-4: Taxa explaining main variance between lake surface samples. The first two components explain 84% of the variance in the data set. Laguna: C = Chaplin, B = Bella Vista, G = La Gaiba, M = Mandioré and S = Soccóros. For full details see appendix XV.

Comparison between figure 8-1 and 8-4 reveals that these two ecosystems are being differentiated similarly in both the trap and lake surface data. The semi-deciduous dry forest trap samples are distinguished by an *Anadenathera* - Palmae (type 2) - Pteropsidia (trilete) undiff. (type 1) assemblage (figure 8-1a), while the lake samples surrounded by the deciduous and semi-deciduous dry forest ecosystem are defined by a Poaceae - *Anadenanthera* - Palmae undiff. assemblage (figure 8-4). The notable differences between the trap and lake assemblages are that the lake samples have: i) more Poaceae, ii) a presence of *Solanum*, and iii) an absence of Pteropsida (trilete) undiff. The importance of Poaceae and *Solanum* to the dry forest is elevated in the lake samples because there are no lake samples from savannah ecosystems for comparison, and the dry forest contains more of these taxa than the moist *terra firma* evergreen forest. The absence of the fern spores is more difficult to explain and may suggest that importance of this taxon in defining this ecosystem is regionally variable. The trap samples collected from the tall *terra firma* evergreen forest show that a Moraceae/Urticaceae undiff. - Melastomataceae/Combretatceae - Palmae (type 1) - *Didymopanax* assemblage is characteristic (figure 8-1a), while the lake surface samples taken from lakes surrounded by the corresponding ecosystem contain a Moraceae/Urticaceae - *Cecropia* - *Celtis* -Melastomataceae/Combretaceae assemblage. These differences show that the lake surface samples contain some of the less abundant taxa identified as important for this ecosystem in the analysis of the traps PAR data (figure 8-1b).

To compare the trap sample and lake surface sample data sets, both data sets were analysed together in a PCA (as described in section 8.2.1) (figure 8-5). If there was no significant difference in the manner in which these two sampling environments collected the pollen rain, then the pollen assemblages obtained from the ecosystems should be positioned in the same area of the graph, regardless of whether they were obtained from pollen traps or lake surface samples.

In figure 8-5a the lake surface samples from the deciduous and semi-deciduous dry forest lakes are shown to be distinct from the moist *terra firma* evergreen forest lakes on the first and second principal component axes. However, the lake samples from both ecosystems are split from the trap samples of the corresponding ecosystem on the second axis by elevated levels of Poaceae. High Poaceae found in the lake samples has resulted in all of them being skewed towards the Cerradão traps. This higher level of grass pollen in the lake surface

a) All major taxa



b) Excluding Poaceae (35)

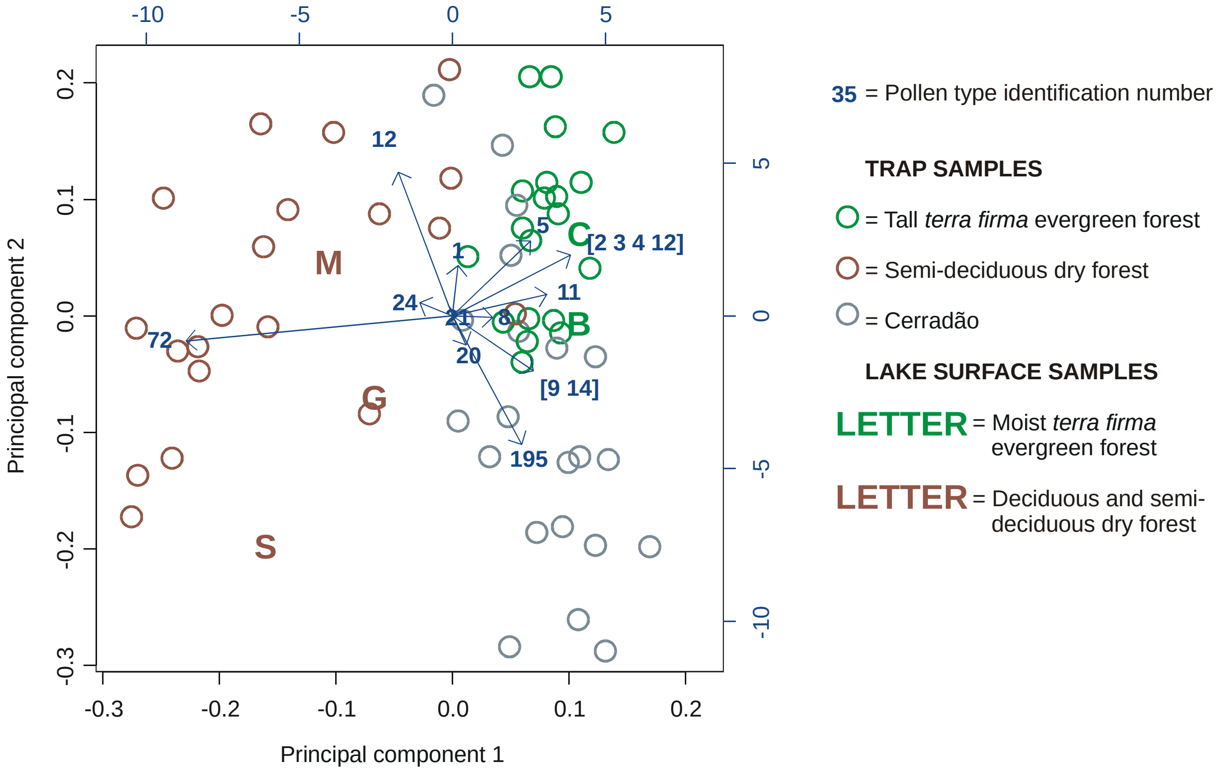


Figure 8-5: Comparison of trap and lake surface sample data. a) Principal components 1 and 2 explain 45% of the variance in the data. b) Principal components 1 and 2 explain 46% of the variance in the data. Laguna: C = Chaplin, B = Bella Vista, G = La Gaiba, M = Mandioré and S = Soccóros. For details of PCA see appendix XV. For reference numbers see table 8-1.

samples is probably a product of aquatic grasses found in and around the lakes and input from grass dominated ecosystems in the region (as discussed in section 8.2.1).

In figure 8-5b the exclusion of Poaceae allows the PCA to place the lake surface samples within the range of values found for the forest ecosystems. However, the differentiation between the forest and savannah ecosystems is lost from component 2, although there is still a split of the majority of the samples between the Cerradão (towards the bottom of the graph) and the tall *terra firma* evergreen forest (towards the top) due to a greater abundance of *Solanum*, *Alchornea* undiff. and Myrtaceae undiff. in the Cerradão.

These analyses demonstrate that the major components of the modern pollen rain data extracted from the pollen traps, as defined in chapter 7, can be used to relate pollen spectra collected from lake surface samples to the ecosystems that surround the lakes. This has been achieved despite the different taphonomic processes that the pollen is subjected to in the two different methods of collection (as was discussed in section 8.2.1). The only caveat to this is that the interpretation of Poaceae should be carried out with caution as aquatic grasses and regional inputs may contribute a significant amount of pollen into lakes.

8.3 Other techniques

In order to determine if further ecological information could be extracted from the modern pollen data collected from the traps, three other methods of analysis were performed looking at different aspects of the pollen spectra: i) the minor taxa, ii) the diversity, and iii) the PARs. The degree to which these analyses were successful is discussed in the following three sub-sections.

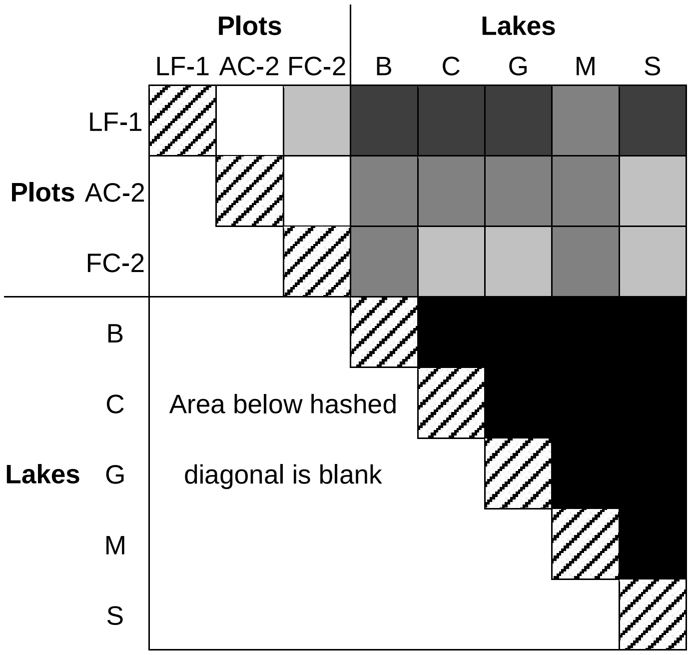
8.3.1 Minor taxa

In addition to the major taxa (discussed above) a list of taxa of minor importance was also constructed for each of the three ecosystems (see chapter 7, sections 7.2.5, 7.3.5 and 7.4.5). These lists contain the pollen taxa that are either represented in the vegetation of the plot or occur in high but spatially and/or temporally restricted abundance in the pollen rain. These minor taxa should therefore also be of diagnostic of the pollen rain from the ecosystems and could supply corroborating evidence for the origin of the pollen rain assigned using the major taxa. This could be particularly useful if the outcome of analysis of the major taxa was not clear-cut.

To discover if any more ecological information could be extracted using the presence of minor taxa, the extent to which the three ecosystems could be further differentiated had to be determined. To achieve this, bivariate analysis was used to determine the extent to which the presence or absence of these taxa correlated between the ecosystems (plots) and the lake surface samples (figure 8-6). The correlation method used was the Sokal and Sneath 1 measurement. This method was chosen because it correlates bivariate data and places greater weight on presences, rather than absences, particularly useful for dealing with these pollen data because only a small number of the taxa are required to assign an ecosystem to a pollen assemblage, i.e. presences are more important than absences.

In figure 8-6a the correlations have been calculated using all the minor taxa. Three observations can be made about how the minor taxa are represented in the pollen rain: i) the three plot samples are all distinctly different, ii) the lake samples are all very similar, and iii) there is no clear pattern of correlation between the lake samples and the plots (ecosystems). This high degree of correlation between the different lake samples and the lack

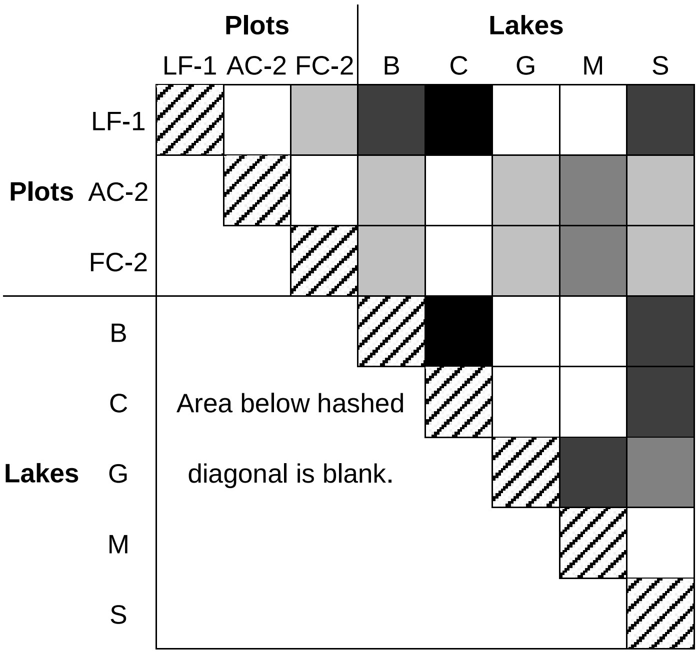
a) All minor taxa



		Plots			Lakes				
		LF-1	AC-2	FC-2	B	C	G	M	S
Plots	LF-1	▨	□	░	▓	▓	▓	▒	▓
	AC-2		▨	□	▒	▒	▒	▒	░
	FC-2			▨	▒	░	░	▒	░
Lakes	B				▨	■	■	■	■
	C					▨	■	■	■
	G						▨	■	■
	M							▨	■
	S								▨

Area below hashed diagonal is blank

b) Selected minor taxa



		Plots			Lakes				
		LF-1	AC-2	FC-2	B	C	G	M	S
Plots	LF-1	▨	□	░	▓	■	□	□	▓
	AC-2		▨	□	░	□	░	▒	░
	FC-2			▨	░	□	░	▒	░
Lakes	B				▨	■	□	□	▓
	C					▨	□	□	▓
	G						▨	▓	▒
	M							▨	□
	S								▨

Area below hashed diagonal is blank.

Key

Strength of correlation coefficient

Minor taxa

Different → Similar

□	0.00 - 0.600	░	0.601 - 0.700	▒	0.701 - 0.800	▓	0.801 - 0.900	■	0.901 - 1.00

B = Bella Vista, C = Chaplin, G = La Gaiba, M = Mandioré and S = Socórros.

Figure 8-6: Presence/absence similarity of minor taxa. Correlations were performed in SPSS v.11.01. For pollen data see appendices VII and XVI. For full details of correlations see appendix XVII.

of correlation between lake samples and ecosystems is because of two factors. Firstly, seven taxa occur in all the lake samples regardless of the surrounding ecosystem. These are: Asteraceae (Asteroide/Cardue) undiff., Cyperaceae, *Acacia*, *Machaerium/Dalbergia/Byrsonima* undiff., Melastomataceae/Combretaceae, Polypodicaceae undiff. and *Trema*. Secondly, because these are presence/absence data the strength of the correlation between the lake samples is increased by the high number of absences from the lake surface samples. To combat these problems the same correlation was carried out on taxa selected using the following criteria: i) the pollen taxa must not be present in lake surface samples from more than one ecosystem, and ii) only the taxa occurring in the lake surface samples were correlated (to remove the problems of correlating absences) (see appendix XVI). The results of this correlation are displayed in figure 8-6b.

Figure 8-6b, like figure 8-6a, shows poor correlation between the trap samples indicating that the ecosystems that they represent each have a distinctly different set of minor taxa. The results from this reduced data set show that the lakes show distinctly different assemblages and have affinities with particular ecosystems (plots). The moist *terra firma* evergreen forest is well defined by the minor taxa as all the samples from this ecosystem, both traps and lakes, are strongly correlated (Laguna Bella Vista, Laguna Chaplin and the LF-1 plot) (figure 8-6b). However, the correlation is less strong between the pollen signals from the deciduous and semi-deciduous dry forest ecosystem traps and lakes. Firstly, Lagunas La Gaiba and Mandioré are shown to be closely correlated, which is expected as they are located within the same region, but they have also been equally correlated to both the semi-deciduous dry forest trap samples (AC-2) and the Cerradão trap samples (FC-2) (figure 8-5b). The reason for this is probably because there is *terra firma* savannah present within the region and that this vegetation is contributing significantly to the pollen captured in the lakes (as described in section 8.2.1). Secondly, Laguna Socórros is strongly correlated with the moist *terra firma* evergreen forest ecosystem plot (LF-1) although this ecosystem does not surround this lake (table 8-3). This strong correlation is based primarily on the absence of taxa (appendix XVI) and so it is essentially artificial. This may indicate that these minor taxa are of limited regional applicability.

These analyses have revealed two things: i) that the minor taxa are distinct to particular ecosystems, and ii) that the signature of the minor taxa can be used to identify the nature of the regional pollen input into the lake sediment. This technique can therefore provide useful supporting evidence to the divisions established by analysis of the major taxa and contribute to an understanding of the regional landscape.

8.3.2 Taxa diversity

The differences in taxa diversity in the pollen samples were examined to determine if it were possible to use them to distinguish between the ecosystems. It was envisaged that this might provide further help differentiate the pollen signatures of the different ecosystems. Some differences in diversity were found between the ranges of diversity values in traps from different ecosystems but the degree of overlap meant diagnostic differences were not obtainable. In addition, comparison of the trap data with the lake surface sample data did not reveal any clear correlation. This suggests that within an single system (such as a lake) it may be possible to use diversity changes to detect variation between (or possibly within) ecosystems but that no absolute characteristic values are obtainable. This is probably due to input from aquatic and/or regionally present taxa. Therefore, these results are included in appendix XVIII and are not discussed further here.

8.3.3 Pollen accumulation rates

To ascertain if differences in the quantity of pollen present in the pollen rain from an ecosystem could be used to distinguish it from the other ecosystems, total PARs were calculated. The relative differences found were then compared to the relative differences calculated for the lake surface samples to establish whether or not these values shed any further light on the interpretation of the lake surface samples. The range of PARs present within the traps was found to fluctuate widely. From the trap data the tall *terra firma* evergreen forest was generally the most productive plant community (c. 8,000 grains cm^{-2} $year^{-1}$), followed by the semi-deciduous dry forest (c. 3,000 grains cm^{-2} $year^{-1}$) and then the Cerradão (c. 1,000 grains cm^{-2} $year^{-1}$). However, no consistent trends were found in comparison to the lake surface samples. Therefore these data are included in appendix XIX for reference only and are not discussed further here.

8.4 Ecological context of palynological divisions

In the above sections the ecosystems found within Noel Kempff Mercado National Park (NKMNP) have been shown to produce pollen assemblages that are reliably distinguishable from one another and it has also been demonstrated that these ecosystem pollen signatures are consistent in samples collected from lakes in other areas. These palynological signals are now considered within the context of the floristic composition of the ecosystems from which they are derived (as discussed in chapter 6).

8.4.1 Moist *terra firma* evergreen forest

The modern pollen rain from the LF-1 plot is distinguished from the other plots by the abundance of Moraceae/Urticaceae undiff., Melastomataceae/Combretaceae, Palm (type 1) and *Didymopanax* (table 8-2). In addition *Alchornea* (type 1), *Cecropia, Celtis* and *Trema* are also important (figure 8-1b). Of these only *Alchornea*, *Celtis* and *Trema* are not recorded as trees >10 cm d.b.h. within the plot (T.J. Killeen, unpublished data; appendix XIV), and are therefore likely to have arisen from plants outside the plot.

Alchornea (type 1) looks like the pollen produced by the species *A. glandulosa* or *A. grandis*. *A. glandulosa* is a small tree (<15 metres) and is found within the tall *terra firma* evergreen forest of the park (Killeen *et al*., 1993; Killeen and Schulenberg, 1998). *Cecropia* is also a small tree found within this ecosystem (Killeen *et al*., 1993; Killeen and Schulenberg, 1998) and in addition this genus produces an abundance of pollen as it is wind pollinated (Holthuijzen and Boerboom, 1982). Therefore, presence of this taxon nearby would probably result in its pollen penetrating into the plot. *Celtis* and *Trema* are present within the ecosystem as either small trees or bushes (Killeen *et al.,* 1993; Killeen and Schulenberg, 1998). These pollen types, identified as characteristic of this ecosystem, therefore are likely to have entered the traps by wind dispersal from plants outside the plot. Other taxa found to be important in the vegetation are not identified in the pollen rain from the plot, e.g. Vochysiaceae which is represented by the two most important species in the vegetation of LF-1 (Panfil, 2001; chapter 6, section 6.3.1).

8.4.2 Deciduous and semi-deciduous dry forest

The pollen rain from the AC-2 plot has been characterized by *Anadenanthera* - Palmae (type 2) - Pteropsidia (trilete) undiff. (table 8-2) and also has a strong influence from Poaceae (figure 8-1b). Panfil (2001) demonstrated that both *Anadenanthera* and palms are important in the vegetation of this plot (chapter 6, section 6.3.2) and they have been shown to occur within the four dry forest plots inventoried (T.J. Killeen, unpublished data). Ferns

(Pteropsidia) are found within a range of ecosystems in the park (Killeen and Schulenberg, 1998) and indeed their spores were found in the majority of the traps (appendix VII). The abundance of fern spores and grass pollen (Poaceae) found within the traps from the semi-deciduous dry forest can be explained by their dispersal mechanisms. These are the only elements of the ground flora in this vegetation type that are wind dispersed (Killeen *et al.*, 1998). Wind pollinated taxa usually produce relatively more pollen than animal and insect dispersed taxa (Janzen, 1975). Animal and insect pollinated taxa that are abundant in the vegetation are not found to be major elements in the pollen rain because they do not produce or disperse much pollen. For example, *Caesalpinia floribunda* was identified as the most important element of the vegetation of this ecosystem (Panfil, 2001; chapter 6, section 6.3.2) but *Caesalpinia* type pollen is only found at low abundances in the pollen rain (chapter 7, figure 7-12). The pollen taxa identified as characteristic of the AC-2 plot reflect the abundant pollen producers within this ecosystem.

8.4.3 *Terra firma* savannah

Poaceae, *Solanum*, *Alchornea* (type 2) and Myrtaceae undiff. were found to be characteristic of pollen rain from the pollen traps located in this ecosystem (table 8-2). Of these only Poaceae was found to be important in the vegetation by Panfil (2001) (chapter 6, section 6.3.3). *Solanum* and Myrtaceae are found within *terra firma* savannah ecosystems of the park (Killeen and Schulenberg, 1998); of these Myrtaceae is more abundant (T.J. Killeen, unpublished data). *Alchornea* (type 2) cf. *schomburgkii/triplinervia* however is not present within the ecosystem (Killeen and Schulenberg, 1998; T.J. Killeen, unpublished data). The parent vegetation for this taxon occurs in riverine or inundated forest and savannah ecosystems (Killeen and Schulenberg, 1998; J. Ratter, *pers. comm.*, 2003). This strongly suggests that this pollen is being sourced from outside the plot and that it may not be diagnostic of this type of ecosystem. This is possible because the plant community that the FC-2 plot is within is close to inundated ecosystems to the south and west (chapter 3, figure 3-2). This finding could indicate that this may be a useful taxon in distinguishing between *terra firma* and inundated ecosystems; further research would be required to clarify this.

In addition to the grasses Panfil (2001) identified five genera that are important in the vegetation of FC-2 (chapter 6, section 6.3.3). Two of these, *Caraipa* and *Emmotum*, are not identified in the pollen from the plot, but pollen types representing the others are: Melastomataceae/Combretaceae, Bombacaceae cf. *Eriotheca* and *Ormosia* (chapter 7, figure 7-8). All these taxa can be present in a range of vegetation types (Killeen *et al.*, 1993) but the latter two were only found in the pollen rain from this ecosystem, i.e. cf. *Eriotheca* and *Ormosia* have not been found in the pollen from tall *terra firma* evergreen forest or semi-deciduous dry forest but have been recorded in the ecosystems vegetation. Given the high diversity of taxa found within this ecosystem and the unreliability of the pollen signal from the dominant taxa (Poaceae). It is necessary to consider the full range of taxa found within this ecosystem to identify it from the pollen rain.

8.5 Summary

In this chapter it has been shown that the moist *terra firma* evergreen forest, deciduous and semi-deciduous dry forest and *terra firma* savannah ecosystems can be differentiated from one another on the basis of their pollen rain (section 8.1). The applicability of these diagnostic assemblages to assign ecosystems to other pollen data sets has been demonstrated by using them to correctly differentiate between samples taken from surface sediments from lakes surrounded by known ecosystems (section 8.2). This exercise lends confidence to the applicability of this method for identifying these ecosystems in the fossil pollen record from lake sediment cores. In addition to the major taxa it has also been demonstrated that analysis of the minor taxa can provide additional ecological information from the pollen rain. The presence or absence of these taxa can identify regional pollen input into lake sediments (section 8.3.1). Two other methods of investigating the modern pollen rain, taxa diversity (section 8.3.2) and PARs (section 8.3.3), did not allow any further ecological information to be extracted from the pollen rain, although some differences were detected between the pollen trap data from different ecosystems. The forest ecosystems were well represented in the pollen rain by a few high pollen producing taxa, but the *terra firma* savannah was more difficult to characterize. The differentiation of the *terra firma* savannah ecosystem was hampered by: i) the inconsistency of the grass pollen signal from this ecosystem, ii) the abundance of grasses within the deciduous and semi-deciduous dry forest signal, and iii) the high diversity of the pollen rain (appendix XVIII). These problems suggest that the full assemblage of major and minor taxa should be considered to confirm the presence of this ecosystem in the fossil pollen record. In the next, and final, chapter of this thesis a summary of the main findings of this thesis is given and further research is outlined.

Chapter 9

Conclusions

Chapter 9

Conclusions

At the beginning of this thesis, in chapter 2 (section 2.3), three key aims were stated. These aims were: i) to establish a reliable and repeatable methodology for the sampling of modern pollen rain in tropical environments (chapter 4), ii) to characterize a range of Neotropical ecosystems by the pollen that they produce (chapter 7), and iii) to determine the extent to which these characteristic taxa can be used to differentiate between these ecosystems (chapter 8). In this concluding chapter, a summary of the key findings is presented and the success to which each of these aims have been met is assessed (section 9.1). Then, in section 9.2, the overall effectiveness of the methodology applied is appraised. In section 9.3, the implications of these conclusions for the understanding of Amazonia's palaeoenvironmental history are discussed and then, in section 9.4, the limitations of the research are acknowledged. Finally, a brief outline of ongoing and future research developed from this thesis is given in section 9.3.

9.1 Summary of findings

9.1.1 Methodology

Methodological advances were made in two areas in this thesis: i) in the collection of pollen rain from tropical environments, and ii) in the preparation of the samples collected.

The first advance was made through field observations. During the three years of pollen trapping carried out in Noel Kempff Mercado National Park (NKMNP) it became apparent that the design of the pollen trap being deployed in this study (described by Bush, 1992) could be improved upon. The principal change was the removal of the one litre bottle that in the

Bush (1992) design was suspended under the funnel trap to act as a reservoir and provide moisture to improve retention of pollen grains. It was discovered that the water held in the bottle was not being transferred to the fibres used to catch the pollen rain. Therefore, the bottle was redundant and could be removed from the traps design without any detrimental effect to the pollen collected (chapter 4, figure 4-3; Gosling *et al.*, 2003).

The second advance was made through laboratory experimentation. The methodology published by Bush (1992) for processing the viscose rayon fibre recommended to trap the pollen was found not to work. Therefore, two problems had to be addressed: i) how to extract the pollen from the hundreds of viscose rayon fibre samples that had been collected, and ii) could an alternative, easily processed, material be found to trap the pollen. The first of these questions was solved by developing the ‘wash’ methodology described by Behling *et al.* (1997) and Bush and Rivera (1998) (chapter 4, section 4.3; Gosling *et al.*, 2003). The second was achieved through experimentation with cotton fibre. This material was found to retain pollen equally as well as the viscose rayon fibre and was easy to dissolve using acetoloysis (chapter 4, section 4.3; Gosling *et al.*, 2003).

By providing this simple and effective methodology it is hoped that in the future modern pollen work from tropical areas will become more comparable and easier to carry out. This improved methodology is already being other researchers in other tropical regions (R. Marchant, *pers. comm.*, 2003). Therefore, it is felt that this aim has been successfully achieved.

9.1.2 Ecosystem characteristics

The characterization of three Neotropical ecosystems has been achieved through the research carried out in this thesis. This was accomplished by considering the nature of the pollen rain within each ecosystem individually (chapter 7: section 7.2 moist *terra firma* evergreen forest, section 7.3 deciduous and semi-deciduous dry forest, and section 7.4 *terra firma* savannah). The factors considered are summarised in figure 9-1.

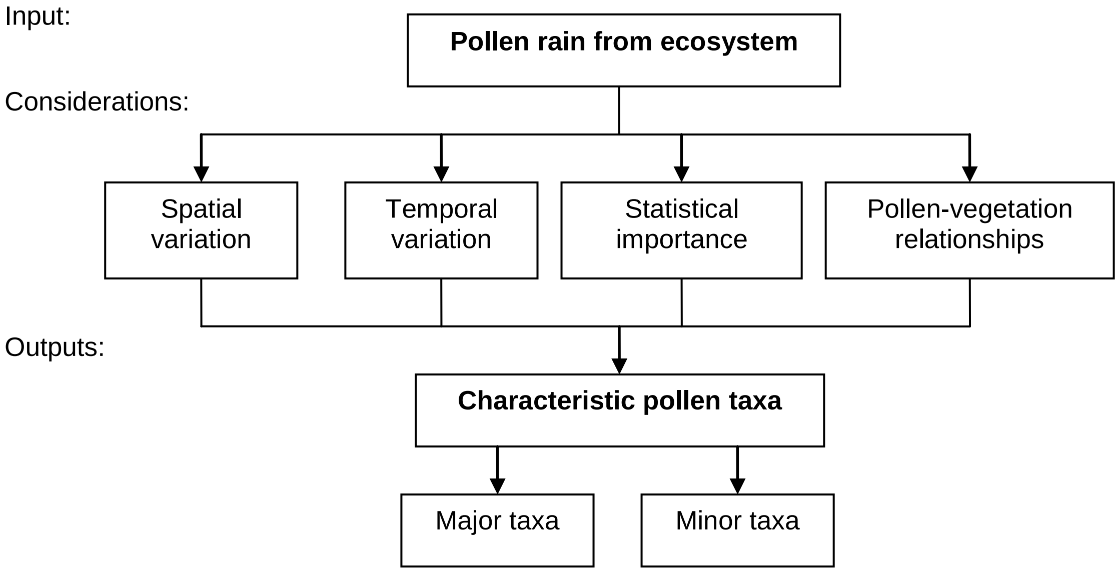


Figure 9-1: Determining a characteristic pollen signature. Factors considered when establishing a characteristic pollen assemblage for an ecosystem.

Through this process two sets of taxa were successfully established as characteristic of the pollen rain from each ecosystem. Firstly, the major taxa consisting of the dominant pollen types found throughout the ecosystem, and a distinct range of values for each taxon occurrence was determined (figure 9-2). Secondly, the minor taxa consisting of pollen present at low abundance or at discrete locations within the plot that could be seen as indicative of the ecosystem when found in association with others (for full lists see chapter 7, sections 7.2.5, 7.3.5 and 7.4.5).

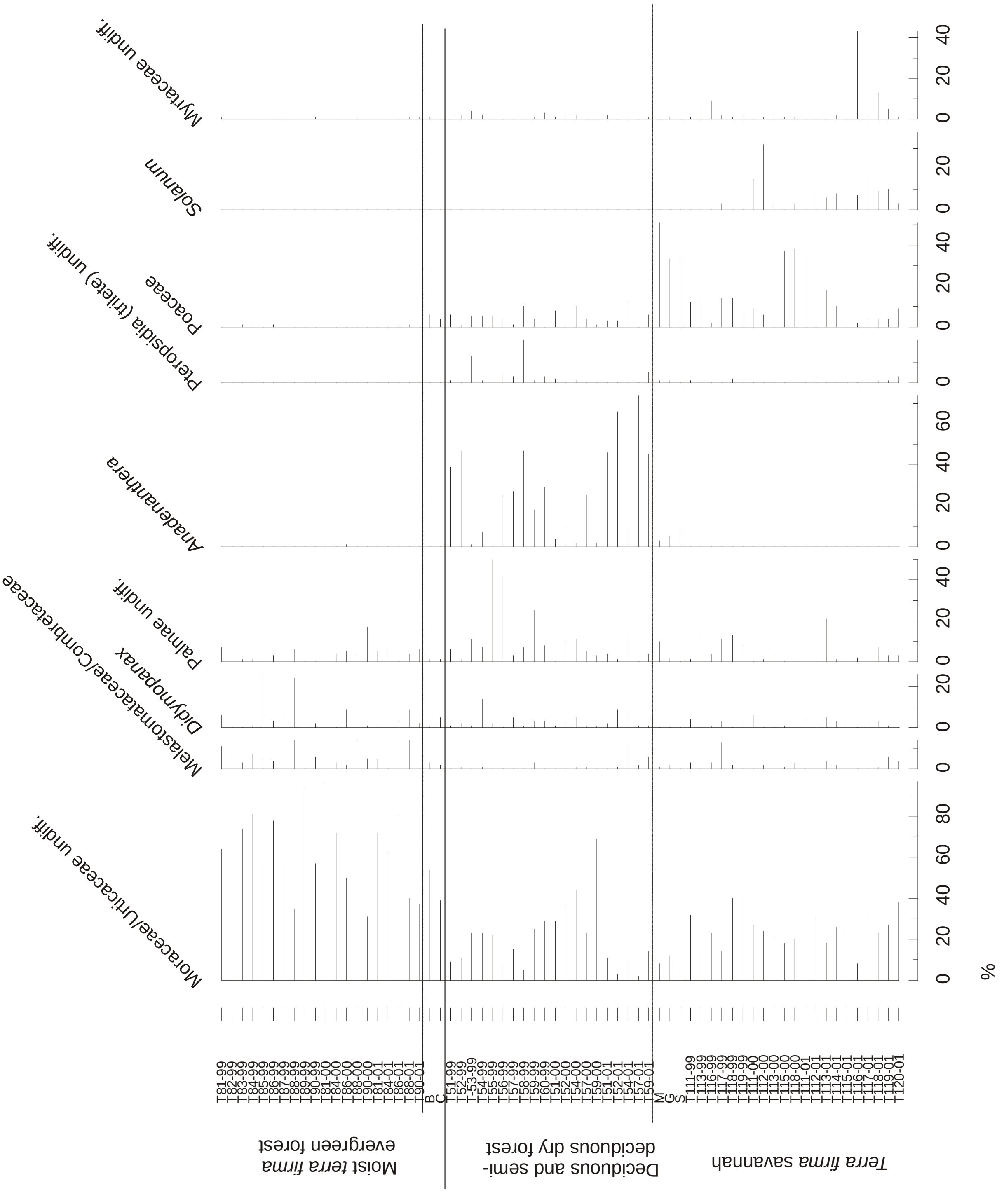


Figure 9-2: Major taxa and their range of variation. Percentage data from traps and lakes: B = Bella Vista, C = Chaplin, M = Mandioré, G = La Gaiba and S = Soccóros.

9.1.3 Ecosystem differentiation

Palynological differentiation of the three ecosystems was achieved through determining the greatest differences in the major taxa identified in the pollen traps in the preceding chapter.

Then the analysis was applied to, and compared with, lake surface samples to gain insight into: i) the applicability of these divisions to an independent data set, and ii) understanding the effects of taphonomic processes on the pollen assemblages (see chapter 8, figure 8-3).

These analyses showed that the proportions of the major taxa within the pollen rain from the traps of the individual ecosystems were sufficiently distinct to allow them to be differentiated (section 8.1). These differences were also found to occur in lake surface samples found within the ecosystems concerned (section 8.2). This verification of the distinctions in an independent data set demonstrates that this method of identifying the ecosystems should be applicable to defining ecosystems in the fossil pollen record (table 9-1). This is a critical discovery as it facilitates an improved interpretation of the poorly understood palaeoenvironmental history of these three ecosystems from the fossil pollen record. The implications for the palaeoenvironmental history of the Neotropics are discussed in the section 9.3.

		Median % abundance		
Ecosystem	**Major pollen taxa**	**Moist *terra firma* evergreen forest**	**Deciduous and semi-deciduous dry forest**	***Terra firma* savannah**
Moist *terra firma* evergreen forest	Moraceae/Urticaceae undiff.	**64**	19	24
	Melastomataceae/Combretaceae	**4**	0	2
	Palmae (type 1)	**4**	2	2
	Didymopanax	**2**	2	1
Deciduous and semi-deciduous dry forest	*Anadenanthera*	0	**25**	0
	Palmae (type 2)	0	**3**	0
	Pteropsidia (trilete) undiff.	0	**1**	0
Terra firma savannah	Poaceae	0	4	**9**
	Solanum	0	0	**3**
	Myrtaceae undiff.	0	1	**1**

Table 9-1: Major distinguishing taxa of the three ecosystem. For full details see appendix VII.

Further still, advances have been made on the understanding of the nature of the pollen signal captured in lake samples. Comparisons of the trap and lake surface sample data indicate that the Poaceae signal found in the fossil record may be related to input of aquatic and/or regional taxa. This finding means that caution must be exercised when interpreting the grass pollen curve in the fossil pollen record.

Additional analysis of other aspects of the modern pollen rain revealed ways in which further ecological information could be gleaned from the different pollen assemblages. The minor taxa were found to be distinct to the ecosystems. When correlated with the lake surface samples this revealed the nature of the regional pollen signal.

9.2 Overview

Due to the differences in the nature of the pollen collected in pollen traps and lakes (as discussed in section 8.2) the applicability of the modern pollen trap data to interpreting the fossil pollen record was a concern. However, the data presented in this thesis reveal that not only is it possible to use modern pollen trap data to better understand the fossil pollen record but that the data can also be used to begin to tease apart the constituents that comprise the pollen found in lake sediments.

Through modern pollen-vegetation study a detailed understanding of the nature of the pollen rain produced by an ecosystem can be gained (as demonstrated in chapter 7). By understanding the pollen characteristics of an ecosystem in isolation it then becomes possible to identify that signal within the more complex pollen record collected in lakes. In chapter 8 (section 8.1) it was demonstrated that the major taxa found within the pollen rain collected in the surface samples of the lakes fell within the range of values for those taxa found within the traps samples, with the exception of Poaceae. This demonstrates that the variation in the pollen rain collected in the pollen traps from each ecosystem encompassed the degree of variation in the pollen signal of lake sediments regardless of the exact floristic composition of the particular vegetation type surrounding the lake, the taphonomic processes in operation and the input of pollen from a variety of sources. This implies that in order to assign a pollen spectrum to an ecosystem only a small number of key taxa and their relative proportions need be identified.

In addition, in chapter 8 (section 8.3.1) it was discovered that the minor taxa, i.e. those occurring infrequently or at low abundances within the pollen trap samples, could be used to identify regional pollen input into lake sediments. The simple presence or absence of groups of taxa known to be associated within an ecosystem, as defined through pollen trap data, allowed a regional picture to be identified for some lakes. This again shows the benefit of understanding the nature of the pollen rain from the ecosystems in isolation in teasing out the complex signal recorded in the lake sediments.

In conclusion, modern pollen data collected from traps allows the pollen rain from an ecosystem to be characterized by a small number of key taxa whose relative abundances occur within defined ranges. These characteristic taxa can then be sought in the fossil pollen record. Strong correlation with an association of taxa from an ecosystem indicates that this ecosystem is contributing significantly to the pollen collected in the lake sediments. The research presented in this thesis therefore achieves its overarching aim of characterizing Neotropical ecosystems by their modern pollen spectra and goes on to demonstrate a robust methodology for applying these findings to aid the interpretation of the fossil pollen record.

9.3 Implications for understanding Amazonian palaeoenvironments

In chapter 2 three theories of vegetation change in Amazonia at the Last Glacial Maximum (LGM) were explored (section 2.1.3): i) Haffer's forest refugia hypothesis (figure 2-2a; Haffer, 1969; Haffer and Prance, 2001), ii) Colinvaux's continual forest hypothesis (figure 2-2b; Colinvaux *et al.*, 1996; Colinvaux *et al.*, 2001), and iii) Prado and Gibbs (1993)'s dry forest arc hypothesis. This modern pollen study provides an assemblage approach for differentiating between ecosystems and casts doubt on the reliability of the indicator taxon approach adopted for the interpretation of many fossil pollen records from Amazonia in the past. The implications of this improved understanding of modern pollen rain for hypotheses of vegetation change in Amazonia are briefly summed up in the next two sub-sections.

9.3.1 The Amazonian aridity debate

The main controversy that surrounds palaeoenvironmental reconstructions of Amazonia at the LGM centres around one main question: What was the nature of the vegetation in the Amazon Basin at the LGM? Palaeovegetation reconstructions have, to date, been based primarily upon indicator species found in the fossil pollen record: Moraceae/Urticaceae pollen to identify forest, and Poaceae to identify savannah. The modern pollen work presented in this thesis has cast doubt on the reliability of these taxa to distinguish these ecosystems.

Moraceae/Urticaceae is ever-present in the pollen traps from all of the ecosystems studied in detail in this thesis, but its parent vegetation is not. The origin of this pollen type in the deciduous and semi-deciduous dry forest and *terra firma* savannah traps is therefore likely to be the nearby moist evergreen forest (<25 km), where Moraceae dominates the vegetation. The high abundance of the Moraceae/Urticaceae pollen suggests that even if plants of the

Moraceae or Urticaceae were present in low abundances in the past vegetation of the Amazon basin it may have still been a major contributor to the pollen rain over the region.

Likewise interpretation of Poaceae pollen is not straightforward. It has been recognised that grasses can flourish under a wide range of conditions, e.g. grass can be abundant in dry savannah environments or can occur as aquatic species. The modern pollen work presented here demonstrates that while the traps from the savannah ecosystem contain a high percentage of Poaceae pollen, the samples from lake surface sediments contain higher grass content than those found in the pollen traps for the equivalent ecosystems. This is thought to be a result of the input of aquatic grasses and regional pollen. The wide range of environmental interpretations possible for of this taxon suggests that it should be interpreted with caution when found in the fossil pollen record.

The identification of a characteristic pollen assemblage for each of these ecosystems in this thesis means that indicator taxa no longer have to be relied upon to differentiate these ecosystems. Future analysis that considers the characteristic pollen assemblages from these ecosystems should mean that a more accurate picture of forest-savannah interaction should be established.

In addition, an insight has been gained into the Pleistocene re-assortment of forest taxa that is suggested by Colinvaux *et al.* (1996). This theory suggests that the elevated abundance of Andean taxa found in pollen cores from the Amazonian lowlands during the LGM indicates that these taxa moved into the lowland forests as temperatures cooled. The two principal taxa considered as evidence for this are *Podocarpus* and *Alnus*, both of which have been found in the modern pollen rain from NKMNP at up to 65 and 74 grains cm^{-2} year^{-1} respectively. The closest *Podocarpus* is c. 600 kilometres to the south of NKMNP and the closest *Alnus* is in the Andean foothills c. 1000 kilometres to the west (T.J. Killeen, *pers. comm.*, 2003). Therefore, the pollen present in the traps must be a product of long distance transport. One source of fossil pollen evidence for the presence of *Podocarpus* in the Amazonian lowlands comes from Laguna Curuça in north-eastern Brazil. At this location this taxon reaches a maximum of 78 grains cm^{-2} $year^{-1}$ during the late glacial period (Behling, 1996) a figure not dissimilar to that found in the modern pollen of NKMNP. These findings suggest that long distance transport may be a sufficient explanation for these values during the late glacial period especially in the light of possible changes in prevailing wind direction or expanded areas of these taxa in the Andes.

9.3.2 The Pleistocene dry forest arc hypothesis

The Pleistocence dry forest arc hypothesis proposed by Prado and Gibbs (1993) suggested, based upon modern species distribution patterns, that the deciduous and semi-deciduous dry forest areas found in the Neotropics were once more extensive and interlinked (chapter 2, figure 2-3). One of the key genera found by Prado and Gibbs (1993) to have a wide-ranging distribution was *Anadenanthera*. The pollen of this taxon has been found to be abundant and characteristic of the pollen rain from the deciduous and semi-deciduous dry forest ecosystem in this thesis. The abundance of this pollen type in the pollen rain from this ecosystem and its near absence from the others (in both trap and lake surface samples) provides a useful tool in recognising the presence of this ecosystem in the fossil pollen record. Preliminary application of this finding suggests: i) that there may be a previously undetected dry forest signal contained in the fossil pollen cores from Laguna Bella Vista and Laguna Chaplin in the NKMNP (Mayle *et al.* 2000), and ii) that the ‘ancient’ dry forest refugia postulated by Prado and Gibbs (1993) may only stretch back to the early Holocene (F.E. Mayle, unpublished data). Further work is required to apply this finding and the other dry forest characteristic taxa to understanding the history of this vegetation type. However, it seems likely that revision of the palaeoenvironmental history of the deciduous and semi-deciduous dry forests of the Neotropics will be required in the light of this research.

9.4 Limitations

The research carried out over the course of this thesis has been primarily limited by time. The main concern with the restricted time is the impact on the pollen count sizes that were achieved for each pollen trap (only c. 100 grains). The statistical reliability of the results could be questioned on the basis of these small count sizes. However, comparison between traps counted for the pilot research, where c. 300 grains were counted, shows a general consistency of the pollen signals obtained from within each of the plots. This suggests that the main variance in the data set is being captured with the smaller counts.

The second concern is the number of samples that were analysed from each year, i.e. for each plot ten traps were analysed from one year and five traps from two years. This may have had affected the results by biasing them towards the year with ten samples, especially given the inter-annual variability shown during the course of this study. Despite this possibility results have been shown to be robust enough to be applicable to an independent data set.

Thirdly, it would have been interesting to apply multivariate statistical techniques other than principal components analysis (PCA) to the data set, such as correspondence analysis, detrended correspondence analysis or canonical correspondence analysis. These alternative methods have been shown to work well with pollen data sets by other authors and it would have been interesting to compare the patterns and associations that would be achieved through these analyses. Unfortunately, due to time and software available, PCA was the only multivariate statistic used in this thesis.

The fourth, and final, major limitation to this study were the samples. It is recognised that extrapolation from one plant community to an entire ecosystem (that is comprised of numerous different plant communities) is not ideal and that the full range of within-ecosystem pollen rain variability is probably not captured. To minimise this problem every effort possible has been made to examine the ‘most representative’ plant community from each ecosystem. Ideally, all the different plant communities found within each ecosystem would be studied to allow a fuller picture of the within ecosystem variability to be gained. Unfortunately this has not been possible in the time available. In addition, the number of lake surface samples available was limited to five, and no lake surface samples were available from within the *terra firma* savannah ecosystem. Ideally, more lake surface samples would provide a more robust independent data set to test the findings of the trap data against.

In conclusion, if this research was undertaken again and more time was available then: i) research would be conducted to verify the count sizes required to capture the variation in the pollen rain of the traps and then those count sizes would be achieved for each trap, ii) an equal number of samples would be analysed from each years data, iii) a variety of multivariate statistics would be applied to the data, and iv) further samples would be obtained from a wider range of plant communities and lakes.

9.5 Ongoing and future research

In the light of these findings two key avenues of research have opened up. First among these is the application of the methodology to identify ecosystems in the fossil pollen record;

starting with the two lakes in NKMNP. This will provide an improved understanding of the vegetation history of the region. Secondly, now that a methodology has been established for the characterization of Neotropical ecosystems by their modern pollen spectra it should be possible to comparatively quickly characterise further ecosystems from the samples already obtained from NKMNP. This will allow further ecological details to be extracted from the fossil pollen record.

In addition, it has become apparent that research into other aspects of Neotropical palynology may enhance understanding of modern pollen rain and therefore provide additional insight when interpreting the fossil pollen record. These areas therefore warrant further investigation: i) pollination biology of taxon dispersal mechanisms (both local and long distance), and ii) the effect of climate on pollen productivity.

Plates

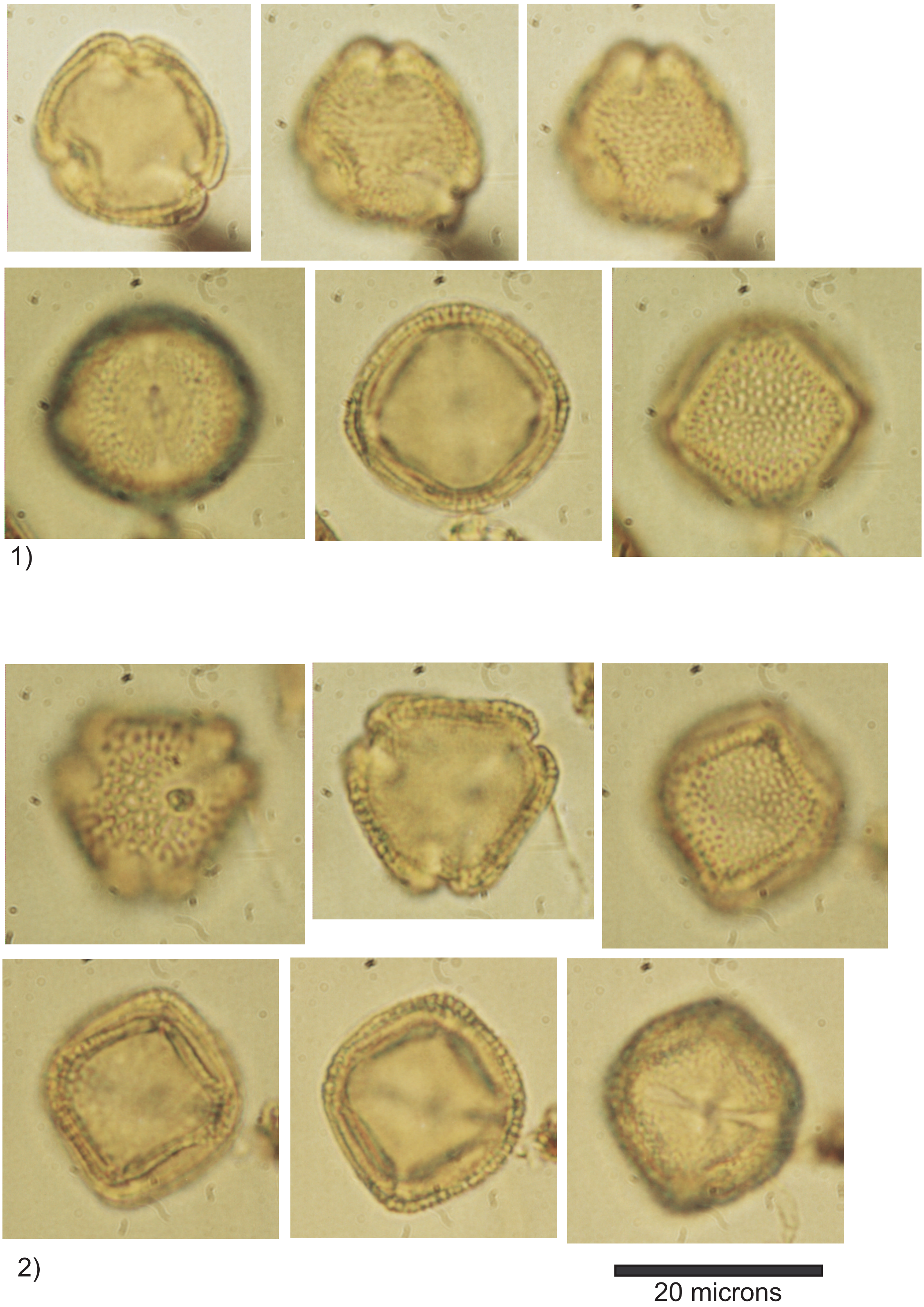


Plate I: 1) Aralacaeae *Didymopanax distractiflorum,* 2) *D. vinosus.*

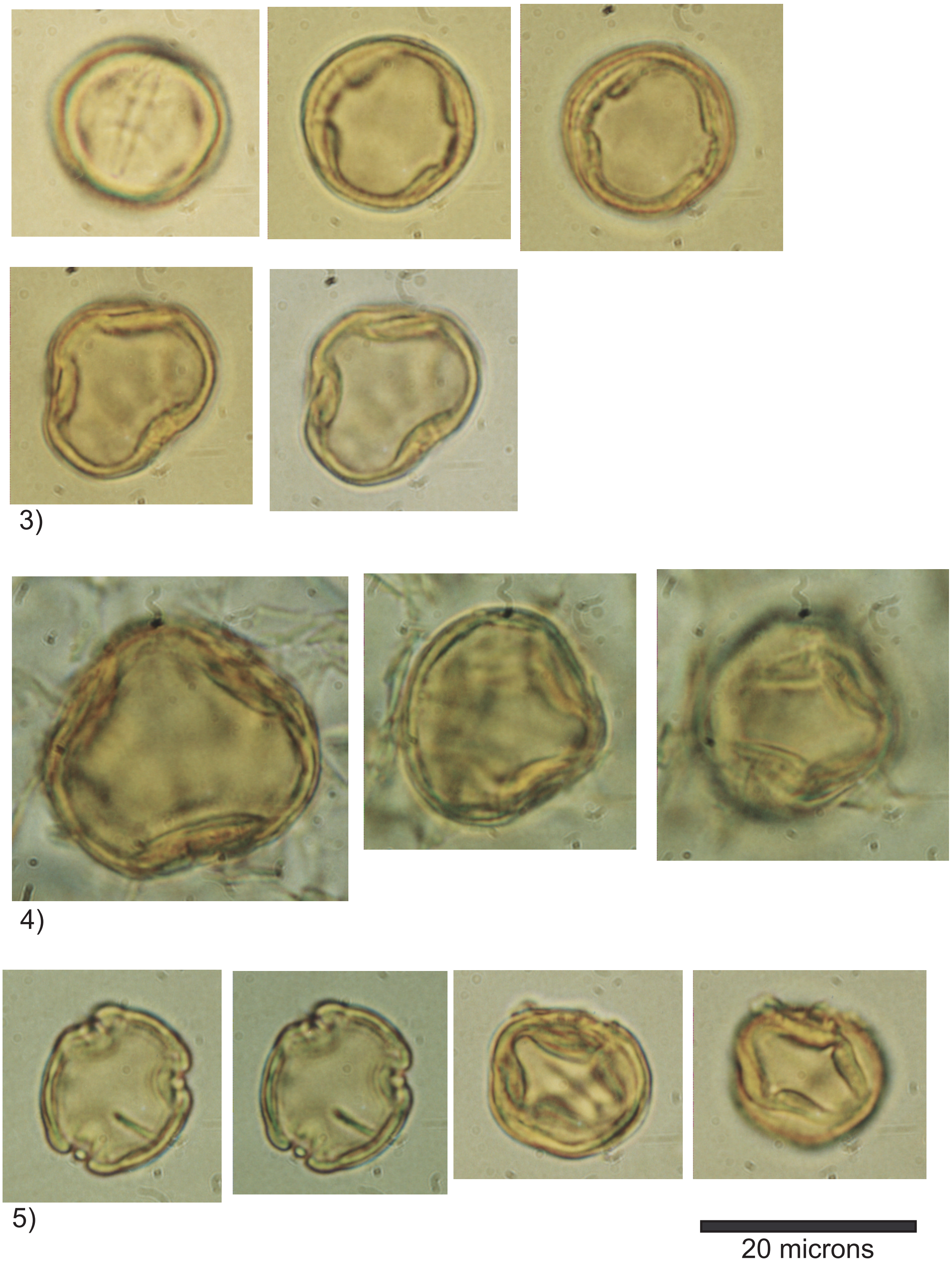
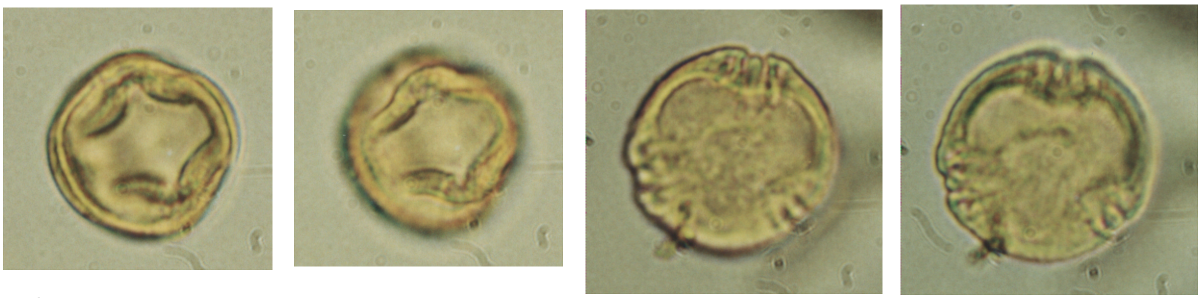


Plate II: 3) Euphorbiaceae *Alchornea glandulosa*, 4) *A. grandis*, 5) *A. schomburgkii.*



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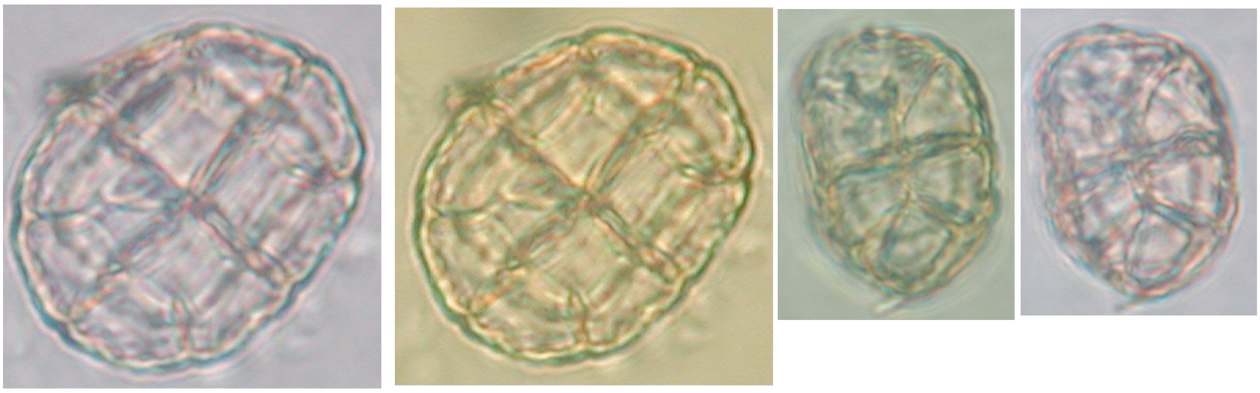

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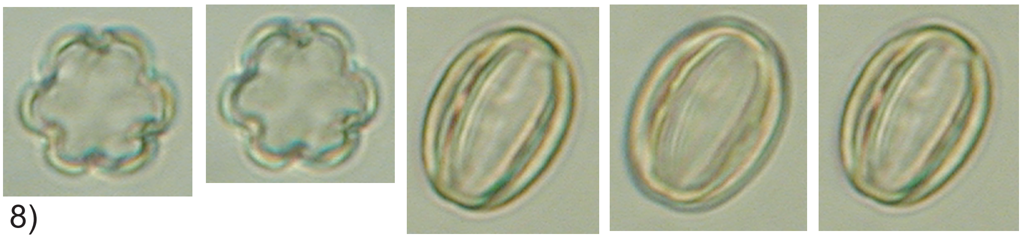

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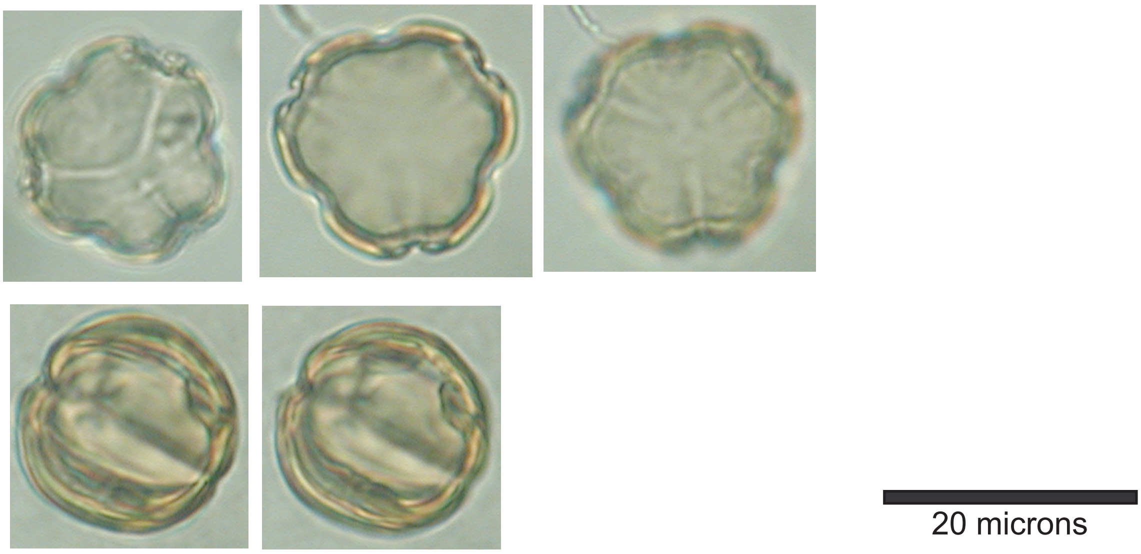
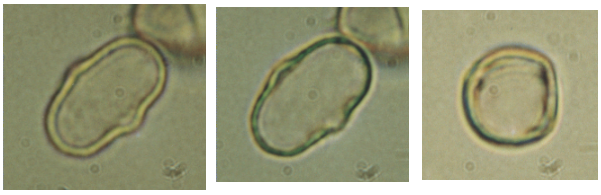


9)

Plate III: 6) Euphorbiaceae *Alchornea triplinervia*, 7) Fabaceae (Mimosoideae) *Anadenathera colubrina,* 8) Melastomataceae *Miconia macrothyrsa*, 9) Combretaceae *Combretum* sp.



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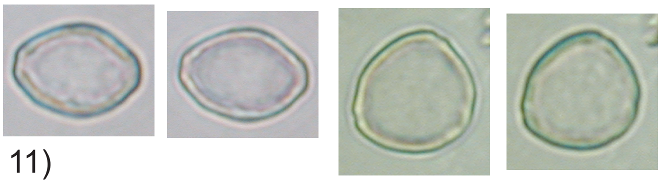

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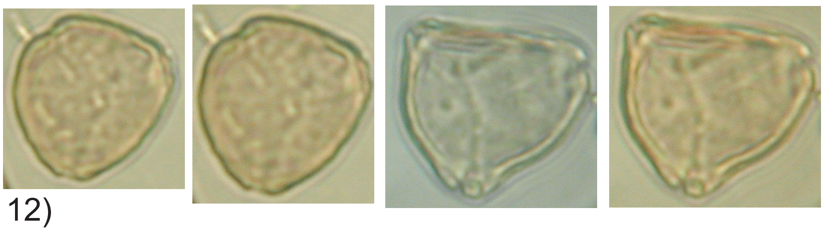
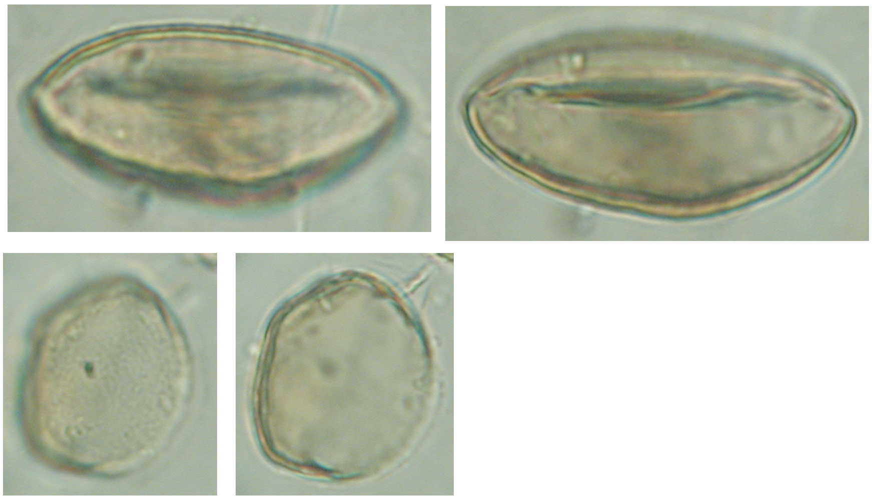


12)



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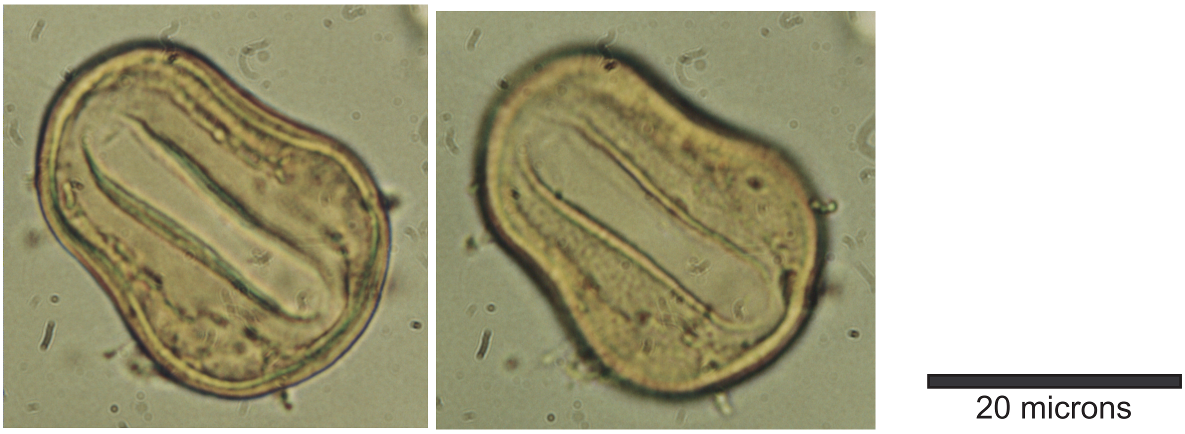

14)

Plate IV: 10) Moraceae *Ceropia concolor*, 11) *Helicostylis tomentosa,*
12) Myrtaceae *Psidium guianense*, 13) Palmae *Euterpe precatoria,* 14) *Attalea marpia.*

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