PATTERNS OF BIODIVERSITY IN NEOTROPICAL DRY FORESTS AND SAVANNAS: CASE STUDIES FROM BRAZIL, PERU AND BELIZE

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degree of Doctor of Philosophy (by Research Publication)

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RESEARCH OVERVIEW

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To my family

Cerrado Landscape. Flora Brasiliensis.

Nova Xavantina, Mato Grosso, Brazil,
22 Oct. '03

To whom it may concern.

This is to state that **Samuel Bridgewater** made an extremely significant (in fact vital) contribution to the following publications:

1. Ratter, J. A., Bridgewater, S. & Ribeiro, J. F. (2001). Espécies lenhosas da fitofisionomia cerrado sentido restrito amplo em 170 localidades do bioma cerrado. Boletim do Herbário Ezechias Paulo Heringer 7: 5-112.
2. Ratter, J. A., Bridgewater, S. & Ribeiro, J. F. (2003). Analysis of the floristic composition of the Brazilian Cerrado vegetation III. Comparison of the woody vegetation of 376 areas. Edinb. J. Bot. 60(1): 57-109.
3. Ratter, J. A., Bridgewater, S., Atkinson, R. & Ribeiro, J. F. (1996). Analysis of the floristic composition of the Brazilian Cerrado Vegetation II: comparison of the woody vegetation of 98 areas. Edinb. J. Bot. 53: 153-180.

Yours faithfully,

[redacted]

Dr. James Ratter
SPSO (retd). RBG Edinburgh

ABSTRACT

South American savannas and seasonally dry topical forests (SDTFs) are two widespread and biologically important vegetation formations which can be highly species-rich (such as the cerrado tree savanna of Central Brazil) and which can show high degrees of endemism (such as the dry forests of northern Peru). Both savannas and SDTFs are highly threatened by agricultural development. Of critical importance in ensuring the protection of their biodiversity is the establishment of reserve areas. However, conservation planning is currently hindered by the lack of base-line floristic data. This work provides floristic data for three areas of priority conservation importance in the Neotropics and examines the patterns of diversity within them. The areas are (i) the cerrado biome of Brazil; (ii) the SDTFs of Peru; (iii) the savannas of Belize. For the cerrado biome, this study also investigates whether diversity patterns are similar to those recently proposed for Neotropical rainforests.

A morphological and biogeographic study of the *Acosmium dasycarpum* complex was undertaken to resolve the taxonomic uncertainties relating to its putative subspecies.

Brazil

(i) Data are presented for 170 floristic surveys conducted in the Brazilian cerrado biome. These surveys target areas which are poorly known floristically, including the states of Tocantins, Mato Grosso, Goiás, Mato Grosso do Sul, Maranhão and Piauí.

(ii) Analyses were made of the floristic composition of 98 areas of cerrado and Amazonian savanna (in the first instance) and subsequently 376 areas, encompassing most of the area of such vegetation in Brazil. A total of 953 species of trees and large shrubs were recorded for these areas of which 334 (35%) occurred at only a single locality. Alpha diversity (the number of tree species occurring in a single community) is often high with more than 100 species of trees and large shrubs growing together. Particular 'hotspots' occur in the drainage of the rivers Araguaia, Tocantins and Xingu but high diversity figures occur in many other areas of the cerrado core, and also in São Paulo state. Amazonian savannas were shown to be species poor, seldom exceeding a dozen species of trees and large shrubs in any one site. The data were analysed by two techniques of multivariate analysis: (a) a divisive hierarchical classification by Two-way Indicator Species Analysis (TWINSPAN), and (b) an agglomerative hierarchical classification by UPGMA (Unweighted Pair-Groups Method using Arithmetic Averages), using the Sørensen Coefficient of Community as a measure of similarity. The results of both methods showed great similarity, demonstrating a strong geographical pattern in the distribution of the cerrado biome. Six floristic provinces are proposed for the cerrado. These comprise: (i) southern sites; (ii) central and south-eastern sites; (iii) north and north-eastern sites; (iv) central-western sites; (v) far-western sites and (vi) disjunct Amazonian sites.

(iii) An analysis of the floristic relationship between the six cerrado phytogeographic provinces revealed great heterogeneity within the biome, principally of the less common species. Of the species recorded, 494 (more than half of the total) are found in only one of the provinces, with only 37 (3.9%) found in all six provinces. Each of the provinces contains a significant number of species which are endemic to it.

A suite of only 121 species forms an oligarchy dominating the total woody flora (c. 1000 spp.) of the cerrado biome. This resembles patterns of dominance recently described in western Amazonian rain forests. Widespread sampling across the biome shows that this suite of species contributes on average 66% of the total species composition, and 75% of the total Importance Value Index in cerrado communities. Informed conservation judgements within the cerrado need to take account of regional floristic patterns to ensure maximum protection of biodiversity and reserves need to be established in each of the six floristic provinces to protect their unique floristic elements. In addition, conservation initiatives should focus on creating many numerous reserves, rather than on the establishment of a few larger ones. This would reflect the heterogeneous nature of the cerrado flora. Special attention should be paid to the biodiversity hotspots in the Araguaia, Tocantins and Xingu basins.

(iv) A morphological and biogeographic study of the *Acosmium dasycarpum* (Vogel) Yakovlev complex (*Sophoreae*, *Papilionoideae*) shows that it is a single taxon and that there is no justification for recognising subspecies *dasycarpum* and *glabratum* (Benth.) Yakovlev as separate entities. Distribution of the two putative morphological forms provides no basis for distinguishing general floristic patterns.

Peru

(i) Inventory data and preliminary floristic lists are presented for two northern Peruvian seasonally dry tropical forests (SDTFs). The 237 woody species recorded in the study comprise only c. 2% of the total species of the areas in which they occur (Tumbes, the Inter-Andean valleys and around Tarapoto). High levels of endemism are shown by SDTFs, with between 13-20% of their tree species recognised as narrow regional endemics. A comparison of disjunct SDTFs patches on the Pacific coast, in the Marañon drainage and around Tarapoto reveals only c. 2% floristic similarity between them, suggesting considerable barriers to species movement. Present day barriers are represented by the Eastern and Western Andean Massifs. However, an examination of the disjunct distribution patterns of three regional endemic species suggest that either species migration over the Andes between the Marañon drainage and the Pacific region has recently occurred via the Porcuya Gap, or these areas were once continuous before the uplift of the Andes. A comparison of Peruvian dry forest plot data with inventories from southern Ecuador and Bolivia indicates that the northern Peruvian Tumbes and Marañon dry forests, and those of southern Ecuador constitute a distinct phytogeographical unit.

Belize

A floristic inventory and preliminary vegetation classification are presented for the tracts of savanna and associated wetland vegetation of the Rio Bravo Conservation and Management Area (RBCMA) in Belize. A total of 258 species were recorded representing ca. 7% of the Belizean flora. Of these, 148 species are characteristic of the drier savanna systems, whilst

47 show a preference for hydrologic savanna and wetland areas. Only 57 species (22% of RBCMA savanna flora) are woody, with the savanna tree flora comprising 15 species. In terms of its woody flora, the savannas of the RBCMA were found to be species poor and typical in floristic composition of the savannas of the Central American and Caribbean region. Although the savannas of the RBCMA do not represent an area of exceptional species diversity (when compared to the cerrado), savanna systems are generally poorly represented in conservation areas in Central America, and due to the diverse range of structural and ecological formations of this vegetation type found within the RBCMA, this reserve constitutes an important protected area.

ACKNOWLEDGEMENTS

I would like to acknowledge the financial support of the Baring Foundation, the European Community and the Department for International Development (DFID) all of whom financially supported this research. Thanks are also due to Philip Smith, my academic supervisor.

Throughout the time I have been based at the Royal Botanic Garden Edinburgh I have had the good fortune to be surrounded by many friends who have made the last ten years an extraordinarily enjoyable and stimulating experience. In particular thanks are due to Dr. James Alexander Ratter - the 'Godfather' of the cerrado – who first saw fit to employ me in his research team, and who has been a great friend and mentor ever since. A great deal of my understanding of the cerrado flora has been derived from time spent with him in the field. He has always been highly supportive and generous to the extreme with his knowledge. Thanks are also due to Joaquim Fonsêca Filho, a technician working for Embrapa-Cerados. Joaquim accompanied me on the majority of my field trips in the cerrado and he has been another great source of inspiration. He is a superb field botanist with an amazing knowledge of the cerrado flora and the 'old ways' of the sertão. Sadly there a few of his kind left. I have extremely fond memories of my time working in the cerrado with these two great colleagues, and these will last for the rest of my life.

I am also indebted greatly to Dr. José Felipe Ribeiro another work colleague and dear friend whose enthusiasm for life and passion for the cerrado has always been infectious. Felipe helped me greatly in all my research visits and made my time in Central Brazil both delightful and productive. Without his support and encouragement, none of the cerrado research presented in this thesis would have been possible.

Thanks are due to many other Brazilians, all of whom have given me a warm welcome whilst in their country, and who have contributed to this research. It has been a great privilege to have worked with them. In particular I would like to acknowledge Ary Oliveira Fiho, Giselda Durigan, Arnildo and Vali Pott, Cassia Munhoz, Carolyn Proença, Terezinha Dias, Bruno Walter, Paulo Ernane Nogueira, Jeanine Felfili, Beatriz Marimon, Edson Cardoso Fabiana Aquino, Joice Ferreira, Tañia Sanaiotti, Eliana de Lima Jacques, Sueli Maria Gomes, Edson de Souza Lima, João Batista dos Santos, Rosana Farias, Marcelo Simon, Gilmar dos Santos, Carlos Cardoso, José de Carmo Lima and Miriam Rodrigues. In addition, I would like to acknowledge Gordon Armstrong and all of the researchers who have participated in the '*Conservation and Management of the Biodiversity of the Cerrado Biome*' project.

Special thanks are due to Toby Pennington who has been one of my closest friends over the last ten years, and with whom I have spent a great deal of time collecting in the field and discussing matters related to South American phytogeography, the latter sometimes whilst completing 'stolen goods' forms in police stations, attending broken vehicles or attempting to cross torrential rivers and mudslides. Our two collecting trips to Peru were an unforgettable experience. The first required many months of therapy to recover from. Many of the ideas and research lines that are discussed in this thesis derive from discussions with Toby and all of my work has benefited from his input. In addition, at the Royal Botanic Garden, I would like to acknowledge the members of the Tropical Group and the library and herbarium staff. In particular, thanks are due to Peter Wilkie, Colin Pendry, Vanessa Plana, Dave Harris, Hannah Atkins, George Argent, Mark Newman, James Richardson, Mary Mendum and Maureen Warwick, all of whom have contributed to the fantastic and inspirational feeling that is unique to the RBGE. Due to their presence at work, I have honestly enjoyed each and every day at the Botanics.

Thanks are due to the hard-working MSc students I have been lucky enough to supervise over the last few years, and whose theses have contributed valuable information on the phytogeography of the Neotropical flora. In particular I would like to acknowledge Alicia Ibáñez Garcia, Reynaldo Limares-Palomino, Joanna Lenthall, Lillis Urban and Simon Queensborough.

For the research conducted in Belize, I would like to acknowledge Chris Minty - formerly Station Manager of the Las Cuevas Research Station – and Peter Furley. Both accompanied me on my first trip to Belize over a decade ago, and showed me the delights of working there (time spent in the mangroves excluded), and of Belikin beer. Both have been very supportive since, are valued research colleagues, and are good friends. In addition, thanks are due to

the students and staff of the Edinburgh University Geography Research Expedition to Belize in 1996. In particular I would like to acknowledge Alicia Ibáñez Garcia (possibly the finest field botanist I have ever had the pleasure to work with), Simon Zisman and Malcolm Murray. In subsequent trips I have collaborated with Neil Stewart and Duncan Moss. Special thanks go to all the staff of the Programme for Belize who manage one of the world's finest and most beautiful conservation areas.

In Peru acknowledgements are due to Carlos Reynaldo and Anecito Daza who, like all my South American colleagues, have been very welcoming, generous of spirit, and without whom none of the field work would have been possible.

Many other people have contributed to this work at one time or another – either by providing insights into South American phytogeography, assisting with determinations or proof reading papers. In particular I would like to thank Gwil Lewis, Lulu Rico, Terry Pennington, Bente Klitgaard, Alex Munro, Caroline Whitefoord, Richard Bateman and the staff of the herbaria of Kew and the Natural History Museum.

I have also been blessed with a number of great friends who have provided inspiration, enthusiasm and support when spirits were flagging. In particular I would like to thank Anna Lake, Julie Jones, William Milliken, Philip Keegan and Gwen Ritchie. Their friendship is of inestimable value.

Finally I would like to acknowledge my family and Carolyn Petersen for their constant love and understanding.

CONTENTS

CHAPTER ONE: INTRODUCTION

Prologue

The seven papers submitted here represent the fruition of seven years' full-time research. Although their focus is geographically dispersed across Central and South America they have one single over-arching theme. They all describe - and attempt to explain - the patterns of plant diversity found within Neotropical savanna and dry forest systems. Five out of the seven papers deal exclusively with the Brazilian cerrado biome. These form the foundation of this collective body of work.

This essay provides background to the submitted papers and gives an overview of the research fields to which they belong. In Chapter One, a brief resumé of all the papers is provided, together with a short description of how (and why) the research originated and developed. This includes a brief section outlining the vital importance of fieldwork to all of the papers submitted. Over three years were spent in the field collecting the data that fuelled the research, and much of it appears as appendices and is therefore easily overlooked. In my opinion the most time consuming, challenging and rewarding component of all my work has been observing and collecting plants in the field. The majority of all sound and lasting theories - such as those attempting to explain the origins of species diversification - have come from scientists with good field knowledge. Although no such great theories are proposed here, the papers are underpinned entirely by field studies, and it is hoped that they have made a useful contribution to their individual scientific disciplines.

Because none of the submitted manuscripts are 'review papers', they assume that the reader already has a degree of understanding of the floristics and ecology of Neotropical savannas and Neotropical Seasonally Dry Tropical Forests (hereafter called SDTFs). Chapter Two attempts to provide such a background. Chapter Three discusses the history of floristic and vegetation studies in the Brazilian cerrado, SDTFs and Belize, placing the research in a historical context.

The papers submitted do not speculate to any great extent about the mechanisms by which the diversity of Neotropical savannas and SDTFs originated and are maintained. However, these are scientific questions that have been taxing biologists for over 150 years. I thought it appropriate, therefore, in Chaper Four to provide a brief discussion of some of the important issues relating to these questions as one of the objectives of my research has been to further our understanding of Neotropical biogeography. In particular, this chapter looks at the evidence for and against the refuge and museum theories of species diversification, considers the possible factors involved in maintaining ß-diversity[1] in the cerrados, and attempts to explain how the complex floristic affinities of the Peruvian SDTFs might have originated. In addition, the chapter briefly discusses the contribution of molecular phylogenetic work to our understanding of Neotropical biogeography. Although this has not formed part of my research, it represents an entirely new line of biogeographic evidence of such fundamental importance, it cannot be ignored.

I hope to continue developing a career in Neotropical botany and Chapter Six outlines some of the future research lines I would like to develop.

Resumé and chronology of research

I began working at the Royal Botanic Garden Edinburgh (RBGE) towards the close of 1992, employed initially to describe the patterns of diversity of the Central Brazilian cerrado (tree savanna) biome. This region is extremely biodiverse with a high percentage of endemic species and is recognised as a global biodiversity 'hot spot' (see Chapter 2). Unfortunately it is also heavily threatened by agricultural expansion, with around 40% of the biome converted to anthropic landscape to date.

At the beginning of the 1990s, although the taxonomy of the woody flora of the cerrado had largely been clarified, there was a very poor understanding of the patterns of species distributions within the biome, and very little inventory data available upon which to base

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[1] ß-diversity is the extent of differentiation of communities along habitat gradients (Whittaker, 1972).

floristic comparisons. The majority of the data that was available was also highly biased to a few geographical regions – namely the states of São Paulo, eastern Mato Grosso and the diminutive Distrito Federal in the heart of the country. As such it was impossible to make informed decisions about the optimum positioning of conservation areas. As the cerrado was being lost to agriculture at an unprecedented level it was clear that wide-ranging floristic inventories were urgently needed to assist in the planning and establishment of protected areas.

At the time of my arrival at the RBGE, there had already been a long-standing research interest in the region, largely due to one of its senior researchers (Dr. J. A. Ratter) being interested in its flora. Indeed, Dr. Ratter participated in the Royal Society Expedition to Xavantina/Cachimbo (Mato Grosso) in 1967. This was one of the first focused studies describing the flora of the region, and was fundamental in highlighting the biological importance of this biome to the scientific community. On completion of an MSc in Forestry at Oxford University, therefore, I eagerly joined his research team. The objectives of the research were ambitious, and ostensibly comprised two components. The first was to design and conduct a floristic survey programme of the whole biome - an area the size of Western Europe. The second was to analyse these data in an attempt to highlight biodiversity 'hotspots' and to investigate whether or not there were clear patterns of plant diversity within the region. The research itself was highly collaborative and carried out under the auspices of a project called the *Biodiversity and Management of the Biodiversity of the Brazilian Cerrados Project* (CMBBC). The success of the botanical field programme owed much to the support of EMBRAPA-Cerrados and the University of Brasília. All of our collaborators - and there have been many throughout Brazil - are fully acknowledged in the papers.

Four of the seven papers submitted here (Bridgewater et al., 2003; Ratter et al., 2003; Ratter et al, 2001; Ratter et al, 1996) have contributed significantly to the scientific understanding of the cerrado biome and elucidated its phytogeographic patterns. The survey programme, for example, doubled the floristic information available for the region. Many thousands of botanical collections were made during this period, and in addition to the years of fieldwork in

Brazil, many more months were spent identifying plant specimens in local and national herbaria. Duplicates of the specimens - identified for the greater part to species level - are deposited in the herbaria of the University of Brasília, the Royal Botanic Garden Edinburgh (RBGE) and Kew. The fieldwork programme has been instrumental in providing the data fuelling a number of regional and national conservation initiatives. The most significant of these was the 1998 Conservation International workshop *'Priority Actions for the Conservation of the Biodiversity of the Cerrado and Pantanal'* (Cavalcanti, 1999) which provided a blueprint for conservation for the biome.

I am second author for three of the papers cited above. I was involved in all the fieldwork (ca. two years were spent in the field conducting over 170 detailed floristic surveys!) and shared the inventory duties fully with Dr. Ratter, the senior researcher throughout the programme. All computer work involved in the research, including the compilation of the data matrices (an odious task taking about six months to complete), the selection, running and interpretation of all the multivariate analyses which elucidated the phytogeographic patterns were done by myself.

A brief resumé of each paper related to the cerrado is provided below:

(1) Ratter, J. A., Bridgewater S. & Ribeiro J. F. 2001. Espécies lenhosas da fitofisionomia cerrado sentido amplo em 170 localidades do bioma cerrado. *Boletim do Herbário Ezechias Paulo Heringer* 7: 5 – 112.

NB. An English translation of this paper is provided.

This presents our floristic survey data set, totalling 170 surveys. A novel rapid survey technique was developed for the fieldwork programme. This has since been widely adopted by other researchers throughout the region. These data provides the foundation of the multivariate analyses used in the three papers below.

(2) Bridgewater S., Ratter J. A. & Ribeiro J. F. (in press). Biogeographic patterns, ß-diversity and dominance in the cerrado biome. *Biodiversity and Conservation.*

(3) Ratter J. A., Bridgewater S. & Ribeiro J. F. (2003). Analysis of the floristic Composition of the Brazilian Cerrado vegetation III. Comparison of the Woody Vegetation of 376 areas. *Edinb. J. of Botany.* 60 (1). 54pp.

(4) Ratter, J. A., Bridgewater, S., Atkinson, R. & Ribeiro, J. F. (1996). Analysis of the Floristic Composition of the Brazilian Cerrado Vegetation II: Comparison of the Woody Vegetation of 98 Areas. *Edinb. J. of Botany.* 53: 153-180.

These three papers use multivariate analyses to describe patterns of diversity within the cerrado and define six distinct floristic provinces within it. Bridgewater et al. (2003) discussed patterns of ß-diversity and dominance within the cerrado and compares these with those hypothesised for Neotropical rain forests. Although there has been much research attempting to describe and explain the extraordinary plant diversity of the tropics, most researchers have focused on tropical rain forests. However floristic data for this ecosystem is poor and hinders the formulation of models which might explain how, and why, diversity varies through space. Due to our survey work, a much better data set is now available for the cerrado; I believe we have compiled one of the largest and most reliable floristic data sets for any diverse tropical biome. Bridgewater et al. (2003) shows that a suite of a little over a 100 'oligarch' species dominates the cerrado biome. This mirrors patterns of diversity hypothesised for western Amazonia rain forests.

(5) Bridgewater, S. & Stirton, C. (1997). A morphological and biogeographical study of the *Acosmium dasycarpum* complex. *Kew Bulletin* 52 (2): 471-475.

In the course of conducting the floristic surveys within Brazil it became clear that there were a number of taxonomic problems hindering floristic survey work. An example of this was the *Acosmium dasycarpum* (Sophoreae, Papilionoideae) species complex. In addition, taxonomic revisions by a number of authors suggested that the floristic provinces identified by our phytogeographic research were supported both by a number of parapatric species distribution patterns. Although I am more of a field botanist than a taxonomist, this work is a taxonomic study of the *Acosmium dasycarpum* complex. It was conducted to resolve the taxonomic ambiguities within the complex, and to see whether the distribution of the two morphological forms of this important woody cerrado species supported these patterns.

(6) Bridgewater S., Pennington R. T., Reynel C., Daza A. & Pennington T. D. 2003. A preliminary floristic and phytogeographic analysis of the dry forest areas of northern Peru. *Candollea* 58 (1): 129 – 148.

In 1997 and 1999, I spent ca. three months in the Inter-Andean valleys of northern Peru, conducting field surveys in the SDTFs of this region. This work resulted from an invitation from the University of La Molina, Lima, to assist in floristically describing the highly threatened forests of this area, and to assess their phytogeographic affinities. This research was a natural extension of the RBGE's cerrado research, SDTFs also being a characteristic of certain areas of the cerrado biome. Prior to this work, a number of researchers had made an attempt at clarifying the patterns of diversity of Neotropical SDTFs, but the lack of floristic data from northern Peru hindered clarification of the status of these forests. This paper provides inventory data for northern Peruvian SDTFs and discusses the evidence to consider these as a distinct phytogeographic unit within South America.

(7) Bridgewater, S., Ibáñez A, Ratter J. A. & Furley, P. (2002). Vegetation Classification and floristics of the savannas and associated wetlands of the Rio Bravo Conservation and Management Area, Belize. *Edinb. J. of Botany* 59 (3): 421-442.

In addition to work in Brazil and Peru, I was also asked to participate in a study to classify the vegetation of the savannas of the Rio Bravo Conservation and Management Area (RBCMA) The RBCMA is the flagship conservation area of the Belizean NGO Programme for Belize. Again, the work was seen as a logical extension of the RBGE's cerrado and dry forest research. The final paper submitted for consideration presents floristic inventory data and a vegetation classification for an area of savanna and associated wetland in Belize. It represents the first complete inventory of these ecologically important habitats in Belize. It involved four months in the field and the collection and determination of over 500 field collections. The paper includes a general discussion of Central American savannas and assesses their floristic affinities.

Approximately half of my seven years research was dedicated to the collection of data. This vital field component comprised conducting (in excess of) 180 floristic surveys, undertaking general collecting programmes in three countries and studying plant specimens in numerous national, regional and local herbaria. A thorough outline of the fieldwork methodology is given in each of the papers, suffice to say here that the importance of the fieldwork component in this research cannot be over emphasised. Throughout my fieldwork in the cerrado I was accompanied by one field assistant Joaquim Fonsêca Filho - a technician working at Embrapa-Cerrados. Although he knows the scientific names of many cerrado species, he prefers to use common names. During the course of our field work I collated these and have included them as an appendix at the end of this introductory essay. They represent the names most commonly used by our collecting team.

CHAPTER TWO: THE DRY FOREST AND SAVANNA VEGETATION OF THE NEOTROPICS: BACKGROUND AND OVERVIEW

Neotropical seasonally dry areas are usually covered by forest (SDTF) or savanna vegetation (Figure 1). Despite the fact that these habitats are far more threatened than rain forest, they have received little attention from conservationists and ecologists (Janzen, 1988; Mooney et al., 1995). In part this is due to the relatively depauperate nature of their floras (SDTFs support ca. 30 tree species species ≥10cm/hectare), when compared with the rain forest (ca. 120 species ≥10cm /hectare), although the cerrado – a type of tree savanna covering much of Central Brazil – is extremely species rich, harbouring over 10,000 species of plants, including ca. 800 species of savanna tree and large shrubs (Dias., 1992). The following sections provide brief overviews of the focal ecosystems of this doctorate, as these are not provided in the papers themselves.

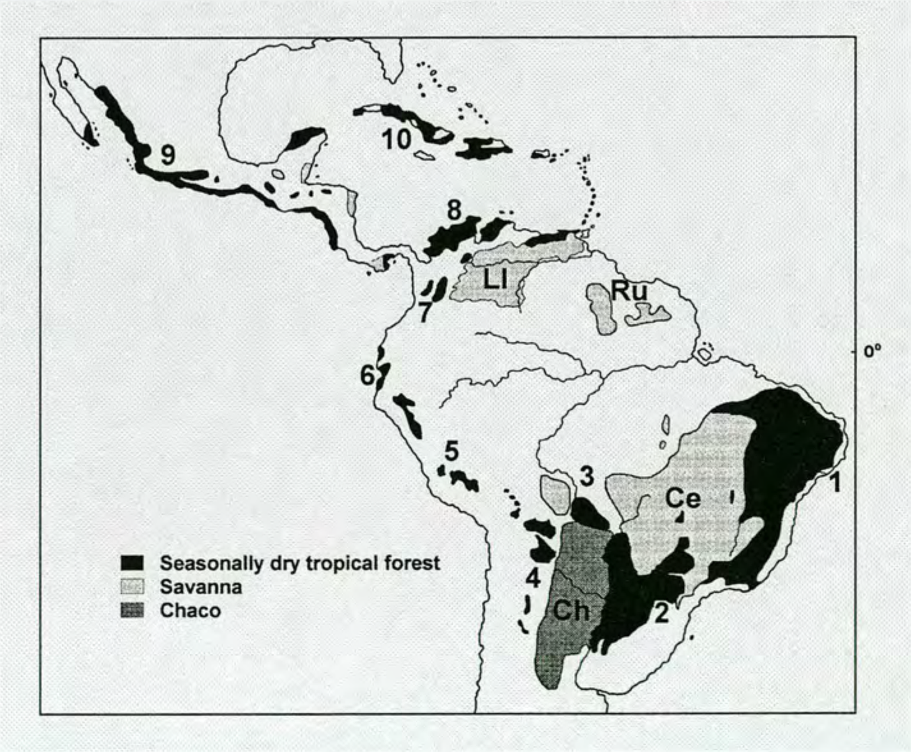

FIG.1. The distribution of seasonally dry vegetation in the Neotropics. Seasonally dry tropical forest; 1. Caatingas. 2. Misiones Nucleus. 3. Bolivian Chiquitano region. 4.Piedmont Nucleus. 5. Bolivian and Peruvian InterAndean valleys. 6. Pacific coastal Ecuador. 7. Colombian InterAndean valleys. 8. Caribbean coast of Colombia and Venezuala. 9. Central America. 10. Antilles. Savannas: Ce. Cerrado. Ll. Llanos. Ru. Rupununi. Ch: Chaco. Source: Pennington et al., 2000)

2.1 The Cerrado

The Brazilian savanna vegetation is called *cerrado* and covered some 2 million km² of Central Brazil (Figure 1), representing about 23% of the land surface of the country. It is the most geographically significant savanna in the Neotropics, and the most floristically diverse savanna system in the world. The core cerrado region extends from the margin of the Amazonian forest to outlying areas in the southern states of São Paulo and Paraná. The climate is typical of moist savannas, with an average precipitation (for over 90% of the area) of 800-2000 mm, and a very strong dry season during the southern winter (approx. April – September), while average temperatures are 18-28°C (Dias, 1992). The soils of most of the area are ferralitic oxisols and ultisols, dystrophic with low pH and availability of calcium and magnesium, and high aluminium content (Lopes and Cox, 1977; Furley & Ratter, 1988). The typical vegetation landscape within the biome consists of cerrado 'tree savanna' on the well-drained interfluves, with gallery forest following the watercourses. The cerrado itself is varied in form, ranging from grassland, sometimes with a sparse covering of shrubs and trees (campo limpo; campo sujo), through a well developed 'tree savanna' (campo cerrado; cerrado) to an almost closed woodland with a canopy height of 12-15m (cerradão) (Eiten, 1972).

Fire is an important ecological factor throughout the biome (Coutinho, 1990), and the woody flora of the cerrado shows adaptations such as thick, corky bark (e.g. *Pterogyne confertiflora*), xylopodia (e.g. *Andira humilis*) and the ability to sprout from lateral buds if the growing apex is killed by fire. The most ecologically dominant families of woody plants are the Leguminosae, Malphigiaceae, Melastomataceae and Rubiaceae; less diverse, but very characteristic of the cerrado is the Vochysiaceae. For example, there are three endemic species of *Qualea* which occur throughout the core area of cerrado (*Q. parviflora*, *Q. multiflora*, *Q. grandiflora)* and their presence essentially defines the biome. Cerrado is floristically distinct from the other types of seasonal vegetation, and whilst cerradão on mesotrophic soils may appear physiognomically rather similar to seasonally dry forest, it is floristically distinct (Ratter, 1992).

Disjunct, isolated areas of cerrado-like vegetation also occur within the Brazilian Amazon rain forest (Eiten, 1972), both in northern sites (e.g. in the states of Amapá and Roraima) and southern sites closer to the cerrados of Central Brazil (e.g. Humaitá - in the state of Amazonas) and even close to the Amazon river itself at Alter do Chão (Pará). These usually occur on poor, sandy soils (Solbrig, 1993) and with the exception of Alter do Chão are depauperate in numbers of species compared to the cerrados of Central Brazil (Sanaiotti, 1994). The southern sites and Alter do Chão have floristic affinities with Central Brazil, whilst the northern sites show affinities to the hydrologic savannas of the Llanos and the Rupununi savannas (Ratter et al., 1996; Sanaiotti, 1996).

Over the last thirty years there has been a great increase in research into the biodiversity of the cerrado biome. This has been fuelled by the increasing realisation that the cerrado is a world 'hot spot' of biodiversity (Dias, 1992; Fonseca et al., 2000; Myers et al., 2000) and that this biodiversity is under great threat, with little over 50% of its original extent now remaining (Alho & Martins, 1995).

2.2 Neotropical seasonally dry tropical forests (SDTFs).

In recent years there has been a dramatic increase in research into South American SDTFs and their floras (e.g. Prado, 1991; Prado & Gibbs, 1993: Gentry, 1995; Kessler & Helme, 1999; Pennington et al., 2000; Bridgewater et al., 2003). The stimulus for this research results from the realisation that as well as this ecosystem being one of the most threatened in the continent (Janzen, 1988), a study of their floras may elucidate patterns of historical vegetation change. From species distribution studies for example, Prado & Gibbs (1993) have suggested that the disjunct SDTF patches that are found today represent fragments of what may have been a larger area of dry forest ranging through the continent during the last glacial maximum - a 'Pleistocene Arc' of dry vegetation.

SDTFs occur where the rainfall is less than 1600 mm yr^{-1}, with at least 5-6 months receiving less than 100 mm (Gentry, 1995; Graham & Dilcher, 1995). The vegetation is mostly deciduous during the dry season, and deciduousness increases as rainfall declines, though in the driest areas there is a marked increase in evergreen and succulent species (Mooney et al., 1995). They are essentially tree-dominated ecosystems with a more or less continuous canopy and in which grasses are a minor element (Mooney et al., 1995). This distinguishes them from savannas which have a xeromorphic, fire-tolerant grass layer. SDTFs occur on fertile soils with a moderate to high pH and nutrient status and low levels of aluminium. Such soils are favourable for agriculture (Ratter et al., 1978), which has resulted in enormous destruction of these forests in many areas (e.g. less than 2% of seasonally dry forests on the Pacific coast of Mesoamerica are still intact; Janzen, 1988), a problem exacerbated by the large human populations in many Neotropical dry forest life zones (Murphy & Lugo, 1995).

SDTSs have a smaller stature and lower basal area than tropical rain forests (Murphy & Lugo, 1995), and thorny species are often prominent. Ecological processes are strongly seasonal. During the dry season, for example, there is a build up of leaf litter because sunlight penetrates to the forest floor and decomposition ceases in the low relative humidity. Flowering and fruiting phenologies are also strongly seasonal, with many species flowering synchronously at the transition between the dry and wet seasons whilst the trees are still leafless (Bullock, 1995). Conspicuous flowers and wind-dispersed seeds are frequent, in contrast to rain forests.

SDTFs vary greatly in form and species composition. Some formations, for example, can be diverse and similar in stature to the tall forest found on moister sites, whilst in the driest areas they take the form of cactus scrub. Many different names are used for the vegetation including tropical and subtropical dry forests, caatinga, mesotrophic, mesophilous or mesophytic forest, semideciduous or deciduous forest, bosque caducifolio and bosque espinoso.

The Leguminosae and Bignoniaceae dominate the woody floras of these forests throughout their range with the Anacardiaceae, Myrtaceae, Rubiaceae, Sapindaceae, Euphorbiaceae, Flacourtiaceae and Capparidaceae also more or less strongly represented (Gentry, 1995). The Cactaceae are prominent in the understorey, particularly at the formation's latitudinal extremes, and are an important element in the diversity of these forests. SDTFs usually have a closed canopy, with a sparse ground flora consisting of rather few grasses, with Bromeliaceae, Compositae, Malvaceae and Marantaceae also represented.

The largest areas of SDTFs in South America are found in northeastern Brazil (the 'caatingas', extending south to eastern Minas Gerais), in two areas defined by Prado and Gibbs (1993) as the 'Misiones' and 'Piedmont' nuclei (Fig. 1) and on the Caribbean coasts of Colombia and Venezuela. Other, smaller and more isolated areas of SDTFs occur in dry valleys in the Andes in Bolivia, Peru, Ecuador, and Colombia, coastal Ecuador and northern Peru, the 'Mato Grosso de Goiás' in Central Brazil and scattered throughout the Brazilian cerrado biome on areas of fertile soils (Ratter et al., 1978). In Central America, SDTFs are concentrated along the Pacific coast from Guanacaste in northern Costa Rica, to just north of the Tropic of Cancer in the Mexican state of Sonora. Within all of these areas SDTFs occur within a complex of vegetation types depending on local climatic, soil and topographic conditions. Phytosociological analysis of diverse woody stands from Argentina to the Brazilian Amazon indicate that seasonally dry tropical forests, including Brazilian caatinga and semideciduous forests of the Paranense province (*sensu* Cabrera & Willink 1973), form a cohesive unit quite distinct from both Chaco[2], cerrado and rain forest (Prado, 1991).

There is good evidence from the contemporary distribution of species in the disjunct areas of seasonally dry tropical forests for historical links among all these areas. Prado and Gibbs (1993) compared dot maps of distributions of individual species and documented 40 phylogenetically unrelated species that are distributed in up to ten disjunct areas of seasonally dry tropical forest, but which are absent from intervening moist and savanna vegetation. There are two possible explanations for these coincident distribution patterns: 1) the separation (vicariance) of formerly continuous distributions, or 2) multiple independent dispersal events among different areas. Because it is more likely that there has been a single vicariance event rather than many independent dispersal hypotheses, Prado and Gibbs concluded that *'these fragmentary and mostly disjunct distributional patterns are vestiges of a once extensive and largely contiguous seasonal woodland formation, which may have reached its maximum extension during a dry-cool period ca. 18,000-12,000 BP, coinciding with the contraction of the humid forest'*.

The SDTFs of Peru itself have been defined by different authors using a multitude of citeria (Linares-Palomino, unpublished manuscript), including their physiognomy, the degree of rainfall, seasonality, level of deciduousness and substrate. These were all published before the broad concept of SDTFs was proposed by Pennington et al. (2000), and have resulted in a very confused terminology for this broad vegetation type in this country. One of the most widely adopted classification systems for vegetation in the Neotropics is that devised by Holdridge (1947). This uses climatic parameters such as temperature, rainfall and humidity to define vegetation types.

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[2] The floristic composition of the Chaco forests is quite different from that of the seasonally dry tropical forests (Prado, 1991; Prado & Gibbs, 1993), and their floristic links are to the dry, temperate Monte and Andean Prepuna formations (Cabrera, 1976). This reflects the regular frosts received by the Chaco vegetation.

In Peru, Holdridge recognised six 'life zones' that ostensibly fall under the category of SDTFs as defined by Pennington et al. (2000). These comprised '*very dry tropical forests*', '*low montane dry subtropical forests*', '*low montane dry tropical forests*', '*premontane dry tropical forests*' and '*tropical dry forest*'. These cover an area in Peru of 44,643 km² - approximately 3.5% of the land area. A few years earlier, Weberbauer (1936) also recognised six distinct regional formations that can be considered as SDTFs. These comprised various xerophytic vegetation types of the InterAndean valleys and 'rainy green' park vegetation in the foothills of the Western Cordilleira of the Andes. However, Weberbauer never defined with rigour the characteristics of his vegetation types, and therefore it is often difficult to know where the boundaries lie between them. Much later, Ferreyra (1988) defined a number of SDTF formations in the north of Peru. One of these he called a '*ceibal*' due to its dominance by *Ceiba trichistandra*, and another '*agarrobal*' which is a type of tree savanna dominated by *Prosopis pallida*. A decade afterwards, the Forest Map of Peru published by INRENA (1995) makes little mention of SDTFs, although four types are classified which fall within the broad definition of SDTF. These comprise '*dry hill forests*', '*montane dry forests*', '*savanna type dry forests*' and '*InterAndean dry forests*'.

In an attempt to standarise the various terminologies of SDTFs in Peru, and to lay to rest the confusion that surrounds them, Linares-Palomino (unpublished manuscript) has adopted the SDTF concept proposed by Pennington et al. (2000), but adapted it to take account of the clear phytogeographic differences between them (Bridgewater et al., 2003; Linares-Palomino et al., in press). He suggests that all SDTFs in Peru should be classified as '*Ecuatorial subhumid*' (those in the departments of Tumbes, Piura, Lambayeque and La Libertad), '*Subhumid InterAndean*' (those of Chamaya, Marañon, Chalhuanca, Vilcanota, Huallaga, Mantaro and Apurimac), and '*Subhumid Eastern*' (primarily those of Tarapoto).

2.3 Belizean savannas

The floristics and structure of Belizean savannas are covered in detail in one of the papers submitted as part of this doctoral thesis. The following text, therefore, concentrates primarily on describing the extent and classification of this vegetation type. In particular, since the manuscript for Bridgewater et al. (2003) was submitted for publication, the Belizean savannas have been re-classified using the UNESCO classification system, and this is briefly reviewed here.

Savannas cover over 2 million km² of the Neotropics of which the cerrado and the Venezuelan llanos comprise the largest areas (Mistry, 2000). Additional smaller extents occur scattered across the continent, including the Gran Sabana of south-eastern Venezuela, the Rio Branco-Rupununi savannas in Guyana and Brazil and the savannas of the Magdalena Valley of northern Colombia. Scattered within Amazonian rainforest there are also patches of seasonal and hyperseasonal savannas[3] (and occasionally cerrado), some of which occur in areas of pure white sand with podzolised soils.

In Central America large patches of savanna occur in southern Mexico in the states of Tabasco, Chiapas, Veracruz, Campeche, Oaxaca and Guerrero, in Belize, Guatemala, south-eastern Honduras and north-eastern Nicaragua and on the Pacific coast of Panama. Savannas also occur in a number of the Carribean islands, the most significant areas being found in Cuba and Hispaniola. These widespread savannas are ecologically varied with the lowland savannas tending to be hyperseasonal in nature (*sensu* Sarmiento, 1983) with both seasonal flooding and drought conditions occuring during each annual cycle, with the upland savannas being usually better drained with reduced ground water effects.

The vegetation of Belize was first mapped in detail by the Land Use Survey Team (Wright et al., 1959), and their classification of savanna and related vegetation (including pine forest) attributed ca. 262,467 hectares to these communities. This constitutes approximately 12% of the surface area of Belize which covers a total of 22,963 km². This classic report classified Belizean savannas and associated forest-type communities into seven broad categories. These included pine and oak forests, orchard and open grass communities, and areas of savanna with scattered pine. Unlike the savannas of South America (such as the cerrado,

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[3] Some authors (see for instance Sarmiento, 1983) have classified Neotropical savannas as being either *seasonal* or *hyperseasonal*. Seasonal savannas have a conspicuous dry season. Hyperseasonal savannas, in additional to having a seasonal climate, also have waterlogged soils during the wet season, and thus are adapted to coping with two contrasting stresses – one induced by drought and the other by soil saturation.

Belizean savannas (and, indeed, many of the savanna areas in Central America) are striking in that the woody component is dominated by species of pine and oak, both of which represent 'northern floristic elements'.

A later study by King et al. (1992) groups all Belizean savannas and pine forests into one group – *pine forest and orchard savanna*. The stage at which '*pine savanna*' ('savanna with scattered pines' or its denser form 'pine ridge') can be differentiated from '*pine forest*' is a moot point, as the species composition of the two can be extremely similar and there is a continuous range of physiognomy uniting them. Most authors agree, therefore, that they should be classified together. Iremonger and Brokaw (1995) updated Wright's classification, and in this work a number of savannas and wetland vegetation types were identified, with general pine savanna classified as '*lowland needle-leaf moist open forests over poor soils*'.

The latest vegetation map for Belize was produced by Meerman & Sabido (2001) as part of the Central America Ecosystems Mapping Project. This map recognises 85 terrestrial ecosystems in Belize classified according to the system adopted by UNESCO (Mueller-Dombois & Ellenberg, 1974). This is essentially a physiognomic vegetation classification system. They classify all savanna communities into six categories which together cover 11% of the area of the country. These are: (1) *Tropical evergreen seasonal mixed needle and broadleaf lowland hill forest*; (2) *Tropical evergreen seasonal needle-leaf lowland dense forest*; (3) *Tropical evergreen seasonal needle-leaf lowland hill forest*; (4) *Tropical evergreen seasonal mixed needle and broadleaf submontane forest*; (5) *Tropical evergreen seasonal needle-leaf submontane forest*; (6) *Short-grass savanna with needle-leaved trees*; (7) *Short-grass savanna with shrubs*. Although it is a slight ecological simplification, categories 1-5 are essentially part of the continuum of pine savanna/forest types found on the Mountain Pine Ridge, whilst 5 and 6 are essentially the predominant pine savanna communities found in the Belize and Orange walk Districts in the north of the country, and in the eastern coastal regions of the Stann Creek and Toledo Districts in the south. Floristically, all these categories are very similar and represent an ecological continuum. A phytogeographic analysis of

Neoarctic savannas (Lenthal et al., 1999) indicated that although the Belizean savannas are floristically a part of a geographically widespread province ranging from northern South America to southern North America (including the Caribbean), they are distinctive in that they usually show an abundance of the palmetto (*Acoelarraphe wrightii*), a multi-stemmed palm typical of low and frequently inundated savannas.

In terms of geology the bedrock of much of Belize consists of limestone, and is a geological continuation of the southern half of the Yucatán of Mexico and the northern Petén of Guatemala. The dominant vegetation of this fertile lime-rich area is sub-tropical moist forest. Where savannas occur they tend to be on eroded littoral sediments deposited on top of the limestone during the Tertiary. The other geological formation supporting savannas in Belize is the Mayan mountains. The northern part of this chain (the Mountain Pine Ridge) comprises ancient igneous (primarily granite) and metamorphic rocks. It is believed that in the late Cretaceous when most of Central America was a shallow sea, the Maya mountains of Belize may well have been one of the few land areas above sea level at the times (Raven and Axlerod, 1974). The soils of this area are highly weathered and nutrient poor and pine savanna/forest is the dominant vegetation cover.

CHAPTER THREE: HISTORY OF BOTANICAL EXPLORATION AND VEGETATION STUDIES IN BRAZIL, PERU AND BELIZE

3.1 Brazil

'Although the country between Parnaguá and Saco do Tanque is comparatively level, yet there is a very perceptible rise; and although the general vegetation has very much the same character as that of other Catinga districts [sic.], many of the trees and shrubs were quite new to me. At this season very few were in flower; of these, the most remarkable was a very large tree to which the name of Sicupira is given by the inhabitants, and which I afterwards found extending far into the province of Goyaz: it belongs to the natural order Leguminosae, and has only very recently been described by Mr. Bentham, under the name of Commilobium polygalaeflorum [Pterodon ploygalaeflorum]: it is easily recognised at a great distance by its numerous large panicles of lilac flowers. An essential oil, which is contained in the fruit is much used by the inhabitants to alleviate the pain of the tooth-ache.... One of the finest trees I ever remember to have seen standing alone, grew by the side of a small brook which flowed at a little distance from the house; it was a species of Qualea, with a clean straight stem about one hundred feet in height, on which it supported a wide spreading top of branches; as it came into flower shortly after our arrival, and as there was no other way of obtaining specimens than by cutting the tree down, Senhor Guimerães himself proposed to do so, as soon as he knew I wished to possess a few specimens. After about two hours' labour on the part of himself and two of my men, this fine tree, which I was sorry to see destroyed, came to the ground with a tremendous crash'
George Gardner. 1849. Travels in the Interior of Brazil.

Concentrated botanical exploration of Central Brazil started a little under 200 years ago when the Bavarian naturalist Karl Friedrich Philipp von Martius first visited the region in 1818. Having completed his studies in medicine at the University of Erlangen and the Royal Bavarian Academy, Martius joined an Austrian expedition to Brazil in 1818, accompanying the future Empress Leopoldina (a Hapsburg princess) on her journey to meet her future spouse, the Emperor Pedro II. Another significant Austrian botanist Johann Emanuel Pohl was also present on this extraordinary voyage. He too was to make a considerable contribution to the scientific understanding of Brazilian botany, publishing his Plantarum Brasiliae, icones et descriptiones (two volumes) between 1827 and 1831, after collecting widely in Brazil for four years.

On arrival in Brazil, Martius embarked on a three-year journey across the country, together with his compatriot and fellow naturalist Johann Baptist von Spix. The botanical result of this journey which passed through the states of Rio de Janeiro, São Paulo, Minas Gerais and Bahia, was an impressive collection of ca. 6,500 plant species, subsequently incorporated into the Munich herbarium. In addition, Martius produced a book about his travels, Reise in Brasilien (Journey in Brazil). For the remainder of his life, Martius was extremely productive. His collections were the basis for the descriptions of many new regional species, the majority of which were published in Nova genera et species plantarum, a three-volumed work partially co-authored with the Italian botanist Joseph Gerhard Zuccarini between 1823 and 1832. His greatest legacy to our understanding of the flora of the region, however, was the initiation of the Flora Brasiliensis. Martius started this audacious project in 1840. Volume I (one of the last produced) comprises an introduction to the Flora, provides accounts of plant collectors and contributors, and some superb plates depicting a range of Brazilian vegetation types. In later volumes (published earlier!) Martius himself provided accounts of the Agavaceae (Volume III) and the Annonaceae (Volume XIII). The final volume of Flora Brasiliensis (Volume 15) was completed in 1906, 38 years after his death. Even today, although now considerably out of date, the Flora Brasiliensis is the only complete flora available for Brazil and remains invaluable to botanists. However, many of the family accounts have since been improved on in the Flora Neotropica. There are also now a number of very useful regional florula projects being developed. Two examples are the Flora of the Distrito Federal and the Flora of Mato Grosso, the former coordinated by the University of Brasília, and the latter by the Swiss botanist Balthasar Dubs (Dubs, 1998).

Another important historical contributor to Central Brazilian botany was the French botanist Augustin Françoise Cesar Prouvençal de Saint-Hilaire, who travelled through South America (although in particular, through Central and South Brazil) between 1816 and 1822. During his five-year sojourn in the Neotropics, Saint-Hilaire collected over 24,000 plant specimens representing 6,000 species, many of them new to science. In addition to his collections, the results of his botanical studies were published in several books and numerous articles in scientific journals. The works by which he is best known are the three-volumed Flora Brasiliae Meridionalis (published in conjunction with de Jussieu and J. Cambessèdes), Histoire des plantes les plus remarquables du Brésil et de Paraguay, Voyage dans le district des diamants et sur le littoral du Brésil and Voyage dans la province de Rio de Janeiro et Minas-Geraes.

Pressing plant specimens in the field

Two of South America's most famous botanical explorers, Friedrich Wilheim Heinrich Alexander von Humboldt and Aimé Jacques Alexandre Bonpland, did not include Brazil in their itinerary, their epic journey across South and Central America (1799 – 1804) focusing instead on northwest South America, and in particular Ecuador, Peru, Colombia. Their impact on Central Brazilian botany, however, was considerable in that they collected many 'generalist' cerrado species having wide distribution patterns outside of the biome. Although they collected a great many new species, it was another botanist - Charles Sigismund Kunth

– who was responsible for naming their collections. Kunth was a German botanist, born in Leipzig in 1788. He became a merchant's clerk in Berlin in 1806, but made the acquaintance of Alexander von Humboldt who encouraged his interest in botany. From 1813 till 1819 Kunth devoted his time to classifying the plants collected by Humboldt and Bonpland. Many of the new species described from their collections resulted from Kunth's endeavours and appeared in the Nova genera et species plantarum (1815 – 1825). In 1820 Kunth became professor of botany at the University of Berlin, and in 1829 sailed for South America, visiting Chile, Peru, Brazil, Venezuela, Central America, and the West Indies. His collections were bought after his death by the Prussian government, and formed a part of the Royal Herbarium in Berlin, although many were later destroyed during World War Two. Kunth also published a number of other significant botanical works related to Brazil including Les Mimosées et autres plantes legumineuses du Nouveau Continent (1819).

Perhaps the greatest historical Central Brazilian collector of all was a Scottish botanist, born in Glasgow in 1812. Like many botanists of the time, George Gardner studied medicine, his interest in botany initially being only a leisure pursuit. Enthused with Humboldt's evocative descriptions of South America, and encouraged by William Hooker, Professor of Botany at the University of Glasgow (later, of course, to become Director of Kew in 1841), Gardner travelled to Brazil in 1836, keen to explore the undescribed areas deep in the Brazilian interior. On arrival in Rio, he remained in the country's then capital for a year, before departing by sea to the northeast province of Ceará. From there he travelled across the entire country, slicing across the states of Ceará, Piauí, Goiás and Minas Gerais. Much of this journey took him through virgin cerrado territory. Gardner returned to Britain in 1841 after collecting 60,000 specimens. These were classified primarily by George Bentham. To a great extent his collections were the initial basis from which a detailed picture of the cerrado flora first emerged. In addition to collecting, Gardner was a keen social observer and his superb book Travels in the Interior of Brazil (1846) gives a wonderful account of life in Brazil at the time. Shortly after arriving back in Britain, Gardner was appointed superintendent of the Peradeniya Botanic Garden in Ceylon, although tragically he died shortly after arriving from 'a fit of apoplexy whilst taking off his boots.' One theory is that Gardner's death resulted from his contraction of Chagas' disease, an illness extremely prevalent in Central Brazil.

In terms of providing a detailed understanding of the ecology and floristics of the cerrado, Johannes Eugenius Bülow Warming was the great pioneer. Warming was born on the island of Mandø, Denmark in 1841, and studied at Copenhagen. Whilst still a student Warming spent three years at Lagoa Santa in Minas Gerais between 1863 and 1866. Although only a tiny village in the interior of Minas, at the time, Lagoa Santa had developed a formidable reputation as a centre of tropical scientific research, primarily due to the endeavours of another Dane - Peter Lund - a palaeontologist. Whilst based at Lagoa Santa, Warming studied the ecology of the cerrado vegetation, as well as undertaking intensive plant collecting. His account of the vegetation of Lagoa Santa (1892) is one of the great classics of Central Brazilian botany, and over a hundred years on, this work is still of great relevance to botanists in providing a sound initial understanding of the vegetation. Warming's work provides a description of the vegetation of the region, and a list of plant species collected in an area of ca. 170 km^2, centred around Lagoa Santa. This comprised 2,600 vascular plants, and his collections were extremely useful for those involved in compiling the Flora Brasiliensis. On return to Europe Warming continued his botanical and ecological studies and became professor at the Royal Institute of Technology in Stockholm, Sweden in 1882.

After Warming's superlative treatise on the vegetation of Lagoa Santa, the next great account on cerrado vegetation appeared in the Journal of Ecology, published by Robert Goodland in 1971. Shortly afterwards, George Eiten - an American botanist living in Brasília - provided a masterly and influential review of the knowledge of the biome at that time (Eiten, 1972). Two other classic texts describing the cerrado vegetation resulted from the Royal Society's Expedition to Xavatina/Cachimbo in 1967 (Ratter et al., 1973, 1977). For a two year period this pioneering expedition focused its studies on an area of vegetation transition between cerrado and rainforest in eastern Mato Grosso, and the resulting publications are still amongst the most detailed concentrated botanical studies ever conducted within the biome. In the last few years there has been an explosion of books describing cerrado ecology and floristics. The two most important of these are the compilations Cerrado: Ambiente e Flora (Sano & Almeida eds, 1998) and the Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna (Oliveira & Marquis eds., 2002).

In addition to those botanists mentioned above, many more have contributed greatly to our understanding of the flora of this biome in the last century. A number merit particular mention. One particularly noteworthy researcher was Carlos Toledo Rizzini, a botanist based at the Jardim Botânico do Rio de Janeiro. Rizzini was the first scientist to produce a list of woody species of the cerrado. This was published in the proceedings of the First Symposium on the Cerrado in 1963. Rizzini's list of woody trees and shrubs comprised 537 species belonging to 242 genera. This list has since been added to, and a number of botanists have published more recent estimates of the diversity of the cerrado flora. These include Mendonça et al. (1998), Castro et al. (1999) and Ratter et al. (2003). The current understanding is that the whole biome contains about 10,000 species, of which at least a third are thought to be endemic. This estimate considers the combined floras of all the vegetation types of the biome including cerrado sensu lato[4], mesophilous and gallery forests, swamp vegetation etc. For the cerrado sensu lato, the current concensus is that the species diversity is between 3,000 and 7,000 species, of which ca. 1,000 are woody.

Throughout the 1960s and 1970s a number of botanists continued to collect prolifically across the biome including Ezechias Heringer (Brasília), Dona Graziella Barrosa (Brasília), George Eiten (Brasília), Howard Irwin (New York), William Anderson (New York) and James Ratter (Edinburgh). Today there are hundreds of collectors working in Central Brazil, the majority of whom are now Brazilian. For example, in Minas Gerais, the research group of Mitzi Brandão and associates have worked over a great area of southern and central Minas Gerais (see for instance, Brandão & Gavilhanes, 1992). In the south-west, Giselda Durigan has surveyed much of the cerrado remnants in São Paulo state (Durigan et al., 2003) whilst in the far north Miranda (1997) has surveyed the disjunct Amazonian savannas of Roraima. The most complete herbarium collections for the cerrado (within Brazil) are those curated by the

Universities of Brasília, Campinas and São Paulo. In addition, the Rio Botanical Garden and the herbarium of the Instituto Brasileiro de Geografia e Estatística (IBGE, based in Brasília) also have fine representations of the Central Brazilian flora. Outside of the country, concentrated collections - including many of the most recent - can be found at the Botanic Gardens of New York, Kew, and Edinburgh.

In the last ten years there has been a surge of research activity attempting to describe the patterns of diversity within the cerrado biome. This has coincided with the realisation that the cerrado is a 'hotspot' of biodiversity (Myers, 2000) and that it is highly under threat. In particular, three initiatives have made significant contributions to our understanding of Central Brazilian phytogeographic patterns. In the late 1990s in the south of the biome, Dr. Giselda Durigan and a team from the University of São Paulo made a floristic comparison of 86 fragments of cerrado found within the São Paulo state boundaries (Durigan, 2001; Durigan, 2003). This work was conducted as part of the project Conservation feasibility of the cerrado remnants in São Paulo state financed by the Biota Programme. In the mid 1990s Dr Alberto Jorge F. de Castro of the Federal University of Piauí (although then a doctoral student at Campinas University) compared the woody flora of the entire cerrado biome using woody species lists from published cerrado inventories. This excellent work (Castro & Martins, 1999) identified three 'supercentres' of biodiversity within the cerrado relating to the south/southeast, the Central Plateau and the northeast regions. The first attempt at a broad examination of cerrado floristics, however, was made by Drs. James Ratter & Tom Dargie (Ratter & Dargie, 1992) who reported a comparison of data for 26 areas of cerrado in the late 1980s.

Two recent important phytogeographic projects are based in Brasília. The first is the Conservação e Manejo da Biodiversidade do Bioma Cerrado (BBC) project, a collaborative venture between Embrapa-Cerrados, the University of Brasília, and the Royal Botanic Garden Edinburgh. In the 1990s this project conducted over 170 floristic surveys in the northern and

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[4] Cerrado *sensu lato* is the term given to the typical tree savanna vegetation of the biome. It comprises a range of physiognomic forms, known by a series of names of vernacular origin.

central-western parts of the cerrado biome filling in many gaps in our knowledge of the cerrado flora. All of the cerrado phytogeographic data presented in this thesis result from this initiative. Another large concurrent and complementary initiative is the Biogeografia dos Cerrados project, coordinated by the Forestry Department of the University of Brasília. This has also conducted many surveys in the cerrado – principally in the extensive Chapadas Pratinha and dos Veadeiros in Central Brazil (Felfili & Silva Jr., 1993; Felfili et al., 1997). This project has also made assessments of regional floristic ß-diversity patterns within these limited areas.

3.2 Peru

An excellent historical account of botanical research in Peru is given by Weberbauer (1911) who chronicles the major botanical explorations in the country during the 18th and 19th centuries. Floristic research in Peruvian dry forests dates from the mid 18th century. Although there has been a long history of exploration and the region has attracted the attention of many botanical 'greats' (including Ruiz and Pavón, Humboldt and Bonpland, Richard Spruce and Al Gentry), for the most part botanical collecting has not been focused or intensive in dry forest areas and today, our knowledge of the flora is still far from complete. Considering that these areas are known to have unique highly endemic floras and are under considerable threat (Bridgewater et al., 2003; Janzen, 1988), further floristic research in the region is desperately needed. Until the patterns of diversity within dry forests are further clarified, then it will continue to be impossible to make well-informed judgements on their conservation.

To give an indication of the present paucity of floristic knowledge of Peruvian dry forests, a collecting trip to the dry forests of northern Peru in 1999 (the data resulting from this are provided in one the papers submitted as part of this doctorate submission), revealed 237 woody taxa. Of these, five were found to be new species, and 66 (i.e. nearly 30% of the total) were impossible to determine to species level, despite being compared in the herbaria at La Molina (Lima), the Royal Botanic Garden Edinburgh, and the Royal Botanic Gardens Kew and using available monographs. Although this reflects in part the normal difficulty encountered when attempting to determine sterile tropical collections - especially in such problematic groups as the Hippocrateaceae, Myrtaceae, Mimosaceae, Combretaceae etc. - much of the difficulty resulted from the fact that many of the species had rarely been collected before, were therefore not represented in the world's herbaria, and had escaped being included in taxonomic accounts. It should also be remembered that all collections in this particular example were made in highly accessible areas, usually along roadsides and often near urban centres. If one was to venture further into the inter-Andean valleys to remoter areas, there is a high probability that there are many more species to be recorded. Indeed, in a recent collecting trip to the Marañon valley Dr. Colin Hughes of Oxford University discovered a new genus of the Legumuinosae tribe Dalbergiae closely related to *Tipuana* (Hughes, pers. comm.).

The first significant botanist to visit northern Peru was Charles Marie de la Condamine who crossed from Loja (Ecuador) to Jaen (Peru) in 1743. Condamine was a mathematician by training and the primary aim of his extended visit to South American was to measure the length of a degree of meridian at the equator as part of an expedition led by Louis Godin. However he was an enthusiastic botanist and one of his significant achievements whilst in Quito (Ecuador) was to send a package of rubber to the Paris Academy with a long memoir describing many aspects of its origins and production. This represented one of the first descriptions of this material. Whilst in northern Peru, Condamine recorded aspects of the flora of the region before making his infamous four month trip down the length of the Amazon from the Marañon – one of its most remote tributaries – to its mouth in Brazil.

Alexander von Humboldt

The French botanist Joseph de Jussieu (who was part of Condamine's expedition) collected around Loja (Ecuador), whilst a little distance over the border in Peru, two Spanish botanists - Antonio de Ulloa and Jorge Juan – collected in Tumbes on their way from Guayaquil to Lima. Half a century later in 1802, the celebrated pairing of Alexander von Humboldt and A. Bonpland collected widely in the region. Although their efforts concentrated mainly in the Andes, they also collected in dry forest areas of the inter-Andean valleys around Ayuabaca, Huancabamba, Marañon and Cajamarca.

A further 50 years were to pass before the arrival of the Yorkshireman Richard Spruce whose prolific collecting across northern South America was to transform our knowledge of the flora of the region. Included in Spruce's astonishing ten-year itinerary was a two year period spent close to an area of dry forest around Tarapoto, to the east of the Eastern Andean massif. Spruce's 7,000 collections from this region are of inestimable scientific value for they form the basis of our floristic knowledge of that area, and many of his collections are the basis of original species descriptions. Few botanists have collected intensively in this region since. Indeed, it is common when studying dry forest herbarium specimens from northern Peru to find only one specimen in a folder. This specimen is invariably Spruce's, and is frequently the type. It is only a slight exaggeration to say that if a modern day botanist is attempting to determine his collections by comparison with specimens in a herbarium, if Spruce collected the species, naming is usually possible. If he did not, then accurate determination can prove to be difficult.

Since Spruce, a number of other botanical collectors have made forays into dry forest areas. These include Constantin von Jelski (around Chota and Cutervo in Cajamarca) in 1878 and 1879, and Weberbauer in the early part of the 20th century around Piura, Jaen, Cajamarca and Tumbes. Perhaps Weberbauer's most significant contribution to our understanding of the region's botany was the production of a vegetation map for the region and the publishing of his 'Phytogeogarphy of the Peruvian Andes' in 1936. Since Weberbauer, there has been sporadic interest in the flora of Peruvian dry forests. In the 1970s, for example, the Forestry Department of Peru made an ecological assessment of the dry forests in Tumbes and Piura

(Brack et al., 1973). This work was fundamental to the establishment of the Cerros de Amotape National park and the El Angolo Game Reserve in 1975. In recent years continuing fieldwork in the dry forests of southern Ecuador and in northern Peru have been conducted by various universities in the north of the country and by researchers from the Royal Botanic Gardens Kew, the Field Museum, Chicago, and the Royal Botanic Garden Edinburgh.

One significant figure of the late 20th century is Alwyn H. Gentry, who at the time of his death in 1993, was one of the leading authorities on the botany of tropical America. In the early 1970s, Gentry started to compile a quantitative data set of tropical and temperate forest samples, with a view to examining the correlations between diversity and a variety of environmental variables, particularly precipitation, elevations, and latitude. As part of this project, Gentry and his collaborators conducted quantitative studies in a plot of a tenth of a hectare close to Tarapoto. Until recently this represented the only existing quantitative data for the region. Subsequent quantitative studies conducted in dry forest areas include those of Klitgaard et al. (1999) in Lojas (Ecuador), and Linares-Palomino (2002) and Bridgewater et al. (2003) in northern Peru.

3.3 Belize

Detailed accounts of the history of plant collecting and botanical studies are given by Balick et al. (2000) and Brokaw (2001). It was only at the beginning of the nineteenth century that botanical collecting for scientific purposes began in Belize. The earliest ecological descriptions of the country were recorded by Captain George Henderson, his account of the British Settlement of Honduras (1811) containing the first detailed descriptions of the natural history of the country. This included information on the timber industry. Many botanists have focused their activities in Belize since this first specimen was collected, with a few deserving particular mention.

Morton Peck, a young American botanist (Harvard University) collected nearly a thousand numbers in Belize between 1905 and 1907, mainly in the Manatee River region of Belize District. His grass collections indicated the West Indian affinities of Belize's flora (Bartlett, 1932). The best known historical collector, however, was William Schipp, an Australian who collected in Belize between 1929 and 1937, and whose specimens were identified by Paul Standley (Field Museum of Natural History, Chicago). Schipp collected in excess of 2,000 numbers, the majority collected in large sets which were distributed to a number of herbaria in America and Europe. Over 150 of these are types. Another botanist who contributed greatly to our knowledge of the Belizean flora was Percival Gentle who devoted the latter half of his life collecting herbarium specimens throughout the country. From 1931 until shortly before his death in 1958, Gentle collected 9,756 numbers making him the most prolific collector of the Belizean flora and it is estimated that he collected approximately 65% of the flora. Cyrus Lundell and John Dwyer (Missouri Botanical Garden) are two other botanists who have contributed much to our knowledge of the Belizean flora, the former collecting 3,000 numbers between 1928 and 1936, and the latter collecting widely in the country starting in 1967. Other recent prolific collectors include Caroline Whitefoord (Natural History Museum), Michael Balick (New York Botanical Garden) and Tom Croat and Alwyn Gentry (Missouri Botanical Garden).

Based on an examination of the collections found in a number of herbaria – Missouri in particular - a number of checklists have been published of the Belizean flora. That of Spellman et al. (1975) - which lists dicotyledons only - also includes an account of botanists who had collected in the country up to that date. A little later, Dwyer and Spellman (1981) produced a checklist of the monocotyledons, whilst Hartshorn et al. (1984) published a detailed list of the trees shortly afterwards. The most recent and comprehensive checklist, however, was published by Balick et al. (2000).

Despite the great interest in Belize during the 18th and 19th centuries on account of its timber reserves – and in particular, the rich abundance of mahogany, logwood and cedar to be found within its borders – there are relatively few early detailed ecological and floristic accounts. The first description of vegetation types in Belize was done by Morris (1883), although the most significant early written contribution to our knowledge of the vegetation and flora of the country came from Standley & Record's *Flora of British Honduras* (1936). The stimulus for this work came from an attempt to provide reliable information on the names of woody plants of British Honduras for the country's Forestry Department. Standley and Record's work comprised two parts. The first gives a superb overview of the vegetation of Belize, including accounts of the economic timber species, whilst the second provides keys and descriptions of (primarily) the woody flora. Shortly afterwards, Lundell (1937) published *The Vegetation of Petén*. Although this work focuses on Guatemala, it contains descriptions of vegetation types and species lists of considerable value to botanists working in Belize.

From 1946, volumes of the *Flora of Guatemala began* to appear, the intention being also to include all species known in Belize. This Flora - which was published in the journal *Fieldiana* (Volume 24) - comprises 12 parts and was completed in 1977. The most up- to-date (but as yet unfinished) guide to the flora of Belize is the *Flora Mesoamericana*. This is a collaborative effort of the Missouri Botanical Garden, the Instituto de Biología of the National Autonomous University of Mexico (UNAM), the Natural History Museum, London. Published in Spanish it describes all the vascular plants growing in the southeastern states of Mexico (including the Yucatán Peninsula) and all the Central American republics. In total the flora is expected to provide taxonomic accounts of about 255 familes (80 of which have been completed to date) and 17,000 species. The project publishes its results on the Internet and eventually will also comprise seven printed volumes.

Stevenson (1938) attempted the first environmental description of Belize, although the country's vegetation was first mapped in detail by the Land Use Survey Team (Wright et al., 1959). The objective of this work was to describe the agricultural potential of Belize. This seminal contribution to our understanding of Belizean soils and vegetation recognised 18 main classes of vegetation and 77 'subtypes'. Iremonger and Brokaw (1995) devised a modernised vegetation classification for Belize, the first significant attempt to update and improve on the earlier work of Wright and his team. The justification for this work was to devise a classification scheme that was readily understood by international conservation community and which used contemporary terminology. To this end, they based it on concepts from the classification system adopted by UNESCO (Mueller-Dombois & Ellenberg, 1974). The most recent vegetation mapping of Belize was done by Meerman and Sabido (2001), conducted as part of the Central America Ecosystems Mapping Project (CAEMP). This was commissioned by The World Bank and the Government of the Netherlands. The primary objective of the CAEMP was to create an ecosystems map on the scale of 1:250,000 for the region using a uniform methodology and nomenclature. The objective of the Belizean section of the project was to update and correct the vegetation map produced by Iremonger and Brokaw (1995).

CHAPTER FOUR: UNDERSTANDING PHYTOGEOGRAPHY

Although the papers submitted for consideration for this doctorate describe patterns of diversity none are 'review papers'. As such they do not speculate to any great extent about the mechanisms by which high levels of tropical species diversity originated and are maintained. These important questions, however, are of great interest to me – and to a number of other researchers based at RBGE - and have been taxing biologists across the world for over 150 years. As such, I believe that a brief discussion of some of the important issues related to them should be included in this broad introduction to my research. In addition, I have also attempted to briefly summarise the new contribution of molecular phylogenetic research to our understanding of historical vegetation change.

4.1 The museum and refuge theories

'The primeval forests of the equatorial zone are grand and overwhelming by their vastness, and by the display of a force of development and vigour of growth rarely or never witnessed in temperate climates…. If the traveler notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction….The absence of the gregarious or social habit, so general in the forests of extra-tropical countries, is probably dependent on the extreme equability and permanence of the climate….Every form of vegetation has become alike adapted to its genial heat and ample moisture, which has probably changed little even throughout geological periods; and the never ceasing struggle for existence between the various species in the same area has resulted in a nice balance of organic forces, which gives the advantage, now to one, now to another species, and prevents any one type of vegetation from monopolising territory to the exclusion of the rest. The same general clauses have led to the filling up of every place in nature with some specially adapted form.'
A. R. Wallace, 1855

The Neotropics, with 90,000 plant species (Thomas 1999), has the most diverse flora on the planet. Most of this diversity is contained in rain forest ecosystems. The plant fossil record suggests that the majority of the species occurring in the tropics must have originated during the past 65 million years of the Cenozoic era (Magallón et al., 1999). However the exact evolutionary basis for angiosperm diversification leading to the phenomenally high species numbers observed the rain forests remains uncertain. Two hypotheses, however, have been proposed.

The first hypothesis held sway for much of the 20th century, and saw the tropics as a 'museum', where relatively stable climates through the Cenozoic resulted in low extinction rates, allowing species to accumulate over time. This idea was first suggested by Wallace in the mid nineteenth century, although it was not proposed as a 'scientific theory' for another 100 years:

> *'The equatorial zone, in short, exhibits to us the result of a comparatively continuous and unchecked development of organic forms; while in the temperate regions there have been a series of periodic checks and extinctions of a more or less disasterous nature, necessitating the commencement of the work of development in certain lines over and over again. In the one, evolution has had a fair chance; in the other, it has had countless difficulties thrown in its way.'*

The "Museum Hypothesis" became scientifically popular only after it was championed by Dobzhansky (1950) and then by Fisher (1960). Their theory was based on 1) the observation that as latitude increases, diversity decreases, and 2) that during past glaciations (such as the Pleistocene), temperate and polar zones underwent severe climate changes causing mass extinctions, whilst it was believed that the climate of tropical regions remained relatively stable, allowing gradual species accruement to very high levels. Dobzhansky suggested that the severe and changing conditions faced by organisms in temperate regions resulted in the evolution of a few generalized species readily able to adapt. In comparison, he believed that natural selection in the tropics was governed more by biotic interactions, resulting in the evolution of increased specialisation.

The Museum Hypothesis was later challenged by evidence that tropical climates, rather than being stable over long geologic periods - as previously thought to be the case - had varied widely over the past two million years of the Pleistocene (Van der Hammen, 1974). This led to hypotheses of a more recent climate driven 'speciation surge' in the tropics, rather than a gradual increase in species over time in a non-changing environment. The most popular of these theories was the 'refuge' model (Haffer, 1969). This suggested that during glacial maxima, the rain forest contracted to isolated pockets (refugia), separated from each other by a dry-adapted vegetation better able to flourish in the colder xeric conditions thought to exist during these periods. It was believed that these forest refugia may have played an important role in biological diversification by fuelling high speciation rates in rain forest areas due to allopatric speciation whilst populations became fragmented. This process of contraction and expansion was not a single isolated incident but occurred many times, coinciding with repeated glaciations. Tropical climates are currently hot and wet, with the forests enjoying a period of maximum expansion. Haffer (1969) proposed this mechanism by reconstructing forest refuges in Amazonia using current distribution patterns of birds and data on rainfall – areas of current high rainfall equating to putative forest refugia. Prance (1973) provided data supporting the theory using evidence from plant distribution patterns using distribution patterns from families such as the Chrysobalanaceae, Lecythidaceae, Dichapetalaceae and Caryocaraceae, although he clearly highlighted the problems with inferring refugial centres from incomplete data sets. Prance also noted that centres of endemism do not necessarily coincide with refugia.

The Refuge Theory was popular in the 1970s and 1980s, but has more recently attracted vociferous criticism, especially for Neotropical biota. This has come from three primary sources. Firstly, palaeoecologists have found pollen signatures from the glacial periods to be consistent with rain forest and that there is little evidence of grass from pollen cores. (e.g., Colinvaux et al., 2001). However, there is significant regional variation in Quaternary pollen signatures. In the south-east of Brazil, for example, Behling (1997) uses palynological evidence to propose that semi-deciduous forest and cerrado was replaced by grasslands and gallery forests during the last glaciation. The work of Colinvaux et al. (2001) suggests long term forest stability in Amazonia, implying that if a dry-adapted vegetation replaced rain forest at times of glacial maxima, that this was not a type of savanna with a distinct grassy layer. Additional evidence for the refuge hypothesis drawn from geomorphology (such as the existence of 'stone lines' in Amazonia which a number of authors took to indicate past aridity) has also been disputed (Colinvaux, 2001). Second, dynamic vegetation model simulations appear to reject the hypothesis of widespread savanna in Amazonia at the last glacial maximum (Cowling et al., 2001). These last studies are based on the belief that carbon dioxide levels fell during Pleistocene glacial maxima. Models of leaf area index suggest that the type of vegetation most likely supported by such carbon dioxide levels would have been forest rather than savanna. Finally, preliminary genetic divergence data based on molecular phylogenies of a number of animal groups (e.g. birds, mammals, lizards, frogs etc.) indicate that speciation in tropical rain forest animals generally pre-dates the Pleistocene, with molecular clocks indicating an earlier Miocene or Pliocene origin (e.g. Moritz et al., 2000). These data together have led to a number of workers dismissing the possibility of Pleistocene speciation.

However, this rejection of the Refuge Theory may be premature because rain forest may have been fragmented by SDTFs (Pennington et al., 2000). This theory is supported by the observation that over 100 phylogenetically unrelated species (e.g. *Amburana cearensis*, *Geoffoea spinosa*) are distributed in up to ten disjunct areas of seasonally dry forest across South America, although they are absent from intervening savanna and moist forest vegetation. This suggests that there may have been a wider expanse of seasonally dry forests in the cool-dry climates of the Quaternary. An alternative explanation, however, is that these current distribution patterns of seasonally dry forest species may have been caused by multiple long-distance dispersal events. However, the former would seem the most likely. As Pennington et al. (2000) comment, '*it is more parsimonious to assume a single event of vicariance rather than many independent dispersal hypotheses*'. In addition, the Pleistocene pollen profiles cited by Colinvaux et al. (1996) as supporting the existence of rain forest are equally consistent with seasonally dry tropical forest. In addition, species of a number fo genera (e.g. *Ruprechtia* and *Pereskia*) show high degrees of endemicity in different patches of SDTF, and vicariance of dry forest patches provides a realistic hypothesis (as to how these endemic species evolved, the mechanism inferred being allopatric speciation.

4.2 β-diversity maintenance and the Brazilian cerrado

One of the great ecological questions that remains unanswered for diverse tropical ecosystems is: 'What mechanisms govern and maintain their high diversity?' Many studies attempting to resolve this question have been conducted in Amazonian rain forest, and although the findings vary and are, as one might expect, far from conclusive, the evidence indicates environmental (e.g. precipitation, dry season severity, temperature etc.) and spatial factors (including plant dispersal capacity) as heavily influencing diversity patterns (see for instance, Duivenvoorden et al 2002; Tuomisto and Ruokolainen 1997; Ruokolainen et al. 1997; ter Steege et al. 2000; Pyke et al. 2001; Condit et al. 2002).). However, Duivenvoorden et al. (2002) show that most of the floristic variation in tropical forests cannot be fully explained by either spatial or environmental ecosystem dynamics, inferring that historical and stochastic processes are responsible for much of the unexplained variation.

Based on multivariate analyses based on the floristic data available to them Castro (1994) and Castro and Martins (1999) suggest the existence eight distinct phytogeographic provinces within the cerrado biome and three 'supercentres of biodiversity'. They correlate these 'supercentres' (southern/southeast; Brazilian Central Plateau; northeast) with climatic factors (especially the presence of droughts and frosts), and suggest that there is a hydrologic soil gradient from the south-east to the north-east and that species distributions can be correlated with this trend. Indeed, simply by observing an average annual rainfall map for the cerrado, a distinct line of disjunction running north-south (roughly following the eastern boundaries of the states of Tocantins and Goiás) can clearly be discerned marking the boundary between the eastern arid areas of the cerrados of Bahia, Ceará, Maranhão and northern Minas Gerais(where rainfall is under 1200mm per annum), and the wetter regions west of this line, the majority of which have rainfall in excess of 1400mm/annum. This line corresponds closely to the boundary of the north-eastern floristic province identified by Ratter et al. (2003) and between the north-east and south-east cerrado 'biodiversity supercentres' of Castro and Martins (1999). The latter authors identify both the occurrence of drought and frosts as primary climatic factors influencing the distribution of cerrado species. Another recent study investigating the environmental factors governing broad ß-diversity patterns within the cerrado (Dias, 1998) also found mean annual precipitation to be a significant factor in explaining regional floristic patterns.

Altitude is another important factor proposed to influence species distributions within the cerrado region (Felfili et al. 2001), and Castro and Martins (1999) suggest that altitude reinforces the separation of their three proposed cerrado biodiversity 'supercentres', these being found in the southeast of the region (generally at low altitude between 0-500m), the central plateau (high altitude between 900-1200m) and in the northeast (medium altitude between 500-900m). This finding is also supported by Dias (1998). One of the strongest factors determining local and regional floristic patterns is undoubtedly the fertility of the soil (see for instance, Ratter et al. 1977; Furley and Ratter 1988; Oliveira-Filho and Martins 1991), with mesotrophic soils (with higher levels of calcium and magnesium) supporting a characteristic suite of species (as observed in the far-western and over much of the central-western floristic provinces for example). At the local level, pockets of more fertile soils bearing characteristic mesotrophic flora can be found in most of the cerrado region in areas where erosion cuts down into base-rich rocks. Interestingly, although soil fertility clearly affects the local species composition of a cerrado community, during our analysis of the 376 cerrado areas, separate analyses were run on dystrophic and mesotrophic sites and both showed occurrence of the same broad geographic provinces (unpubl. data), indicating the importance of other factors in governing patterns at the regional level. In this case it appears that the significance of a floristic differentiation based on relatively few mesotrophic species is overwhelmed by the background regional similarity of the many other species present.

Historic factors are likely to be of great significance in explaining present day diversity patterns, although the paucity of past data (both for the cerrado and Amazonian rain forest) prevents any rigorous analyses, despite a great deal of interesting and worthwhile informed speculation. Silva (1995), for example, has suggested that biotic diversity within the cerrado increased through interchange with adjacent regions during the Quaternary climatic-vegetational fluctuations. A number of authors (e.g. Cole 1986; Oliveira-Filho and Ratter 2002) attribute the great diversity of the cerrado to its great age, and recent research using data on endemic birds classified into palaeoendemic and neoendemic evolutionary categories supports this (Silva and Bates, 2002).

4.2 Explaining the phytogeographic patterns of northern Peru

Inventory data for northern Peruvian SDTFs indicate high levels of endemism and low degrees of floristic similarity between disjunct patches separated by the Eastern and Western Andean Massifs (Bridgewater et al., 2003). A broader multivariate analysis of 62 samples from representative dry forests in Latin America (Linares- Palomino et al., in press) support the division of these dry forest formations into three broad phytogeographical groups: (1) a Central American–Caribbean group (including northern South America), (2) a Ecuadorian-Peruvian group, and (3) a Bolivian-Argentinean group. This contradicts the phytogeographical divisions for dry plant formations suggested by Sarmiento (1975) who proposed four South American arid flora regions: (1) from southern Mexico, through Central America, to northern South America southwards to Peru, (2) north-eastern and Central Brazil and the Chaco forests of Bolivia and Paraguay, (3) the Chaco forests themselves and (4) the mediterranean evergreen scrub and forests of south-central Chile.

The origin of each of the three phytogeographical groups cannot be easily explained, as the geological and climatological factors influencing these patterns are complex. Although Quaternary glacial and inter-glacial events have undoubtedly been important in diverging the floras of these regions, plate tectonic events and the Andean uplift have also been crucial in shaping present day vegetation distribution patterns in the Neotropics.

An important factor in explaining the clear separation of the Central American-Caribbean SDTFs is the isolation of South America from any other landmass for approximately 80 million years, beginning with the rifting from Africa and ending with the closure of the Isthmus of Panama approximately 3.5 – 3.1 Ma (Burnham & Graham, 1999). There is geological evidence that brief connections between northern South America and *proto* Central America might have existed in the latest Eocene/early Oligocene (35 – 33 Ma) (Iturralde-Vinent & MacPhee, 1999), but little paleobotanical and paleozoologocal evidence exists to support migration events, and it is thought that these connections would never have been continuous. However, this possible migration route offers one explanation for the apparent close floristic link of Costa Rican with northern South American sites in the multivariate analyses. Furthermore, from the Eocene-Oligocene transition, through the middle Miocene, and especially during high sea-level stands in the late Miocene, an epicontinental sea in the present-day Orinoco river basin might have isolated north-western South America from the rest of the continent (Iturralde-Vinent & MacPhee, 1999). This may have reinforced the floristic differences between northern South American sites and the rest of the continent, which are demonstrated in this study.

Several authors have proposed a dynamic relationship between moist/wet forests and dry vegetation formations (savannas and dry forests) in the Neotropics during glacial and inter-glacial cycles in the Quaternary (e.g. Haffer, 1969; Prado & Gibbs, 1993). The moist/wet forests have been proposed as expanding their geographical range during inter-glacial cycles (such as that of the present day), in which more humid and warmer climates are predominant. As a consequence, the dry vegetation formations, once more widespread in distribution, have receded to areas of low rainfall, forming dry forest and savanna refugia. During glacial maximum times, evidence suggests that the climate was drier and cooler by around 2-8ºC (Burnham & Graham, 1999) and the sea level lower by around 100 – 200m (Gregory-Wodzicki, 2000). These events would have been important factors in promoting the retreat of moist/wet forests into refugia and the expansion of drier vegetation formations around the region. The periodic fragmentation and reuniting of the vegetation formations may have facilitated speciation by allopatry and hybridisation, and was proposed as one mechanism accounting for the high diversity of the lowland biota (Burnham & Graham, 1999; Richardson et al., 2001).

This model of Pleistocene vegetation shifts may be a more recent factor reinforcing the separation between coastal Pacific and Andean SDFTFs in Ecuador and Peru, and those in Colombia and Venezuela. Gentry (1982) postulated that the super-humid Chocó region in western Colombia may have always kept these areas separated. The Chocó presently has a high record of precipitation (around 11.6m/year) and during drier glacial maxima it may have been a moist barrier to the expansion of the drier Pacific vegetational formations in South America and Central America and Caribbean Colombia and Venezuela.

Such Pleistocene vegetation dynamics may also explain the floristic dissimilarities between the Ecuadorian-Peruvian and the more northern situated sites based on the Chocó region, the humid barrier region of the Amazon rain forest providing a barrier between this region and the SDTFs in southern South America. This represents a huge area that may have made it impossible for dry forest species to cross to northern South America, and then follow the Pacific coast southwards. The few sparsely distributed species characteristic of dry forests found in Amazonian rain forests (Pennington et al. 2000) would suggest this. Furthermore, palynological evidence indicates much of Amazonia remained humid throughout the Pleistocene (Colinvaux et al., 1996).

The factors causing the weak floristic affinities between the Ecuadorian-Peruvian and the Bolivian-Argentinean phytogeographic groups are complex, although Andean uplift events and Quaternary climatic changes may have been important. Orographic factors could also have assisted in causing the isolation of the SDTFs of the dry Inter-Andean valleys of southern Peru from those located in more southern regions, especially the ones in the Bolivian Andes. Even though up to 10Ma the elevation of the Bolivian Altiplano was only half of its present elevation of about 4000m, organisms which had the ecological conditions to disperse across medium elevations still had to disperse across at least two of the Cordilleras (Eastern and Central), if not three (Eastern, Central and Western). This suggests that the high peaks of the Andes have played a role in isolating these different SDTF areas for over 10 million years. It is probable that the links of dry Inter-Andean valleys of La Paz with the Chiquitos region (or even the Piedmont or Misiones nuclei) reflect past extension of extending Chiquitano forests during dry periods of glacial cycles.

4.3 Molecular techniques, Evolutionary Rates Analysis and Phytogeography

Even though many dispute the refuge theory, historical climate change has undoubtedly impacted on the distribution and evolution of plant species in the Neotropics. What is in doubt, however, is exactly how much these climatic changes have driven speciation. This question has been addressed by a number of different authors in recent years using new molecular techniques such as Evolutionary Rates Analysis (ERA) (Pennington et al., in press). Although beyond the scope of this thesis, this line of enquiry is certainly worthy of brief mention here as ERA is a powerful new analytical tool providing insights into diversification. Although this field is in its infancy, it is already clear that it will contribute greatly to our understanding of species diversification and historical biogeography.

The basis of ERA is to look at the shape of phylogenetic trees to ascertain whether diversification patterns within certain clades have been gradual or rapid. Absolute dates can be placed in the nodes of the phylogenetic trees either by using molecular clocks calculated for non-coding DNA in other taxa, or by placing a roughly known date on a single node using fossil evidence and extrapolating from this. Pennington et al., (in press) have used ERA on nuclear ribosomal ITS sequence data on a number of taxa found in Neotropical seasonally dry forests. These include Ruprechtia (Polygonaceae), Chaetocalyx and Nissolia (Fabaceae), and Loxopterygium (Anacardiaceae). These authors found evidence for species diversifications both during and before the Pleistocene in Central America, although the data suggested that diversification was primarily pre-Pleistocene in South America. These results support both the model that predicts tropical species diversity to be recent (and which invokes a role for Pleistocene climatic change), and that which considers it ancient (thereby implicating geological factors such as the Andean orogeny and the closure of the Panama Isthmus, etc.). These authors also attempted to identify common factors underlying evolution in these groups using Cladistic Vicariance Analysis (looking for similar phylogenetic patterns in unrelated taxa thus inferring common historical processes driving their diversification), although their analyses did not clarify common patterns.

Richardson et al. (2001) carried out a similar molecular investigation of Inga, an extremely speciose genus of about 300 species, the majority of which grow in Neotropical rain forest. In this study a molecular clock approach estimated genetic diversification to have occurred within the last two million years suggesting that speciation occurred during the Pleistocene.

CHAPTER 5: THE FUTURE

The last decade has seen great leaps forward in our understanding of the nature of the incredible plant diversity of the Neotropics. Finally, it seems, we are beginning to form a picture not just of which plants occur where, but how and why whole species assemblages evolved. This slow but gradual clarification of phytogeographic patterns and their origins has resulted from multi-disciplinary collaborations including scientists from the fields of systematics and floristics, molecular biology and palaeoecology. Although we have unravelled some of the mysteries of the Neotropical flora, there is much still to be discovered. It is an exciting time to be a Neotropical botanist! Great areas of the Neotropics remain botanically unexplored, for example, and although we now have many theories relating to the origins of the Neotropical flora, as yet these remain only theories. Nothing has been proved conclusively. Piecing together the final picture will be difficult and time consuming necessitating the continued collaboration between scientists from many disciplines. There is also a great sense of urgency in this work as deforestation rates continue to accelerate. One of the ecosystems considered in this doctoral submission – the SDTFs, are especially threatened. For example, even a decade ago, less than 2% of the SDTFs of Mesoamerica were still intact (Janzen, 1988).

Fieldwork programmes need to expand to continue to provide the basic species checklists that form the backbone of phytogeographic work. Many of the great and ground-breaking theories in biology – such as the theory of evolution, for example, have been put forward by field scientists who have spent many years observing, recording and asking questions about nature. All theories must also be tested against field observations if they are to be validated. In addition, field collections also provide the vital specimens and molecular material needed by taxonomists to monograph plant groups and build a detailed phylogeny of plant diversity.

In this chapter a number of potential (and in my view) important future research lines related to my areas of study are outlined. These seek to provide some answers to a number of important biological questions, and in so doing add another small piece to the incredibly diverse biological jigsaw puzzle that is the Neotropical flora. Some involve concentrated field surveys and floristic analyses. Others are more orientated towards molecular biology and are proposals that have been arrived at after many discussions with colleagues. A few are already underway.

5.1 Examining patterns of ß-diversity in the Brazilian cerrados

The formulation of a conservation strategy for a highly fragmented and degraded ecosystem such as the cerrado depends on a sound understanding of its parts. Of critical value to decision makers is knowledge on how the species components of the biological system interact, and how - and why - their local and regional distribution and abundance patterns vary across space. Of fundamental importance to understanding diversity and its maintenance is the concept of ß-diversity, which is the extent of differentiation of communities along habitat gradients. A thorough understanding of ß-diversity is vital for the selection of conservation areas. If the species composition of a geographically widespread biome does not change with distance, for example, then the location of reserves is not important. If, however, there are considerable floristic differences, careful study of the composition of local sites is essential to ensure that selection of reserves adequately protects all species.

The research findings of this doctoral submission have gone some way towards elucidating patterns of diversity within the cerrado. This work has been based on various multivariate analyses of what is arguably the most comprehensive dataset for any diverse tropical biome and permits far more accurate assessment of distribution patterns than is currently available for the other diverse systems such as the Amazon rain forest. In addition, in comparison with Amazonia, there is a far less biased concentration of surveys in areas close to research centres. A final strength of this dataset is that the majority of the taxa recorded are identified to species level, and that identifications have been cross-checked by the same workers for all sites. This removes the taxonomic uncertainty that plagues many rain forest inventories, where identifications merely to family or genus are common, and where identifications between sites made by different workers have not been cross-validated.

Although a series of papers on cerrado diversity patterns have been published in recent years (a number of which are submitted here), much work remains to be done. There is great scope to further investigate the many relationships between the species components of the cerrado, and to better understand how - and why - their local and regional distribution and abundance patterns vary across space. I believe the following research lines would be extremely fruitful:

1) In recent years a number of different authors have investigated diversity patterns within the cerrado. These include Bridgewater (in press), Ratter et al (2003), Durigan et al (2003), Simon and Proença (2000), Felfili et al. (1997) and Castro (1994). Although their methods differ, their research findings are, on the whole, complementary. Unfortunately, to date there has been no attempt to bring these works together and arrive at a consensus on floristic patterns. It would therefore be very productive for each of these research groups to pool their data, perhaps through the mechanism of a research workshop. Durigan et al. (2003) for example, has a superb dataset for the state of São Paulo. This region is under-represented in the dataset of the other authors. Simon and Proença (2000), have taken a different approach to the other authors by hypothesising patterns of cerrado diversity based on studies of the genus *Mimosa.* These should be matched with those patterns derived from total woody floristic comparisons. *Mimosa* is a particular apt genus for this work as it was taxonomically revised by Barneby (1991) and has a major centre of diversification in Central Brazil.

2) A simple piece research project building on the work of Ratter et al. (2003) and Bridgewater (in press) is to look at the similarity links of sites within and between their putative phytogeographic provinces. Clearly demarcating these phytogeographic zones will be of vital importance in planning conservation measures in the cerrado. The phytogeographic divisions elucidated by these authors reflect the fact that individual cerrado species often have

restricted distributions. Pairs of sister species (e.g., *Andira cordata* and *A. cujabensis*), or subspecific taxa (e.g., in *Diptychandra aurantiaca*) are also distributed according to the boundaries demarcating these phytogeographic zones, indicating that they reflect historical events such as the historical movement of vegetation types caused by climatic change (Pennington, 2003). Using the Sorensen index of similarity, floristic differences can be assessed between all pairs of sites in their data matrix. If the floristic boundaries are real entities, in theory, links should be stronger between pairs of sites within a province than between pairs of sites from different provinces.

3) The existence of clear phytogeographic zones in the cerrado biome can also be tested using molecular methods. Although the floristic patterns reflect suites of species having restricted distributions (e.g. *Hirtella ciliata* and *Parkia platycephala* to the north-east of the region) many species are widespread, occurring across all phytogeographic zones. As such, they are not informative in phytosociological analyses. However, one would expect that these species would have been affected by the same historical events as other cerrado taxa, and that these events might be reflected in the geographic partitioning of their genetic variation. Future research could test this hypothesis, and therefore the generality of the cerrado phytogeographic zones, by examining genetic variation in widespread cerrado species such as *Qualea grandiflora* (Vochysiaceae) and *Copaifera langsdorfii* (Leguminosae).

4) There is a large quantity of published edaphic and environmental data available for the cerrado biome, although this is currently in disparate sources. If this could be gathered together, it would allow multiple regressions of species distribution data to be made against edaphic and environmental variables, and would assist our understanding of the mechanisms determining ß-diversity patterns. An estimate of the time required to build up a dataset of this nature would be around four months. Furley and Ratter (1988), for example, have clearly demonstrated the preference for fertile soils of a number of cerrado species (e.g. *Callisthene fasciculata*, *Magonia pubescens*, *Terminalea argentea*) and these species are particularly prevalent in cerrados found in Mato Grosso do Sul. These sorts of relationships between species distributions and edaphic factors could be proven through Canonical Correspondence

Analysis (CCA) i.e. the distance decay of Cerrado floristic similarity could be compared with the distance decay of environmental variables (climate variables, soil nutrient concentrations, elevation etc.).

5.2 Understanding the floristics of Belize

As Brokaw (in press) points out, much of the biological research conducted in Belize has focused on vegetation mapping. As a result, there are now superb vegetation maps available for the country, the latest being produced by Meerman and Sabido (2001). In addition, there has also been considerable research effort spent on investigating macro and micro environmental and plant distribution patterns (see for instance, Queensborough, 2000; Furley et al, 2001), soil-moisture-plant relationships (e.g. Furley, 1976, 2001) and vegetation dynamics (e.g. Kellman and Miyanishi, 1982; MacDougall and Kellman, 1992). However, despite the popularity of Belize as a research study area, unfortunately there is still a great paucity of information on the country's flora. Despite a provisional checklist being produced for the country (Balick et al., 2000) our knowledge of the flora does not match our understanding of broad-scale vegetation patterns. Where species lists occur for a vegetation type, more often than not they still only comprise a few of the dominant tree species. Where attempts have been made to provide more detailed checklists for certain areas, these have also usually been derived from forest inventories focusing on trees above 10cm dbh (diameter at breast height). Some of the best vegetation-specific floristic information on woody species, for example, was compiled by Bird (1998) who established 30 permanent sample plots between 1992 and 1997. The aim of these plots was to provide structural and long term forest dynamic data to assist forest management for timber. Although this work is superb, any plant less than 10cm dbh was excluded for the purposes of the study. Shrubs, herbaceous species, epiphytes and lower plants always seem to be overlooked - in terms of their presence being documented - and it is time this was addressed.

An obvious line of research – and one that I would be keen to become involved with – would be to conduct detailed floristic inventories within the main Belizean vegetation types and to provide complete checklists for them. Balick's *Checklist of the Vacular Plants of Belize* (2000) is a very useful starting point, but it is still only provisional, and gives no indication of the habitat preferences of species. To emphasise how inadequate our knowledge of the Belizean flora still is, an MSc student based at RBGE (supervised by myself) conducted her thesis on the riverine forest close to Guacamallo Bridge in the Chiquibul Forest (Urban, 2003). This is an area that has been much frequented by botanists as it is a watering hole for scientists en route to the Las Cuevas Research Station managed by the Natural History Museum. Her study - which comprised only three weeks in the field - revealed two new generic and two new species records for Belize, and a potentially new species of *Inga* (T. D. Pennington, pers. comm.). Her study indicates that there is clearly much exciting base line botanical work to be done. The paper submitted as part of this doctoral thesis focused on a small area of savanna within the Rio Bravo Conservation and Management Area. This provided the first detailed species list for this vegetation type in Belize. A subsequent detailed species list for the pine savanna at Monkey Bay Wildlife Sanctuary was published by Laughlin (2002). There are few other lists available. In the near future I would be keen to:

1) Provide a checklist for the Chiquibul forest. This forest is a continuation of the forests of the Petén and is the largest single extent of forest left in Central America. Although this forest area has been relatively well collected in Belize, herbarium data has not been used to compile a useful species list. As such, its broad floristic affinities and patterns of diversity are still not understood. A florula would also be extremely useful.

2) Collect widely and provide a species checklist for the Belizean karstic forest. These limestone forests are very poorly known floristically, and are rare formations in the tropics.

3) Conduct an inventory and phytogeographic analysis of the Belizean riverine forests. Riverine forests are poorly described throughout Central America (Urban, 2003; Kellman & Meave, 1997). In Belize, a detailed floristic survey of this nature is urgently required as over 80% of the riverine forest of the important Macal and Raspacula rivers are shortly to be lost because of a dam project that is due for completion in 2005.

5.3 Understanding the floristics of Neotropical Seasonally Dry Tropical Forests

Although our understanding of the Belizean flora may be poor, our knowledge of floristics of Peruvian SDTFs is inadequate considering their high levels of endemism and the degree to which they are threatened. One of the papers submitted as part of this doctorate provides preliminary floristic information on this much neglected ecosystem and assessed its phytogeographic affinities. This work, and the research findings of other researchers such as Linares-Palomino (in press) has clearly identified the need for floristic inventories within Peruvian SDTFs. In the short term the following lines of research would be extremely profitable and would assist in conservation planning of this beleagured vegetation type:

1) Floristic inventories of the SDTFs in the Quillabamba Valley (Cuzco), the Apurimac Valley, and the Sandia valley (Puno). No information is currently available for these areas.

2) Provisional research in the SDTFs around Tarapoto have revealed them to be floristically unique, and their affinities remain obscure, despite a recent phytogeographic analysis attempting to elucidate regional floristic patterns (Linares-Palomino, in press). More data is required to clarify the flora of the disjunct Tarapoto SDTFs.

3) At a more general level, the museum and refuge hypotheses can be tested by using molecular analyses to examine the genetic structure of representative, widespread seasonally dry forest species such as *Geoffroea spinosa* (Leguminosae) and *Astronium urundeuva* (Anacardiaceae). Although molecular analyses fall outside the scope of this doctoral submission (which is primarily floristic), the preceeding chapter has hopefully illustrated the potential of such work to assist our understanding of historical biogeography. The use of

such molecular characters as chloroplast loci and microsatellite markers now enable the genetic structure of widespread and disjunct species to be assessed and allow a correlation of species' genetic structure with geographic distribution.

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APPENDIX: COMMON NAMES OF WOODY SPECIES GROWING IN CENTRAL BRAZIL

The following list results from three years spent working with local collectors in the cerrado. Most have been learnt from Joaquim Fonsêca Filho, a technician working at Embrapa-Cerrados. A Mineiro by birth, Joaquim has spent much of his life working in the cerrado and there are few alive who have his extraordinary knowledge of the flora of Central Brazil. I was extremely fortunate to have been accompanied by Joaquim on the majority of my field excursions. He was one of my mentors as well as being exceptionally good company. Although he knows the scientific names of many cerrado species, he prefers to use common names, and the list below reflects those most commonly used by our collecting team.

Common Namnes	**Scientific names**
Açaí	*Euterpe* spp.
Açoito cavalo	*Luehea* spp.
Açucena	*Coussarea hydrangeaefolia* Benth. & Hook. f Rub
Acurí	*Attalea phalerata* Mart.
Aderno	*Emmotum nitens* (Benth.) Miers
Algodão bravo/do bugre	*Cocholospermum regium* (Schrank) Pilg. *C. vitifolium* Spreng.
Almécega	*Protium brasiliense* Benth. *P. heptaphyllum* (Aubl.) E. K. Marchal
Almécega vermelha	*Tetragastris unifoliata* (Engl.) Cuatrec.
Amarelão	*Apuleia leiocarpa* J. Macbr.
Amargosa	*Vatairea macrocarpa* (Benth.) Ducke
Amargosinha	*Acosmium dasycarpum* (Vogel) Yakovlev
Amburana	*Amburana cearensis* (Allem.) A.C. Sm.
Angelim	*Andira* spp.
Angelim branco	*Andira cuiabensis* Benth.
Angico Branco	*Albizzia niopoides* (Spruce ex Benth.) Burk. *Anadenanthera colubrina* (Vell.) Brenan
Angico preto	*Anadenanthera peregrina* (Benth.) Speg.
Angiquinho	*Calliandra* spp.
Araçá da mata	*Gomidesia lindeniana* O. Berg
Aráticum	*Annona crassiflora* Mart. *A. paludosa* Aubl.
Aráticum cagão	*Annona coriacea* Mart.
Arnica	*Lychnophora ericoides* Mart.
Aroeira	*Astronium urundeuva* Fr. Allem.
Aroeirinha	*Lithraea molleoides* (Vell.) Engl
Assa peixe	*Vemonia ferruginea* Less.
Ata	*Annona coriacea* Mart.
Ata Brava	*Talauma ovata* A. st.-Hil.
Babaçu	*Attalea speciosa* Mart.
Bacopari do cerrado	*Salacia crassifolia* (Mart.) Peyr
Bacopari da mata	*Salacia elliptica* G. Don
Bacuri	*Attalea phalerata* Mart. *Platonia insignis* Mart.

Balsaminho	*Diptychandra aurantiaca* (Mart.) Tul.
Banha de galinha	*Swartzia flaemingii* Raddi
Barbatimão	*Stryphnodendron* spp.
Barriguda	*Ceiba speciosa* (A.St.-Hil.) Gibbs
	Cavanillesia arborea K. Schum.
	Ceiba (*Chorisia*) spp.
Bate caixa	*Palicourea rigida* Kunth
	Salvertia convallariodora A. St.-Hil.
Biribá	*Rollinia* cf. *mucosa* (Jacq.) Baill.
Boca boa	*Buchenavia tomentosa* Eichler
Bocaiuba	*Acrocomia aculeata* (Jacq.) Lodd. ex Mart.
Boldo bravo	*Hyptidendron canum* Pohl ex Benth.
Bôlsa do pastor	*Zeyheria montana* Mart.
Bolsinha	*Aspidosperma tomentosum* Mart.
	A. macrocarpon Mart.
Bosta de rato	*Hirtella glandulosa* Spreng.
	H. gracilipes (Hook. f.) Prance
Bráuna	*Schinopsis brasiliensis* Engl.
Breu branco	*Protium brasiliense* Benth.
	P. heptaphyllum (Aubl.) E.K.Marchal
Breu curuba	*Tetragastris unifoliolata* (Engl.) Cuatrec.
	Trattinickia rhoifolia Willd.
Breu vermelho	*Tetragastris balsamifera* (Swartz) O.K.
Brinco da agua	*Ferdinandusa speciosa* Pohl
Bugre	*Rudgea viburnioides* (Cham.) Benth.
Buriti	*Mauritia flexuosa* L. f.
Buritirana	*Mauritiella armata* (Mart.) Burret
Burra leiteira	*Sapium longifolium* (Müll. Arg.) Huber
	S. marginatum Müll. Arg
Butiá	*Butia leiospatha* (Mart.) Becc.
Cabeça de frade	*Mouriri elliptica* Mart.
Cabeça de negro	*Bulbostylis paradoxa* (Spreng.) Standl.
Cabo de machado	*Pouteria torta* (Mart.) Radlk.
Cabrito	*Rhamnidium elaeocarpum* Reissek
Cachimbeiro	*Cariniana rubra* Miers
	C. domestica Miers
Cafezinho	*Myrsine* spp.
Cagaita	*Eugenia dysenterica* DC.
Cagaiteiro	*Eugenia dysenterica* DC.
Cajá	*Spondias mombin* L.
Cajazeira	*Spondias mombin* L.
Caju	*Anacardium occidentale* L.
Caju rasteiro	*Anacardium humilie* Engl.
	A. pumilum Walp.
Cajueiro	*Anacardium occidentale* L.
Calunga	*Simaba glabra* Engl.
Cambará	*Vochysia divergens* Pohl
	Gochnatia polymorpha DC.
Cancileiro	*Machaerium acutifolium* Vogel
	Platypodium elegans Vogel
Canela de ema	*Vellozia squamata* Pohl
Cangicão	*Byrsonima crassifolia* (L.) Kunth
Cangiquinha	*Byrsonima orbignyana* A. Juss.
Cangerana	*Cabralea canjerana* (Vell.) Mar
Canjerana amarela	*Vochysia divergens* Pohl
Canjerana branca	*Qualea ingens* Warm.
Canjerana preta	*Qualea wittrockii* Malme
Canjerana vermelha	*Vochysia ferruginea* Mart.
	V. pyramidalis Mart.
Cansanção	*Jatropha vitifolia* Mill.
Canudeiro	*Mabea fistulifera* Mart.
Capeiba do brejo	*Hieronyma alchorneoides* Fr. Allem.
Capitão	*Terminalia brasiliensis* Eichler
	T. actinophylla Mart.
	Terminalia spp.
Capitão do cerrado	*Terminalia argentea* Mart. & Zucc.
Capitão garote	*Terminalia argentea* Mart. & Zucc.

Capitiu	*Siparuna guianensis* Aubl.
Caraíba	*Tabebuia aurea* Benth. & Hook.
Caraipé	*Licania* spp.
Carandá	*Copernicia alba* Morong ex Briton
Carapanaúba	*Aspidosperma nitidum* Benth.
Carapixu	*Krameria tomentosa* A. St. Hil.
Carapixu de negro	*Triumfetta semitriloba* Boj.
Caripé	*Licania spp.*
Caripé branco	*Licania blackii* Prance
Caripé vermelho	*Licania kunthii* Hook. F.
Carnaúba	*Copernicia prunifera* (Miller) H.E. Moore
Carne de vaca	*Roupala montana* Aubl.
Caroba	*Jacaranda caroba* (Vell.) DC.
Carobinha	*Jacaranda caroba* (Vell.) DC.
Carvalho	*Physocalymma scaberrimum* Pohl
Carvão-vermelho	*Diptychandra aurantiaca* (Mart.) Tul.
Carvoeiro	*Sclerolobium paniculatum* Vogel
Catiguá	*Trichilia catigua* C. DC.
Catoaba	*Erythroxylum* spp.
Cebola brava	*Clusia sellowii* Schltdl.
Cedro	*Cedrella fissilis* Vell.
Cega machado	*Physocalymma scaberrimum* Pohl
Cerveja do pobre	*Bredemeyera floribunda* Willd.
Chapeudinho	*Heisteria densifrons* Engl.
	H. ovata Benth.
Chichá (Xixá)	*Sterculia striata* A. St.-Hil. & Naud.
Cinco dedos	*Zeyheria montana* Mart.
Cinzeiro	*Terminalia argentea* Mart. & Zucc.
Cipó costela de anta	*Coccoloba* spp.
Cipó cururu	*Serjania* spp.
Cipó de fogo	*Davilla nitida* (Vahl.) Kubitzki
	D. multiflora (DC) A.St.-Hil.
Cipó escada de jabotim	*Bauhinia guianensis* Aubl.
	B. outimouta Aubl.
	B. punctata Burch.
	B. splendens Kunth
Cipó Japecanga	*Smilax brasiliensis* Spreng.
Cipó quina	*Strychnos* spp.
Coari-coari	*Lacistema hasslerianum* Chodat
	L. aggregatum (Berg) Rusby
Copaíba	*Copaifera langsdorfii* Desf.
Copaibinha	*C. martii* Hayne
Coração de negro	*Piptocarpha rotundifolia* (Less.) Baker
	Eremanthus glomerulatus Less.
	Connarus suberosus Planch
Coroa de frade	*Mouriri elliptica* Mart.
Criolim	*Mouriri elliptica* Mart.
Crista de galo	*Heliotropium indicum* L.
Cumaté	*Chaetocarpus echinocarpus* (Baill.) Ducke
Cumbuquinha	*Mezilaurus crassiramea* (Meissn.) Lacre
Cundurú	*Unonopsis lindmannii* R.E. Fries
Curiola	*Pouteria ramiflora* (Mart.) Radlk.
Curitiu	*Aspidosperma nobile* Müll. Arg.
Dedaleira	*Lafoensia pacari* A.St.-Hil.
Douradinha	*Rudgea viburnioides* (Cham.) Bent
Embiraçu	*Eriotheca gracilipes* (Schum.) Robyns
	E. pubescens (Mart. & Zucc.) Schott. & Endl.
	Pseudobombax longiflorum (Mart. & Zucc.) Robyns
Embireira	*Guatteria* spp.
Escorrega macaco	*Vochysia haenkeana* Mart.
Espinheiro	*Acacia* spp.
Farinha seca	*Licania* spp.
Faveira	*Dimorphandra mollis* Benth.
	D. gardnerianum Tul.
Faveira bolota	*Parkia platycephala* Benth.
Fedegoso	*Senna rugosa* (G.Don) Irwin & Barneby
Feijão de arara	*Antonia ovata* Pohl

	Pera glabrata (Schott.) Baill.
Figo	*Ficus* spp.
Folha larga	*Salvertia convallariodora* A. St.-Hil.
Frei jorge	*Cordia alliodora* (Ruíz & Pav.) Oken
	C. trichotoma (Vell.) Arrab.
	C. glabrata (Mart.) A. DC.
Fruta de morcego	*Euplassa inaequalis*(Pohl) Engl.
	Roupala montana Aubl.
Fruto de urubu	*Casearia rupestris* Eichler
Fruto do lobo	*Solanum* spp.
Fumo do campo	*Cordia insignis* Cham.
Gameleira	*Ficus* spp.
Gameleirinha	*Ficus guianensis* Aubl.
Garapa	*Apuleia leiocarpa* J. Macbr.
Gariroba	*Syagrus comosa* (Mart.) Mart.
Garote	*Terminalia argentea* Mart. & Zucc.
Genipapo	*Genipa americana* L.
Genipapo bravo	*Tocoyena formosa* (Cham. & Schltdl.) Schum.
Gomeira	*Vochysia thyrsoidea* Pohl
Gonçaleiro	*Astronium fraxinifolium* Schott
Gonçalo alves	*Astronium fraxinifolium* Schott
Grão de galo	*Abuta selloana* Eichler
	Pouteria ramiflora (Mart.) Radlk
	P. torta (Mart.) Radlk.
Gravatá	*Dyckea* spp.
Gritadeira	*Palicourea rigida* Kunth
Guapeva	*Pouteria torta* (Mart.) Radlk.
Guatambu	*Aspidosperma subincanum* Mart.
Gueroba	*Syagrus oleracea* (Mart.) Becc.
Imbaúba	*Cecropia* spp.
Imburana	*Amburana cearensis* (Fr. Allem.) A.C.Sm.
	Commiphora (*Bursera*) *leptophloeos* (Mart.) J.B. Gillet
Ingá	*Inga* spp.
Inharê	*Sorocea guilleminiana* Gaudich.
	Brosimum gaudichaudii Trécul
Ipê amarelo	*Tabebuia serratifolia* (Vahl.) Nich
Ipê roxo	*Tabebuia impetiginosa* (Mart.) Standl.
Ipê verde	*Cybistax antisyphilitica* Mart.
Jaca brava	*Richeria grandis* Müll. Arg.
Jacarandá do cerrado	*Dalbergia miscolobium* Benth.
Jacarandá muchiba	*Machaerium opacum* Vogel
Jacarandá preta	*Dalbergia miscolobium* Benth.Ppl
Jacaré	*Callisthene fasciculata* (Spreng.) Mart.
	Qualea dichotoma (Mart.) Warm.
Jacitara	*Desmoncus* spp.
Jamacaru	*Cereus jamacaru* DC.
Jatobá da mata	*Hymenaea courbaril* L. var. *stilbocarpa* (Hayne) Lee & Langenh.
Jatobá do cerrado	*Hymenaea stigonocarpa* Mart. ex Hayne
Jatobá roxa	*Peltogyne confertiflora* (Hayne) Benth.
Juá mole	*Neea spruceana* Heimerl.
	Guapira spp.
Juá preta	*Humiria balsamifera* A.St.-Hil.
Juá vermelha	*Sacoglottis guianensis* Benth.
Lacre	*Vismia* spp.
Landim	*Calophyllum brasiliense* Cambess.
Laranjeira do mato	*Esenbeckia febrifuga* A. Juss.
Laranjeira do cerrado	*Styrax ferrugineus* Nees & Mart
Larga galho	*Pseudolmedia laevigata* Tréc.
Lixeira	*Curatella americana* L.
Lixeirinha	*Davilla elliptica* A. St.-Hil.
Lobeira	*Solanum* spp.
Louro	Lauraceae spp.
Louro dourado	*Ocotea guianensis* Aubl.
Louro pardo	*Cordia trichotoma* (Vell.) Arrab.
Louro preto	*Cordia glabrata* (Mart.) A. DC.
Macambeira	*Bromelia* spp.
Macaúba	*Acrocomia aculeata* (Jacq.) Lodd. ex Mart.

Macucu sangue	*Diptychandra aurantiaca* (Mart.) Tul.
Mama cadela	*Brosimum gaudichaudii* Trécul
Maminha de porca	*Zanthoxylum rhoifolium* (Lam.)
	Z. riedelianum Engl.
Mamonarana	*Pseudobombax longiflorum* (Mart. & Zucc.) Robyns
	P. tomentosum (Mart. & Zucc.) Robyns
Mandacaru	*Cereus jamacaru* DC.
Mandioca brava	*Manihot* spp.
Mandiocão	*Didymopanax* spp.
Mandiocão da mata	*Didymopanax morototoni* Decne. & Planch.
Mandiocão do cerrado	*Didymopanax macrocarpum* (Cham. & Schltd.) Seem.
	Didymopoanax distractiflorum Harms
Mangaba	*Hancornia speciosa* Gomez
Mangaba brava	*Lafoensia pacari* A.St.-Hil.
Mangabeira	*Hancornia speciosa* Gomez
Marfim	*Agonandra brasiliensis* Miers
Maria mole	*Ferdinandusa elliptica* Pohl
	Pisonia noxia Netto var. *noxia*
Mariana	*Ormosia* spp.
Maria preta	*Blepharocalyx salicifolius* (Kunth) O. Berg
Marinheiro	*Guarea guidonia* (L.) Sleum.
Marmelada de pinto	*Alibertia concolor* (Cham.) K. Schum.
Marmelada do bezerro	*Alibertia edulis* (L.Rich.) A.Rich.
Marmelada do cerrado	*Alibertia edulis* (L.Rich.) A.Rich.
Marmelo	*Austroplenckia populnea* (Reissek) Lundell
Marolo	*Annona paludosa* Aubl.
Mata barata	*Andira humilis* Mart. ex Benth
	A. vermifuga (Mart.) Benth
Mata cachorro	*Simarouba versicolor* A. St.-Hil.
Mata calado	*Ryania* spp.
Mata gado	*Palicourea marcgravii* A. St.-Hil.
Mata matá	*Eschweilera* spp.
Mbeju de porco	*Ephederanthus parviflorus* S. Moore
Mijo de guará	*Roupala montana* Aubl.
Miringiba	*Terminalia glabrescens* Mart.
	Terminalia spp.
Morcegueira	*Andira inermis* (W. Wr.) DC.
Moreira	*Maclura tinctoria* (L.) Don ex Steudel
Mororó	*Bauhinia bongardii* Steud.
	B. cupulata Benth.
Morototó	*Didymopanax morototoni* Decne. & Planch.
Mulateira	*Albizzia niopoides* (Spruce ex Benth.) Burk.
Mulher pobre	*Dilodendron bipinnatum* Radlk.
Mulungu	*Erythrina dominguezii* Hassler
Murici	*Byrsonima* spp.
Murici de ema	*Byrsonima basiloba* A. Juss.
Murici de galinha	*Byrsonima inodorum* S. Moore
Murici de vargem	*Byrsonima crassifolia* (L.) Kunth
	B. orbignyana A. Juss.
Murici vermelho	*Byrsonima coccolobifolia* Kunth
Mussambé	*Terminalia fagifolia* Mart. & Zucc.
Mutamba	*Guazuma ulmifolia* Lam.
Negramina	*Siparuna guianensis* Aubl.
Novateiro	*Triplaris americana* R. H. Schomb.
Oitirana	*Couepia grandiflora* (Mart. & Zucc.) Benth.
Olho de boi	*Diospyros* spp.
Olho de cotia	*Cupania vernalis* Cambess.
	Matayba guianensis Aubl.
Olho de pomba	*Casearia grandiflora* Cambess.
	C. sylvestris Sw.
Ora por nobre	*Ximenia americana* L.
Pacari	*Lafoensia pacari* A.St.-Hil.
Paineira	*Eriotheca gracilipes* (Schum.) Robyns
	E. pubescens (Mart. & Zucc.) Schott. & Endl.
	Pseudobombax longiflorum (Mart. & Zucc.)
	P. tomentosum (Mart. & Zucc.)
Paineira do campo	*Pseudobombax longiflorum* (Mart & Zucc.) Robyns

Pajeú	*Triplaris americana* R. H. Schomb.
	Triplaris spp.
Pau bosta	*Sclerolobium aureum* (Tul.) Benth
Pau d'arco amarelo	*Tabebuia serratifolia* (Vahl.) Nich.
Pau d'arco roxo	*Tabebuia impetiginosa* (Mart.) Standl.
Pau de alho	*Cordia alliodora* (Ruíz & Pav.) Oken
Pau de arara	*Salvertia convallariodora* A. St.-Hil.
Pau de canga	*Trichilia catigua* C. DC.
Pau de jangada	*Apeiba tibourbou* Aubl.
Pau de leite	*Himatanthus articulatus* (Vahl) Woodson
Pau de leite (cont.)	*H. obovatus* (Müll. Arg) Woodson
Pau de moeda	*Simira hexandra* (S. Moore) Steyerm.
Pau de olho	*Copaifera langsdorfii* Desf.
	C. martii Hayne
Pau de vidro	*Linociera hassleriana* (Chodat) Hassler
Pau do novato	*Triplaris americana* R. H. Schomb.
Pau ferro	*Machaerium scleroxylon* Tul.
Pau marfim	*Agonandra brasiliensis* Miers
Pau pombo	*Tapirira guianensis* Aubl.
Pau pra tudo	*Tabebuia aurea* Benth. & Hook.
Pau santo	*Kielmeyera* spp.
Pau terra da folha grande	*Qualea grandiflora* Mart.
Pau terra liso	*Qualea multiflora* Mart.
Pau terra roxo	*Qualea parviflora* Mart.
Pau tucano	*Vochysia tucanorum* (Spreng.) Mart.
Pau-doce	*Vochysia elliptica* (Spreng.) Mart.
	V. pruinosa Pohl
	V. cinnamomea Pohl
	V. rufa (Spreng.) Mart.
Pente de macaco	*Apeiba tibourbou* Aubl.
Periquiteira	*Trema micrantha* Blume
Peroba	*Aspidosperma cylindrocarpum* Müll. Arg.
Peroba do campo	*Aspidosperma tomentosum* Mart.
Peroba-rosa	*Aspidosperma cylindrocarpum* Müll. Arg.
Peúba roxa	*Tabebuia impetiginosa* (Mart.) Standl.
Pimenta de macaco	*Xylopia aromatica* Lam.
Pindaiba do brejo	*Xylopia emarginata* Mart.
Pindaiba preta	*Xylopia emarginata* Mart.
	Xylopia sericea A. St.-Hil.
Pindaiba-vermelha	*Xylopia sericea* A. St.-Hil.
	X. amazonica R. E. Fries
Pinho	*Jacaranda copaia* D. Don
Piqui	*Caryocar coriaceum* Wittm.
	C. brasiliense Cambess.
Piquirana	*Lamanonia ternata* Vell.
Piquizeiro	*Caryocar brasiliense* Cambess.
	C. coriaceum Wittm.
Piririma	*Syagrus flexuosa* (Mart.) Becc.
Piririma vassoura	*Butia leiospatha* (Mart.) Becc.
	B. paraguayensis (Barb. Rodr.) L. H. Bailey
Pitomba	*Talisia edulis* Radlk.
	T. subalbens Radlk.
Puçá	*Mouriri pusa* Gardner
Quaresma	*Tibouchina candolleana* Cogn.
Quebra colhão	*Hirtella gracilipes* (Hook.f.) Prance
	H. racemosa Lam.
Quina do cerrado	*Strychnos pseudoquina* A. St.-Hil.
Quina da mata	*Aspidosperma* spp.
Rabo de arara	*Norantea goyazensis* Cambess.
	N. guianensis Cambess.
Saca-rolha	*Helicteres* spp.
Sambaiba	*Curatella americana* L.
Sambaibinha	*Davilla elliptica* A. St.-Hil.
Sangue de agua	*Croton urucurana* Baill.
Sangue de cristo	*Sabicea brasiliensis* Wernhamn
Sapucaia do cerrado	*Eschweilera nana* (Berg) Miers
Sobre	*Emmotum nitens* (Benth.) Miers

Sucupira branca	*Pterodon polygalaeflorus* Benth.
	P. pubescens Benth.
Sucupira preta	*Bowdichia virgilioides* Kunth
Sucuuba	*Himatanthus bracteatus* (A. DC.) Woodson
Suucubinha	*Himatanthus obovatus* (Müll. Arg.) Woodson
Tachi	*Triplaris americana* R. H. Schomb.
Taipoca	*Aspidosperma multiflorum* A. DC.
	Tabebuia roseoalba (Ridley) Sandw.
Tamboril	*Jacaranda brasiliana* Pers.
	J. cuspidifolia Mart.
Tamboril, Timboúva	*Enterolobium contortisiliquum* (Vell.) Morong
Tapicuru	*Callisthene cf. hassleri* Briq.
	C. microphylla Warm.
	C. minor Mart.
	C. major Mart.
Tarumã	*Vitex* spp.
Tatareina	*Sclerolobium aureum* (Tul.) Benth.
Taxi branco	*Sclerolobium paniculatum* Vogel var. *rubiginosum* (Tul.) Benth.
Tento	*Ormosia* spp.
Timboúva	*Enterolobium contortisiliquum* (Vell.) Morong
Tinge lingua	*Myrcia splendens* (SW.) DC.
	Myrcia spp.
Tinguí	*Magonia pubescens* A. St.-Hil.
Tinguí bosta	*Sclerolobium aureum* (Tul.) Benth.
Trapiá	*Maprounea guianensis* Aubl.
Tucumá	*Astrocaryum* spp.
Ubim	*Geonoma* spp.
Ucuúba	*Virola sebifera* Aubl.
	V. subsessilis Warb.
	V. urbaniana Warb.
Umiri	*Humiria balsamifera* A.St.-Hil.
Unha de boi, Mororó	*Bauhinia bongardii* Steud.
	Bauhinia spp.
Unha de gato	*Uncaria guianensis* (Aubl.) Willd.
Urucurana	*Sloanea* spp.
	Alchornea iricurana Casar.
Urundeuva	*Astronium urundeuva* Fr. Allem.
Utirana	*Couepia grandiflora* (Mart. & Zucc.) Benth.
Uvinha	*Micropholis venulosa* (Mart. & Eichler) Pierre
Vaqueta	*Combretum duarteanum* Cambess.
	C. leprosum Mart.
Veludo	*Guettarda viburnioides* Cham. & Schltdl.
Vinhático cascudo	*Enterolobium gummiferum* (Mart.) J. Macbr.
Vinhático	*Plathymenia reticulata* Benth.
Xixá	*Sterculia striata* A. St.-Hil. & Naud.