PALAEOECOLOGY OF THE BOLIVIAN PANTANAL:

A 45,000 year history of vegetation and climate change in tropical South America

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Declaration of Originality

All the work included in this thesis is original and my own, unless otherwise stated. The research presented in this thesis has not been submitted for any other degree or professional qualification.

Thesis Abstract

The Quaternary palaeoecology of lowland tropical South America remains largely unexplored. Hiatuses and slow sedimentation rates in many lacustrine records limit analysis at key intervals in the earth's climate history, such as the last glacial maximum (centred at 21.0 cal. ka BP) and the glacial-Holocene transition. These issues are confounded by the scarcity of palaeoclimate proxies independent of pollen analysis; the effects of temperature, precipitation, and atmospheric CO_2 concentrations on vegetation change are not easily disentangled in the interpretation of pollen diagrams. Therefore, key questions concerning past vegetation and climate of the lowland neotropics are greatly debated or remain unanswered. These include: (1) whether the lowland tropics experienced aridity during the last glacial period; (2) climate and vegetation change across the glacial-Holocene transition, and whether North Atlantic climate events, such as the Younger Dryas (12.9 to 11.6 cal. ka BP), influenced tropical lowland climate; (3) the relative extent of forested and savannah biomes during the last glacial period, and whether current biogeographic patterns are reflective of the past distribution of ecosystems.

This thesis improves the understanding of past vegetation and climate in tropical South America through a detailed palaeoenvironmental reconstruction of a site in lowland Bolivia. Pollen, geochemical, and algal analyses, chronologically constrained by 18 AMS ^{14}C dates, were performed on a sediment core extracted from a large, shallow lake, Laguna La Gaiba (17º45'S, 57º40'W) (LLG). LLG is surrounded by the Chiquitano seasonally-dry tropical forest (SDTF), but it is situated along the course of the Rio Paraguay on the western margin of the Pantanal, the world's largest tropical wetland. Key findings indicate: (1) The glacial landscape, prior to 19.5 cal. ka BP, was dominated by open, herbaceous vegetation. Colder temperatures, in combination with aridity and lower atmospheric CO_2 concentration, limited the growth of tropical forest in the region. (2) Early post-glacial warming allows for the establishment of tropical forest, but precipitation remains low until

12.2 cal. ka BP. (3) There is no evidence of a climatic event in association with the YD chronozone, but rapid flooding at 12.2 cal. ka BP mirrors the pattern of deglaciation found in southern South America, suggestive of a southern hemisphere climatic influence. (4) The recent development of SDTF at 10.0 cal. ka BP indicates this region did not form part of an extensive dry forest biome proposed by biogeographers to have existed at the height of the last glaciation. (5) The region experienced aridity from 10.0 to 3.0 cal. ka BP, but the hillslopes around LLG maintained closed-canopy SDTF. Instead, aridity influenced the abundance of key SDTF taxa and diversity (palynological richness). (6) Changes in the relative abundance of *Pediastrum* species are reflective of Holocene lake level change; thus, this genus of green alga is highlighted as a potential palaeoclimatic proxy to be used in conjunction with pollen analysis.

Preface

This thesis is formatted in journal style, and as is typical of research submitted to peer-reviewed journals, some of the data included in the three research chapters have been collected by collaborating authors. These authors are listed at the beginning of each chapter, and the contribution of each is detailed below.

Chapter 2 incorporates a vegetation survey around the shores of the field site, Laguna La Gaiba, conducted by Ezequiel Chavez and René Guillén of the Muséo de Historía Natural Noel Kempff Mercado, Santa Cruz, Bolivia, and Michael J. Burn differentiated the pollen of Moraceae and Urticaceae in twenty-five horizons. Toby Pennington of the Royal Botanic Gardens, Edinburgh, has been crucial to data interpretation and discussion.

The research in Chapter 3 also relies on the field surveys of Ezequiel Chavez and René Guillén, as well as the finer-scale pollen differentiation provided by Michael J. Burn. This chapter also includes carbon isotope data obtained by Neil J. Loader and Alayne Street-Perrott, Swansea University, Wales, and elemental data collected by Francis E. Mayle and Michael H. Marshall (Aberystwyth) at the Itrax® XRF scanner facility, University of Aberystwyth. As in the preceding chapter, Toby Pennington has played an integral role in the ecological interpretation and climatic significance of changes in the inundation-tolerant forest.

The data obtained for Chapter 4 were collected entirely by my own hand, but the interpretation of these data was improved by contributed work of my co-authors in the previous two chapters.

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I could not have completed this degree without the army of fellow postgrads and numerous Edinburgh publicans who were with me for the highs, and especially the lows, of PhD research. Thanks also to my palaeofellows, Mike Burn, Huw Jones, and Katharine Fitzpatrick, who were also always up for a pint or an argument, and more often than not, both. It is unlikely I ever would have landed in Glasgow airport in January 2005 without the early academic guidance of Les Cwynar, who I credit with first interesting me with microscopic dead things preserved in mud, and in his own, sometimes aggravating manner, he has ensured that I stuck with palaeoenvironmental research. Thanks also to my family in New Brunswick who have been with me every step of the way, and who will be anxious to tell all their friends that I got my P-h-D.

And finally, I could not have completed this degree without the unconditional love and support of my husband, Will Thomas, who has put up with rather a lot over the past few years… to speak lightly.

I. General Introduction

II. Long-term dynamics of the Chiquitano seasonally-dry tropical forest, eastern Bolivia

III. The Glacial-Holocene transition in the Bolivian Pantanal: Rapid flooding and vegetation change at 12.2 cal. ka BP

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I. General Introduction

1.1. Prologue

Assessing the impact of anthropogenic climate change on tropical ecosystem biodiversity and stability requires studies of vegetation-climate interactions on timescales much longer than those offered by conventional ecology. However, palaeoecology and palaeoclimatology in tropical South America are nascent fields. Long thought to have exhibited stability over glacial-interglacial cycles, and considered exempt from pollen analysis because of the profusion of animal-pollinated plant taxa, the ecosystems of tropical South America are now capturing the attention of Quaternary scientists. However, despite this recent interest, few archives from tropical South America extend beyond the early Holocene when global climate experienced high magnitude fluctuations. As a result, comparatively little is known of tropical climate and vegetation dynamics over glacial-interglacial timescales, particularly in lowland regions. The paucity of data has resulted in extrapolation of a few records to the entirety of the lowland tropics, often encouraging heated debate. The central premise of this thesis is to improve understanding of glacial-interglacial vegetation and climate change in tropical South America through high resolution analysis of a sedimentary record from lowland Bolivia spanning the past 45,000 years.

1.2. The glacial climate of lowland tropical South America

Andean regions of tropical South America contain robust, well-dated climate archives spanning the last glacial-interglacial transition from Lake Titicaca and the Salar de Uyuni, located on the Altiplano above 3500 m asl (Fig. 1.1). These records indicate that precipitation was high during the Last Glacial Maximum (LGM, centred on 21 cal. kyr BP); lake levels in Titicaca were above their present outflow (Baker et al. 2001a), and lacustrine sediments were deposited in the currently moisture-deficient Salar de Uyuni, indicative of greater effective moisture (Baker et al. 2001b, Baker et al. 2005).

However, there are few lacustrine records in the lowlands that extend uninterrupted beyond the early Holocene. Those that do are often poorly dated, and slow sedimentation rates disallow high temporal resolution of analysis. The paucity of lowland archives has led to the extrapolation of Andean palaeoclimate to the lowland tropics, a practice justified by the argument that at present, the climate of Andean and lowland regions is coupled (Baker et al. 2001a). Moisture from the Amazon basin is currently advected into Andean regions, but the assumption this relationship holds true over glacial-interglacial cycles, and that high precipitation in Andean regions is representative of a 'wet' lowland climate during the last glacial period is questioned (Absy et al. 1991, van der Hammen and Absy 1994, Hostetler and Mix 1999, Burbridge et al. 2004, Punyasena et al. 2008).

An early model for climate and vegetation change over glacial-interglacial cycles in the lowland tropics of South America was proposed by Haffer (1969), who hypothesized that 'biodiversity hotspots' in the Amazon rainforest existed as refugia in glacial periods, separated by large tracts of open, seasonally-adapted vegetation favoured by an arid glacial climate. The biodiversity hotspots are currently in areas of higher rainfall in the Amazon, thus it is argued that evergreen forest could have persisted in these regions despite the overall drier climate of glacial periods. Haffer (1969) drew on potential analogues of glacial-aged savannahs from African palaeoecology, and undated aeolian features variably distributed across the lowland tropics of South America, argued to have formed under a drier glacial climate, to lend support to the refugia model of rainforest dynamics over glacial-interglacial cycles. However, for several decades, Haffer's hypothesis remained untested.

Recently, two pollen records have been presented in as evidence against the refugia hypothesis; a lacustrine record from Lake Pata, a small basin situated in central, equatorial Amazonia (Colinvaux et al. 1996), and a marine core from the Amazon delta, argued to reflect a broad regional pollen signal from the Amazon

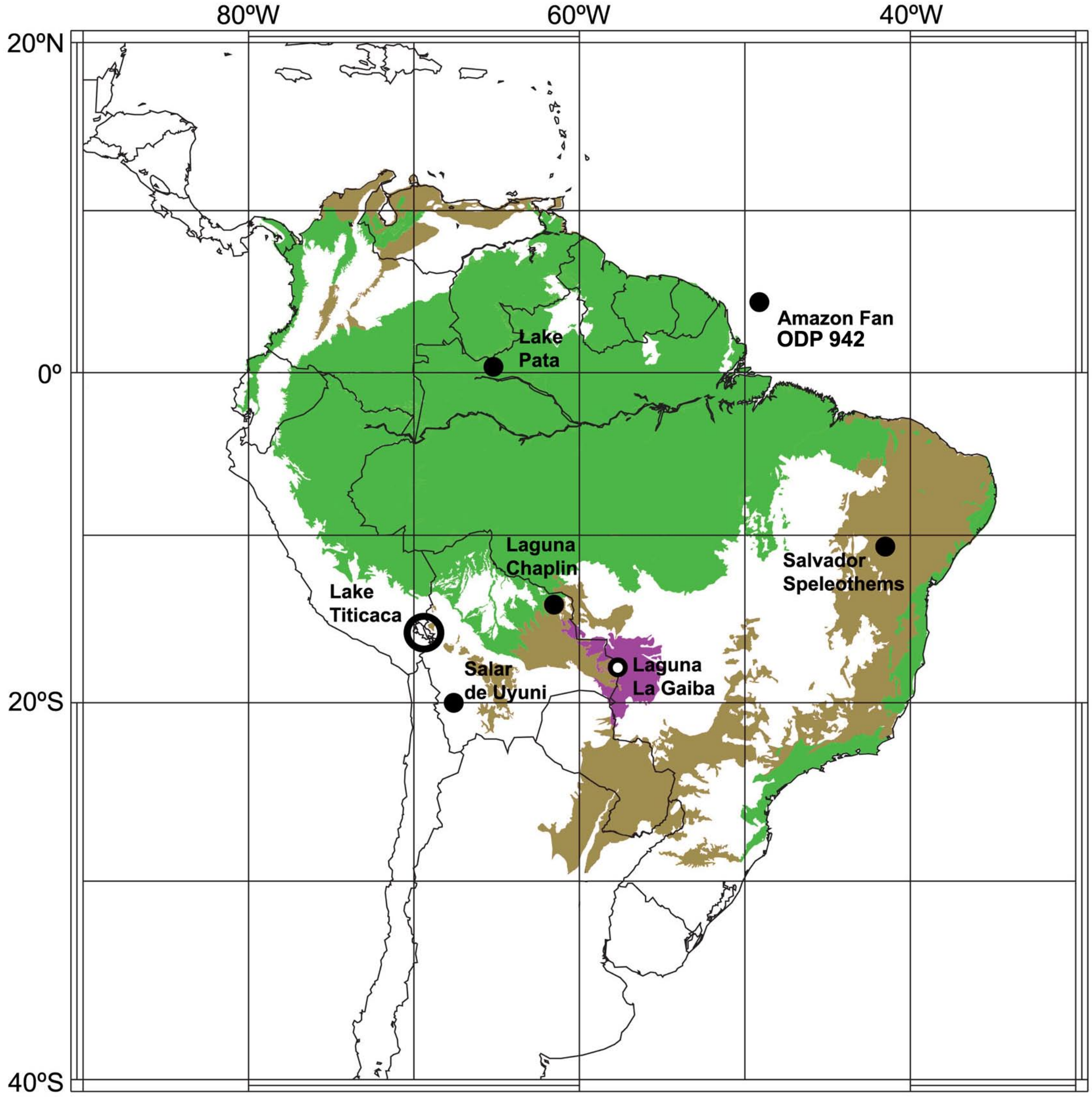

Fig. 1.1. Key sites in the reconstruction of glacial climate (all sites), and climate during the Younger Dryas chronozone (Salvador, Titicaca, Salar de Uyuni) in tropical South America. Also featured are ecoregions central to the discussion of glacial vegetation and climate in tropical South America: evergreen rainforest (green), and seasonally-deciduous tropical forest (SDTF) (brown), the Pantanal wetlands (purple). The study site, Laguna La Gaiba, is situated on the boundary between the Chiquitano SDTF and the Pantanal. Ecoregion data were obtained from Olson et al. (2001).

basin (Haberle and Maslin 1999). The absence of savannah indicator types, particularly Poaceae, and abundance of tree pollen in both these records are argued to refute the existence of large, ice-aged savannahs in the Amazon basin (Colinvaux et al. 2000). The authors argue the pollen evidence of continuous forest cover in the Amazon basin, along with evidence of high moisture availability in Andean regions, demonstrate that the glacial climate of lowland, tropical South America was not arid as previously hypothesized (Colinvaux et al. 1996, Colinvaux et al. 2000, Bush et al. 2004). Rather, the invasion of Andean taxa in lowland areas indicates Amazonia experienced a cool, moist climate during the LGM. Furthermore, detractors of the refugia hypothesis argue the mechanism by which the relict 'aeolian' features were created is under question, and it is unknown whether they formed during the last glacial period because of poor chronological control (Colinvaux et al. 2000).

The glacial aridity hypothesis is further complicated by Croll-Milankovitch theory. Variations in summer insolation due to the precessional cycle are thought to positively correlate with the strength of the South American summer monsoon (SASM). High summer insolation steepens the land-sea thermal gradient, thereby intensifying the SASM, thus precessional 'highs' correspond to periods of increased moisture availability (Baker et al. 2001a, Cruz et al. 2005). Insolation maxima due to the precession cycle are in antiphase in the northern and southern hemisphere tropics, complicating the climatic trend across the lowland tropics. However, a large proportion of the Amazon basin lies south of the equator, therefore moisture availability across much of this region is likely to follow the southern hemisphere pattern of varying summer insolation. During the LGM, summer insolation peaked in the southern hemisphere, resulting in high precipitation on the Altiplano (Baker et al. 2001a,b), and in coastal regions of tropical and subtropical Brazil (Auler et al. 2004, Cruz et al. 2005), thus it is argued the continental, lowland southern hemisphere tropics would have also experienced high moisture availability.

1.3. The failure of glacial aridity in the lowland tropics?

Despite the evidence in favour of a cool, moist LGM climate in lowland, tropical South America, recently published palaeoecological studies have shown that glacial-aged savannahs occupied regions currently located within the boundaries of evergreen rainforest, indicative of a drier glacial climate (van der Hammen and Absy 1994, Mayle et al. 2000, Burbridge et al. 2004). It is also argued the widespread occurrence of hiatuses and/or reduced sedimentation rates in lacustrine records during the LGM are reflective of drying of lake basins, thus indicating lower available moisture compared to present (Ledru et al. 1998).

Furthermore, the absence of Poaceae and evidence of closed-canopy forest at the LGM in the Amazon pollen records is not necessarily indicative of moist, evergreen rainforest and similar-to-modern precipitation levels. Seasonally-dry tropical forests (SDTF) are closed-canopy formations with few grasses in the understorey. Critically, SDTF occur under climatic conditions identical to savannahs; receiving 1000 – 1600 mm of mean annual precipitation with a pronounced dry season of several continuous months experiencing < 100 mm of rainfall. Floristically, evergreen rainforest and SDTF have many families and genera in common; at the family-level, the flora of SDTF is best described as a subset of evergreen rainforest, with the exception of three families (Capparidaceae, Cactaceae, Zygophyllaceae) that occur principally in SDTF (Gentry 1995).

The taxonomic resolution of pollen analysis is rarely finer than family or generic level, and without the presence of indicator types, rainforest is not easily distinguished palynologically from drought-tolerant seasonally-dry tropical forest (SDTF). Pennington et al. (2000) argued the LGM pollen signal at Lake Pata could equally be representative of SDTF, and the lower precipitation and thermal regime of the glacial environment favoured the formation of an unique Pleistocene assemblage in the Amazon basin, containing drought-tolerant taxa characteristic of SDTF. This hypothesis is an extension of previous biogeographic research (Ratter et al. 1988, Prado and Gibbs 1993, Oliveira-Filho and Ratter 1995) on the floristic affinities

Table 1.1. Summary of the debate over the precipitation regime of lowland, tropical South America; main hypotheses, supporting evidence, and key criticisms

HYPOTHESES	KEY POINTS	SUPPORTING DATA	KEY CRITICISMS	CRITICAL TESTS	REFERENCES
Similar-to-modern precipitation in the lowland tropics	Limited evidence of a decoupled precipitation regime; Moist and cool glacial climate allowed for continuous forest cover	Amazonian sediments contain abundant tree pollen; high precipitation inferred from Andean records	Sedimentary hiatuses in lowland lakes (including Pata) are indicative of drought; Forest is not indicative of a wet climate because pollen in Amazonian records (e.g., Pata) could represent drought-tolerant vegetation	An independent climate proxy; or Higher taxonomic resolution of pollen analysis to differentiate rainforest from SDTF	Baker et al. 2001a Bush et al. 2004 Colinvaux et al. 1996 Colinvaux et al. 2000 Maslin & Haberle 1999
Arid glacial climate in the lowland tropics	Glacial precipitation regimes of lowland and Andean regions were decoupled; Lowland ecosystems characterized by drought-tolerant vegetation	Biodiversity ‘hotspots’ in areas of higher rainfall; Sedimentary hiatuses in lowland lakes; Aeolian landforms indicative of drying	Contradicts climate predicted by Milankovitch forcing; Little grass pollen (indicative of savannah) in lowland records; Andean records show wet glacial climate	Pollen records from forest-savannah ecotonal regions **this study**	Burbridge et al. 2004 Haffer 1969 Mayle et al. 2000 van der Hammen & Absy 1994

drought-tolerant formations across the Neotropics. In particular, the widespread occurrence of five taxa in the currently disjunct blocks of SDTF are argued to reflect widespread distribution of SDTF in the Pleistocene (vicariance), rather than the result of migration and multiple colonization events.

Dry forest biogeographers propose the disjunct blocks of SDTF are refugia of a once extensive “Pleistocene dry forest arc”. Favoured by a drier glacial climate, they hypothesize this biome spanned much of the lowland, tropics of South America, elements of which encroached into the Amazon basin. Proponents of the “Pleistocene dry forest arc” hypothesis argue that extensive coverage of drought-tolerant forest during the last glacial period reconciles the Amazonian pollen data with evidence of drying from lacustrine sediments and the relict aeolian features (Prado and Gibbs 1993, Pennington et al. 2000). However, there are few palaeoecological data available from SDTF to test the validity of the “Pleistocene dry forest arc” hypothesis.

1.4. The glacial-Holocene transition in tropical South America

The extent to which high frequency climate fluctuations in the North Atlantic during the glacial-Holocene transition influenced the global climate, particularly in the southern hemisphere, remains a matter of some debate (Blunier et al. 1998, Markgraf and Seltzer 2001, Sugden et al. 2005, Ackert et al. 2008). The most studied of these events, the Younger Dryas (GS-1 stadial, 12.9 to 11.6 cal. kyr BP), is thought to influence the precipitation regimes of tropical South America, Asia, and Africa (Gasse 2000, Yuan et al. 2004, Wang et al. 2004, 2007, Garcin et al. 2007). In particular, reduced overturning circulation in the North Atlantic during the Younger Dryas cooling event, resulting in a steepened pole-equator thermal gradient in the Northern Hemisphere, is hypothesized to have forced the mean position of the Intertropical Convergence Zone (ITCZ) southward, thereby inducing aridity in the northern hemisphere tropics of South America, and increasing precipitation south of the equator (Dahl et al. 2005).

Several well-dated palaeoclimate reconstructions from tropical South America demonstrate decreased (north of 10ºS) and increased (south of 10ºS) precipitation during the YD chronozone. In particular, high lake levels in Titicaca and the Salar de Uyuni (Baker et al. 2001b, Placzek et al. 2006) and travertine growth, indicative of running water, in the currently moisture-deficient region of northeast Brazil (Salvador) (Auler et al. 2004), are robust evidence in favour of higher precipitation during the YD chronozone in areas located south of the equator (Fig. 1.1). However, records of sufficiently high temporal resolution and chronological control for a detailed examination of climate across the YD chronozone are situated in Andean and coastal regions. Due to the relatively young basal age and low sedimentation rates in most lacustrine records from the continental interior of South America, it is unknown whether a precipitation anomaly occurred during the YD chronozone in this region.

1.5. The palaeoclimate proxy gap

Most palaeoenvironmental reconstructions in lowland, tropical South America are based on fossil pollen data obtained from lacustrine and marine cores. However, the confounding effects of atmospheric CO_2 concentrations, temperature, and precipitation (including the timing and seasonal distribution of rainfall) on vegetation are not easily disentangled in the interpretation of pollen diagrams. Water use efficiency in plants is reduced in under conditions of lower atmospheric CO_2 concentrations, thereby confounding the effects of aridity and CO_2 levels in the interpretation of glacial precipitation from past vegetation (Cowling and Sykes 1999). Also, estimated temperature lowering of 5 – 6ºC in Amazonia during the last glacial period (Stute et al. 1995) would reduce evaporative transpiration, thereby moderating the impact of aridity on tropical vegetation (Colinvaux et al. 2000). Moreover, changes in the timing and distribution of rainfall (seasonality) are strong ecosystem determinants. Regions exhibiting sufficiently high mean annual precipitation to support evergreen rainforest will favour the expansion of SDTF where there is a pronounced dry season (Gentry 1995). Therefore, changes in the seasonality and duration of rainfall can also alter tropical vegetation at the biome level.

The inference of South American palaeoclimate through fossil pollen has recently been improved through modern calibration data, used to generate quantitative estimates of past temperature and precipitation in lowland Bolivia (Punyasena 2008, Punyasena et al. 2008). However, without independent climate proxies, ecological questions concerning the (in)stability of tropical ecosystems to changing climate, the adaptability of ecosystems, and ability and speed of plants to migrate to suitable climates remain unanswered. These type of ecological data are crucial for predicting the response of tropical biomes in light of future anthropogenic climate change, and independent palaeoclimate proxies for the lowland tropics are needed to disentangle at least some of these effects. The "palaeoclimate proxy gap" is a major hinderance in the understanding of long-term vegetation-climate dynamics in lowland, tropical South America.

1.6. Thesis aims

This thesis has both broad and focused research aims. Broadly-speaking, I aim to characterize late Quaternary vegetation and climate change of the Pantanal-Chiquitanía region in lowland Bolivia. Fossil pollen, algae, and geochemical analyses were applied to a sediment core spanning the past 45,000 years, extracted from a large lake located on the western edge of the Pantanal, the world's largest tropical wetland. The Pantanal is a 140,000 km^2 basin located mainly in western Brazil, but extending into eastern Bolivia, and together with the western Brazilian highlands, forms the headwaters of the Rio Paraguay. Therefore, past variations in precipitation inferred from the Pantanal region is likely to reflect a regional signal. Also, relict deflation basins and palaeodunes have been identified in the Pantanal. These aeolian features, currently fixed by overlaying vegetation, are hypothesized to have been formed under an arid glacial climate, although work on the dating of these features is ongoing (Clapperton 1993, Assine and Soares 2004). Although situated within the Pantanal basin, the study site, Laguna La Gaiba, is engulfed by the eastern edge of the Chiquitano SDTF, the largest remaining intact block of dry forest in South America (Miles et al. 2006), and a proposed component of the 'Pleistocene dry forest arc' (Prado and Gibbs 1993, Pennington et al. 2000, Miles et al. 2006).

The focused aims of the thesis are presented over three chapters, and formatted for submission as journal papers.

- Chapter 2 discusses the long-term changes in SDTF and Pantanal composition and diversity, and the probable climatic drivers of these changes. In particular, I aim to ascertain whether the Chiquitano SDTF was extant during the last glacial period in accordance with the 'Pleistocene dry forest arc' hypothesis.
- Chapter 3 focuses in detail on the climate and vegetation changes across glacial-Holocene transition. In particular, I attempt to determine whether there is any evidence of a precipitation anomaly during the YD chronozone.
- Chapter 4 reports on the results of a pilot study exploring the potential of *Pediastrum*, a genus of green algae, as a proxy for reconstructing lake levels in tropical regions, thereby attempting to reduce the "palaeoclimate proxy gap".

The papers will be submitted to Journal of Biogeography (Chapter 2) and Journal of Paleolimnology (Chapter 4). Chapter 3 has been submitted for publication in a special issue of Global Change Biology: Proceedings of "Tropical paleoecology and global change: records from terrestrial and main archives" symposium at the 12th International Palynological Congress IPC-XII, Bonn, Germany.

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II. Long-term dynamics of the Chiquitano seasonally-dry tropical forest, eastern Bolivia

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2.1. Abstract

Conventionally, debate over long-term ecosystem change in the South American tropics has focused on the relative extent of open savannahs and evergreen rainforest during the last glacial period. Recently, attention has been drawn toward seasonally-dry tropical forest (SDTF), hypothesized to have extensively covered tropical South America during glacial times. However, there are few palaeoecological data from Neotropical SDTF available to investigate the long-term history of these ecosystems. Here we present a 45,000-yr record of vegetation and climate change from the eastern margin of the Chiquitano SDTF in lowland Bolivia, the world's largest remaining intact block of SDTF. Fossil pollen analysis was applied to 94 sediment samples from a core extracted from a large, shallow lake, Laguna La Gaiba (LLG) (17º45'S, 57º40'W), situated on the western edge of the Pantanal wetlands, and adjacent to the Chiquitano SDTF. The scarcity of tree pollen in the glacial assemblages (> 45.0 to 19.5 cal. ka BP) indicate tree density was low, and SDTF was absent during the last glacial period. Warming at 19.5 cal. ka BP allows for the establishment of inundation-tolerant vegetation in low-lying seasonally-inundated areas under conditions of lower flooding. An early forest develops on the bedrock hills after 18.0 ka BP, but the community consists of a depauperate flora compared to the modern Chiquitano SDTF. Lake levels remain lower than present until 12.2 ka BP, when rapid flooding eliminates the seasonally-inundated community, but the early dry forest on the bedrock hills demonstrate little change. The expansion of the Chiquitano SDTF occurs after 10.0 ka BP, as shown by the appearance of *Anadenanthera,* and rising *Astronium* pollen, possibly due to a final temperature increase marking the onset of the Holocene. Although the floristic composition of

the Chiquitano SDTF remains largely unchanged throughout the Holocene, palynological richness (diversity) declines, and the relative abundance of drought-tolerant SDTF types increase in response to early- to mid-Holocene aridity (10.0 to 3.0 cal. ka BP) centred at 6.7 cal. ka BP. Precipitation rises in the late Holocene, decreasing the abundance of drought-tolerant taxa in the Chiquitano SDTF, and increasing palynological richness. Overall, the record from LLG indicates that changing precipitation affected the relative abundance of SDTF taxa and palynological richness of the pollen samples, but temperature is inferred to be the key driver of floristic composition in the Chiquitanía-Pantanal region over glacial-interglacial timescales.

2.2. Introduction

Debate over the glacial precipitation regime of lowland, tropical South America is heated and polarized. Several proponents argue for cool, but wet climate during the Last Glacial Maximum (LGM, centred on 21.0 ka BP), evidence for which is extrapolated from the well-dated and robust palaeoclimatic records of the Altiplano (Baker et al 2001a,b), speleothem growth in coastal Brazil (Wang et al. 2004), and the existence of closed-canopy forest in central Amazonia (Colinvaux et al. 1996, Haberle and Maslin 1999). On the other hand, there is some palaeoenvironmental evidence in favour of a dry glacial environment in the lowland tropics; sedimentary hiatuses in lowland lacustrine records are reflective of moisture-deficient basins (Ledru et al. 1998); aeolian features, such as palaeodunes, assumed to have formed during the LGM, are distributed across the lowland tropics (Clapperton 1993, Assine and Soares 2004); and in ecotonal regions, savannah once occupied sites that now lie within rainforest (Absy et al. 1991, van der Hammen and Absy 1994, Sifeddine et al. 2001, Burbridge et al. 2004).

Further evidence in favour of glacial aridity is drawn from current biogeographic patterns, argued to reflect variation in the extent of drought-tolerant and moisture-dependent biomes, driven by glacial (dry) and interglacial (wet) cycles (Haffer 1969, Prado and Gibbs 1993, Pennington et al. 2000, Wüster et al. 2005). Haffer (1969), who first proposed this hypothesis, argued that under an arid glacial climate, extensive savannahs occupied areas now dominated by rainforest, the latter having survived as isolated refugia in regions that experienced higher precipitation. Haffer’s proposal is hotly contested; high abundance of arboreal pollen, indicative of closed-canopy forest, and the absence of grass pollen in Amazonian records are presented as evidence against glacial aridity and the rainforest refugia hypothesis (Haberle and Maslin 1999, Colinvaux et al. 2000).

However, the absence of grass is not necessarily indicative of moist, evergreen rainforest. Seasonally-dry tropical forest (SDTF) are drought-tolerant ecosystems that occur under climates similar to savannahs; capable of withstanding

Table 2.1. Summary of key hypotheses for glacial vegetation of lowland tropical South America, their supporting evidence and main criticisms

HYPOTHESES	KEY POINTS	SUPPORTING DATA	KEY CRITICISMS	CRITICAL TESTS	REFERENCES
Rainforest Refugia Hypothesis	Glacial-age rainforest refugia within open, shrubby vegetation	Biodiversity ‘hotspots’ in areas of higher rainfall; aeolian ‘arid’ landforms	Aeolian landforms are undated; no evidence of savannah in Amazon fan sediments	Long records from areas in central Amazonia hypothesized to have been occupied by open vegetation	Haffer 1969 Wüster et al. 2005
Continuous Rainforest	Moist and cool glacial climate allowed for continuous forest cover	Amazonian sediments contain abundant tree pollen; high precipitation inferred from Andean records	Sedimentary hiatuses in lowland lakes (including Pata) are indicative of drought; the pollen signal in Pata could represent SDTF	Higher taxonomic resolution of pollen analysis to differentiate rainforest from SDTF	Colinvaux et al. 1996 Maslin & Haberle 1999 Colinvaux et al. 2000 Bush et al. 2004
Pleistocene Dry Forest Arc	SDTF occurs in the same climatic regime as savannah, and occupied large parts of the lowland tropics	Broad distribution of five key SDTF taxa suggestive of vicariance; reconciles pollen data of closed canopy forest with evidence for aridity	Biogeographic data indicative of dissimilarity between some adjacent SDTF; few pollen records from SDTF to support this hypothesis	Long records located within the proposed ‘dry forest arc’ ****this study****	Prado & Gibbs 1993 Pennington et al. 2000 Pennington et al. 2006

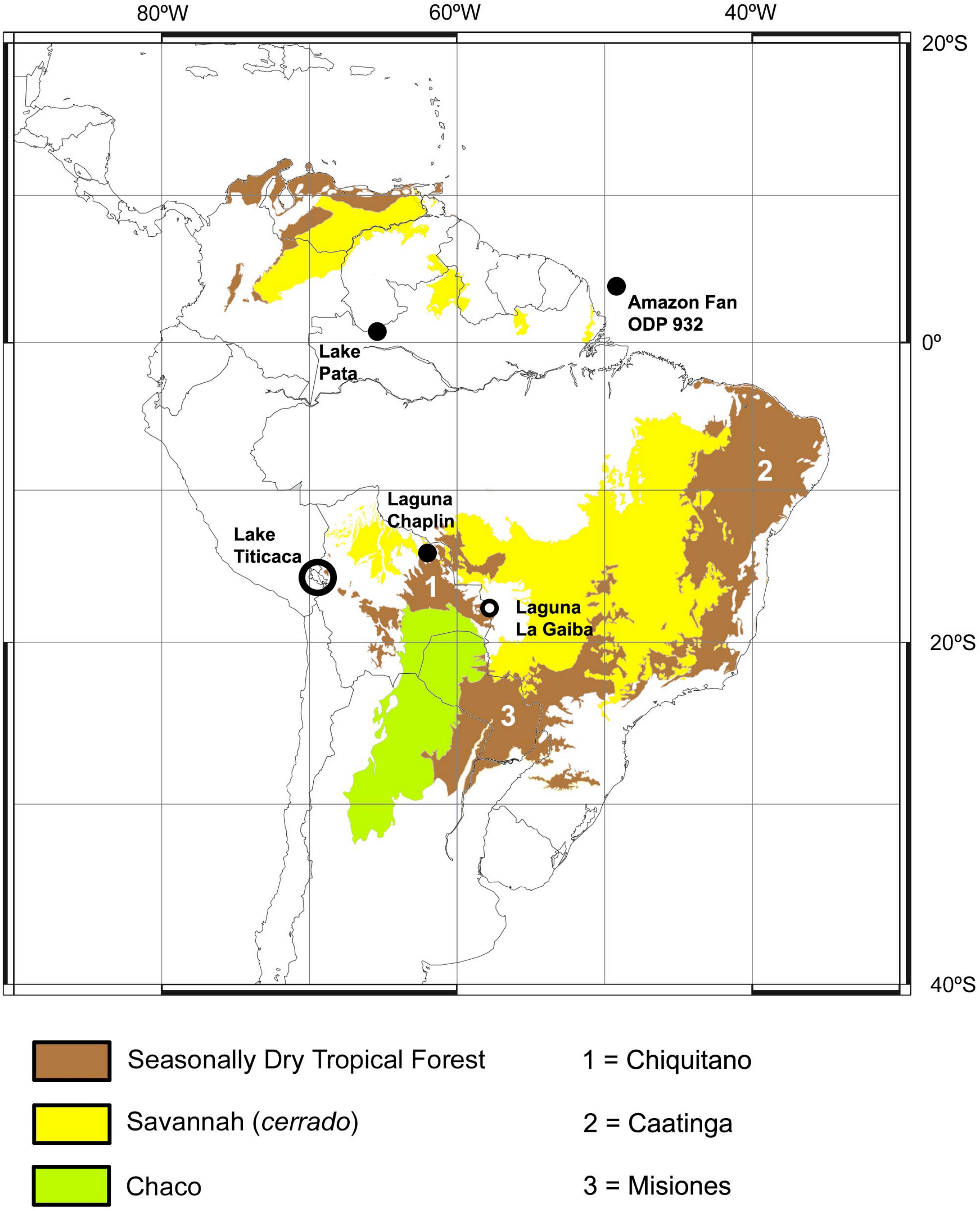

Fig. 2.1. Schematic distribution of SDTF, savannah and Chaco vegetation in tropical and subtropical South America (adapted from Pennington et al. 2000). Also shown is the position of Laguna La Gaiba (this study) on the eastern edge of the Chiquitano SDTF (square), and Laguna Chaplin (circle) discussed in the text.

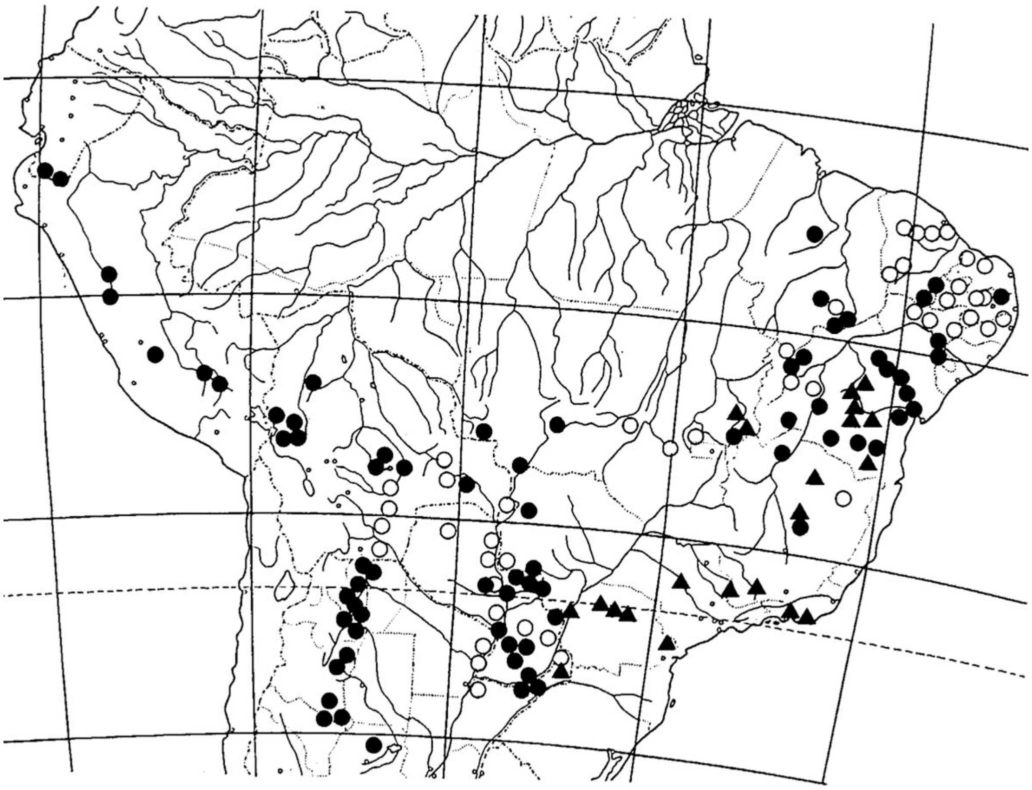

Fig. 2.2. Distribution of *Anadenanthera colubrina* in tropical and subtropical South America. Circles and triangles denote *Anadenanthera colubrina* var. *cebil* and *Anadenanthera colubrina* var. *colubrina*, respectively. Open symbols refer to citations in floristic lists and solid symbols refer to herbarium specimens or citations in monographs. Adapted from Prado and Gibbs (1993).

prolonged dry seasons and low annual precipitation, though SDTF differ from savannahs in that they grow on more fertile soils, often calcareous and containing low levels of aluminium (Gentry 1995, Pennington et al. 2006). Although of lower stature than moist, evergreen rainforest, SDTF are closed-canopy ecosystems and contain little grass in the understorey (Gentry 1995). Proposed as an alternative to extensive glacial-aged savannahs (Prado and Gibbs 1993, Pennington et al. 2000), the incursion of SDTF in Amazonian regions during the last glacial period does not contradict the palaeoecological data. At the family level, rainforest and SDTF are floristically similar, and owing to the coarse taxonomic resolution of pollen analysis, the fossil assemblages in central Amazonian records could equally be interpreted as reflecting SDTF (Pennington et al. 2000).

Evidence in favour of more extensive SDTF in glacial periods are floristic affinities among currently disjunct blocks of Neotropical SDTF, argued to reflect past linkages between these regions (Pennington et al. 2000) (Fig. 2.1). The widespread, arc-shaped distribution of some species of Neotropical SDTF, such as *Anadenanthera colubrina* (Fig. 2.2), is argued to reflect the glacial extent of SDTF (Prado and Gibbs 1993, Pennington et al. 2000). In central Brazil, now dominated by *cerrado* (savannah) biome, greater coverage of SDTF during the last glacial period are thought to have acted as migration corridors, linking the eastern Caatinga and southwestern Misiones dry forest nucleii (Fig. 2.1) (Prado and Gibbs 1993, Pennington et al. 2000). That central Brazil once supported greater forest coverage is backed by widely occurring fire-intolerant taxa in cerrado forest islands, such as species of Cactaceae, that are incapable of migrating across this broad and frequently burned ecosystem (Pennington et al. 2000).

Advocates of a ‘Pleistocene dry forest arc’ argue that a humid interglacial climate favoured the expansion of rainforest in Amazonian regions, and in central Brazil, higher precipitation caused soil-leaching and acidification, rendering the region unable to support forest, thereby favouring the expansion of cerrado (Ratter et al. 1988, Oliveira-Filho and Ratter 1995). Contraction of Pleistocene-aged dry forests resulted in the currently disjunct blocks of SDTF, restricted to fertile soils in areas that experience a pronounced dry season, as well as the widespread distribution of several species characteristic of SDTF (Murphy and Lugo 1986, Pennington et al. 2000).

Although an attractive hypothesis, the distribution and dynamics of SDTF over glacial-interglacial timescales is largely unknown (Mayle 2006). Furthermore, the floristic affinities of SDTF in Argentina, Brazil, and Paraguay strongly support the ‘Pleistocene dry forest arc’ hypothesis, but floristic data from Bolivia and Peru emphasize difference rather than similarity between SDTF in inter-Andean valleys and Brazilian seasonal forests, indicative of spatial complexity in the past distribution of SDTF (Pennington et al. 2006). Moreover, palynological evidence of from a forest-savannah ecotone in northeast Bolivia demonstrate that extensive savannahs, not SDTF, occupied the southern margin of the Amazon rainforest during the last glacial period (Mayle et al. 2000, Burbridge et al. 2004).

The Chiquitano SDTF, situated in eastern, lowland Bolivia, is located within the proposed ‘Pleistocene dry forest arc’. Preliminary evidence suggests this region experienced aridity during the last glacial period; the eastern margin of the forest borders the Pantanal wetlands that contain relict aeolian features hypothesized to be active during the last glacial period (Clapperton 1993, Assine and Soares 2004), thus an arid glacial climate would likely favour SDTF. The aims of this research are (1) to determine history of the Chiquitano SDTF through the analysis of fossil pollen; (2) to infer the palaeoclimate of this region from past vegetation; (3) to establish whether SDTF occupied this region during the last glacial period as predicted by the ‘Pleistocene dry forest arc’ hypothesis.

2.3. Study Area

The Chiquitano is the largest intact block of SDTF in South America, comprising nearly a quarter of the world’s total (Miles et al. 2006). Overlaying Precambrian bedrock on the western edge of the Brazilian shield, the Chiquitano SDTF forms a transition between humid rainforest to the north, and dry Chaco scrub to the south (Killeen et al. 1998). Typical of SDTF, the Chiquitano experiences 900 – 1200 mm mean annual precipitation, and a pronounced dry season lasting several months in the austral winter. Temperature is also highly seasonal; the annual average is 24ºC, and values range from 3ºC to 40ºC (Jardim et al. 2003).

The Chiquitano flora is typical of Neotropical SDTF (Jardim et al. 1993), comprising a subset of the families present in moist evergreen forest (Gentry 1995). Bignoniaceae and Leguminosae are the most speciose families (Gentry 1995) and Anacardiaceae, Apocynaceae, Cactaceae, Euphorbiaceae, Myrtaceae and

Sapindaceae are well-represented (Killeen et al. 1998, Jardim et al. 2003). Families considered to be characteristic of moister, evergreen forest occupy moist, low-lying areas, such as Annonaceae, Chrysobalanaceae, Lauraceae, Melastomataceae, Moraceae, Myristicaceae, Palmae, and Sapotaceae (Jardim et al. 2003). The Chiquitano SDTF possesses one of the highest α-diversity of any Neotropical SDTF, containing as many as 87 species of trees and lianas (> 2.5 cm dbh) in 0.1 ha, and also exhibits a high degree spatial heterogeneity (β-diversity) (Killeen et al. 1998). Characteristic of Neotropical SDTF, the canopy-height and basal area of the Chiquitano is lower than moist, evergreen rainforest. The understorey contains few grasses, and species of Bromeliaceae and Cactaceae are common ground cover. Lianas are also abundant, typically of the Bignoniaceae (Gentry 1995, Killeen et al. 1998).

Bordering the eastern edge of the Chiquitano SDTF, the Pantanal is the world's largest tropical wetland (~140,000 km^2), located mainly in western Brazil, but extending into easternmost Bolivia (Alho 2005) (Fig. 2.3). The Pantanal is not a single biogeographical unit, rather it is comprised of a combination of xeric, mesic and inundated plant communities, the distribution of which is dependent on topography and the flooding regime (Dubs 1992, Alho 2005, Nunes da Cunha et al. 2007). Endemism is low; vegetation of the Pantanal incorporates elements of humid rainforest, dry Chaco and Brazilian cerrado vegetation (Prance and Schaller 1982). River levées support inundation-tolerant gallery forests, and permanently-flooded wetlands occupy areas of lowest elevation immediately behind these levées. In the eastern Pantanal, seasonally-inundated savannahs occupy low-lying areas that endure greater flooding, and SDTF inhabit higher elevation soils, the result of termite activity or shifting rivers. Alho (2005), Nunes da Cunha et al. (2007), and Prance and Schaller (1982) give comprehensive overviews of the vegetation types of the Pantanal.

The study site is Laguna La Gaiba (LLG) (17°45'S, 57°40' W), a large, shallow lake within the eastern margin of the Chiquitano SDTF, but located along the

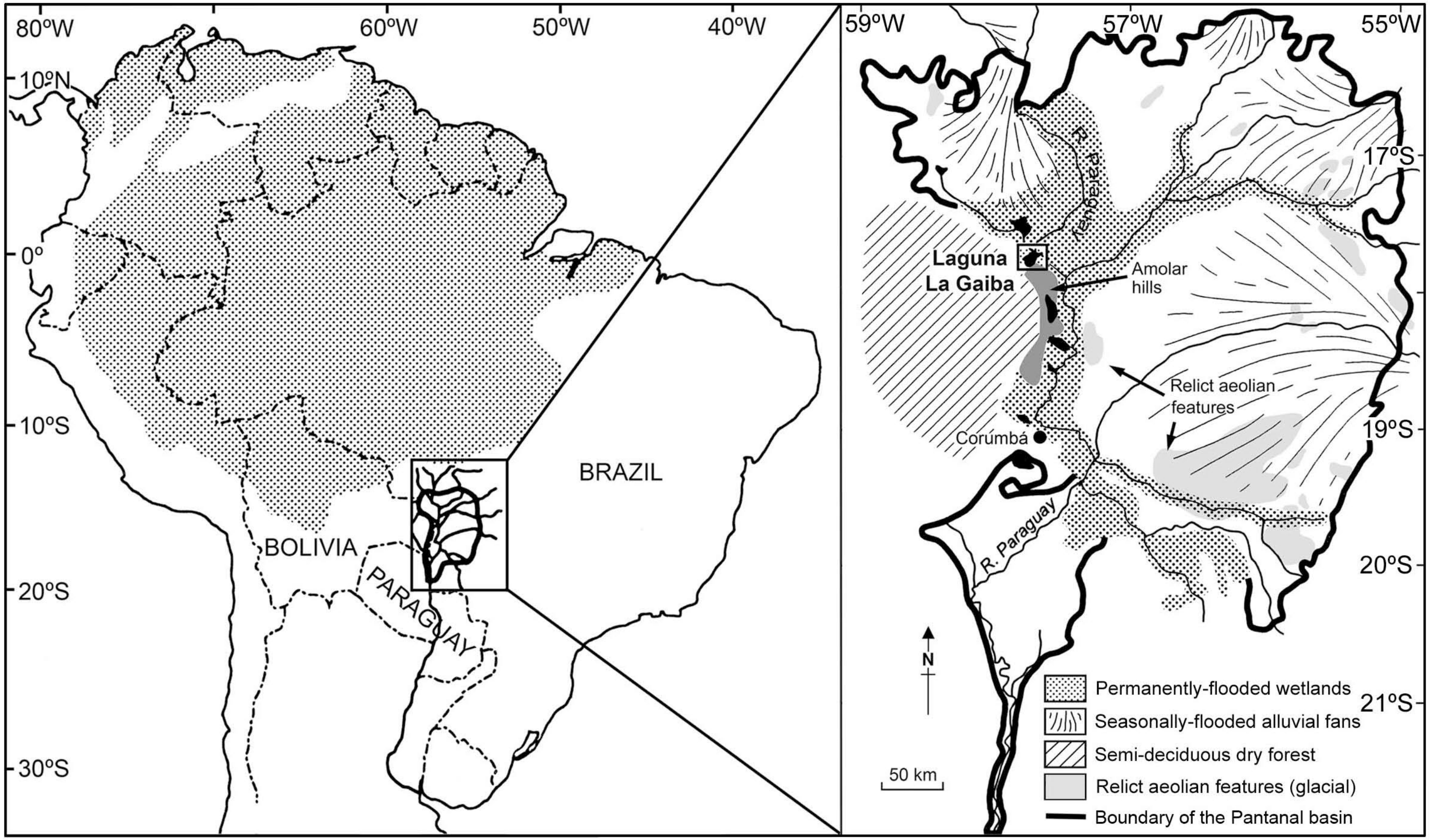

Fig. 2.3. (a) Location of the Pantanal basin relative to the Amazon rainforest (stippled). (b) The study site, Laguna La Gaiba, is situated along the Rio Paraguay and lies between the permanently flooded wetlands and gallery forests of the Pantanal (stippled) and the Chiquitano SDTF (hashed). Seasonally-inundated savannahs overlay alluvial fans to the east of the Rio Paraguay (radiating lines). Relict aeolian features from Clapperton (1993) are shaded in light gray.

course of the Rio Paraguay, thus the lake is hydrologically connected to the Pantanal wetlands and savannahs (Fig. 2.4). LLG is nestled among SDTF that dominates the hillslopes of the Amolar-Urucum formation, rising steeply above the lake to reach a maximum elevation of 550 to 1000 m asl (Alho 2005). Deciduousness increases with elevation (Fig. 2.5a), and the highest summit on the hills to the southeast of LLG is occupied by upland savannah (Prance and Schaller 1982). The northeast lake margin merges with the Pantanal wetlands, but the remaining lake margins are constricted by the Amolar hills (Fig. 2.5b). Narrow, sediment-rich beaches on the south and southwestern shores of the lake support moister, evergreen vegetation, the composition of which differs somewhat from the SDTF on the Amolar hills (Fig. 2.5c).

A qualitative vegetation survey conducted in August 2008 demonstrates the forest surrounding LLG is characteristic of the Chiquitano SDTF. Taxa abundant in terra firme formations include *Anadenanthera colubrina*, *Astronium fraxinifolium*, *A. urundeuva*, *Capparis spp*., and species of Bignoniaceae, mostly lianas. Few herbs are present, but bromeliads and Cactaceae (*Cereus spp*.) are abundant in the understorey. Lower elevation forest, such as the assemblages located on the lake shore and on sediment-rich soils, contain elements characteristic of moister, evergreen forest, such as *Inga* spp. and *Annona* sp. Inundation-tolerant *Albizia inundata*, *Inga* spp., and *Vitex* sp. are common along lake and river margins, and floating mats of *Eichhornia* spp., *Polygonum* spp., Asteraceae and Poaceae dominate the lake margins (Table 2.1).

2.4. Methodology

2.4.1. Coring

In 2001, two parallel overlapping sediment cores were extracted from a floating platform in the centre of the south basin using a Colinvaux-Vohnout drop-hammer modified Livingston piston corer (Colinvaux et al. 1999). The cores, measuring 5.6 m and 4.8 m and extending to ~ 45 ka BP, were shipped in their

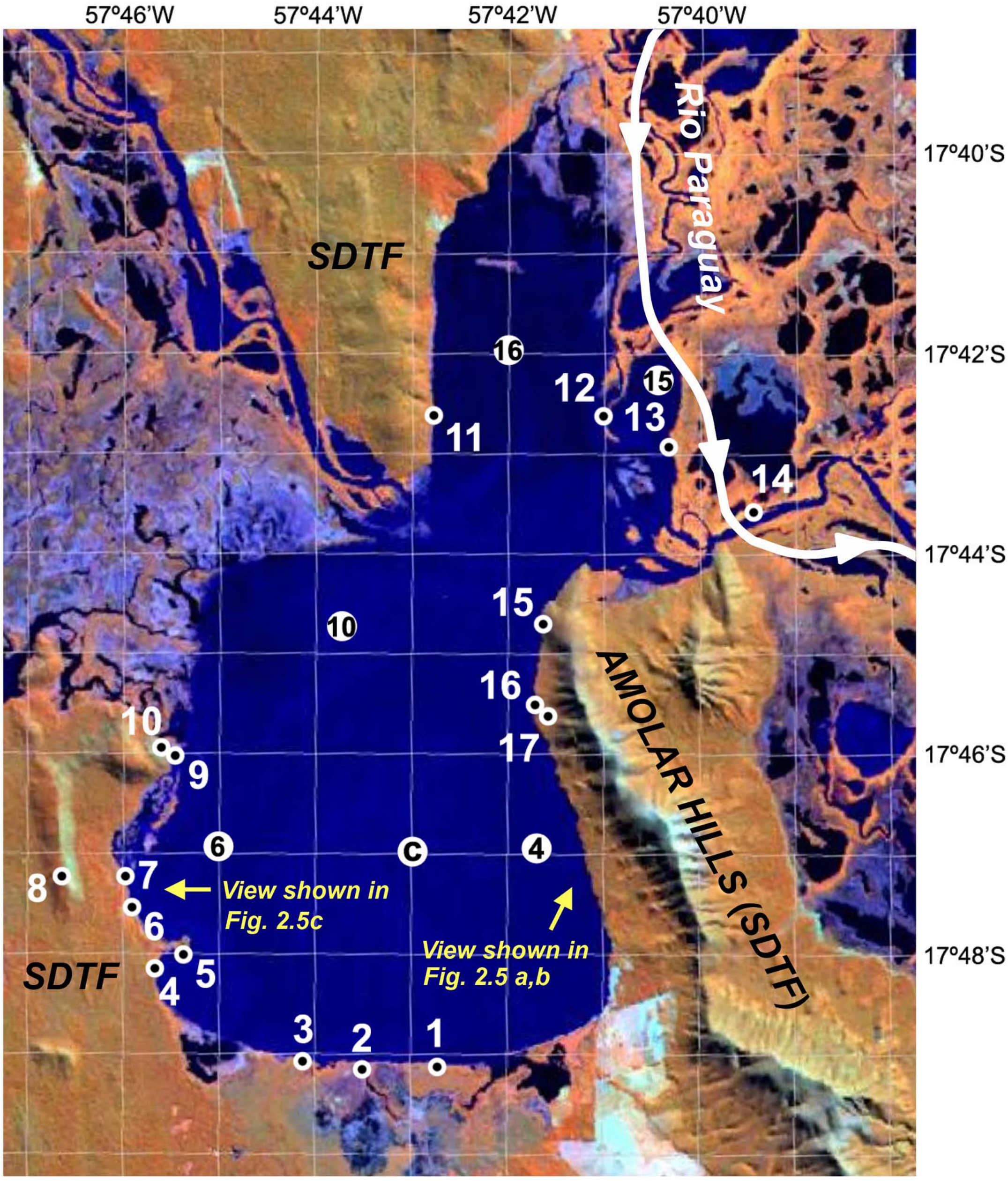

Fig. 2.4. Landsat image of LLG indicating its situation in the Chiquitano SDTF. The south basin of LLG is surrounded by dry forest on steep hills, and the shallow north basin merges with the Rio Paraguay and the Pantanal wetlands. Also shown are the locations of the vegetation survey (hollow circles) (Table 2.1), and positions of six surface sediment samples including the core site (solid circles) analyzed for modern pollen (Fig. 2.9). See Figs 2.5a-c for photographs of the surrounding vegetation.

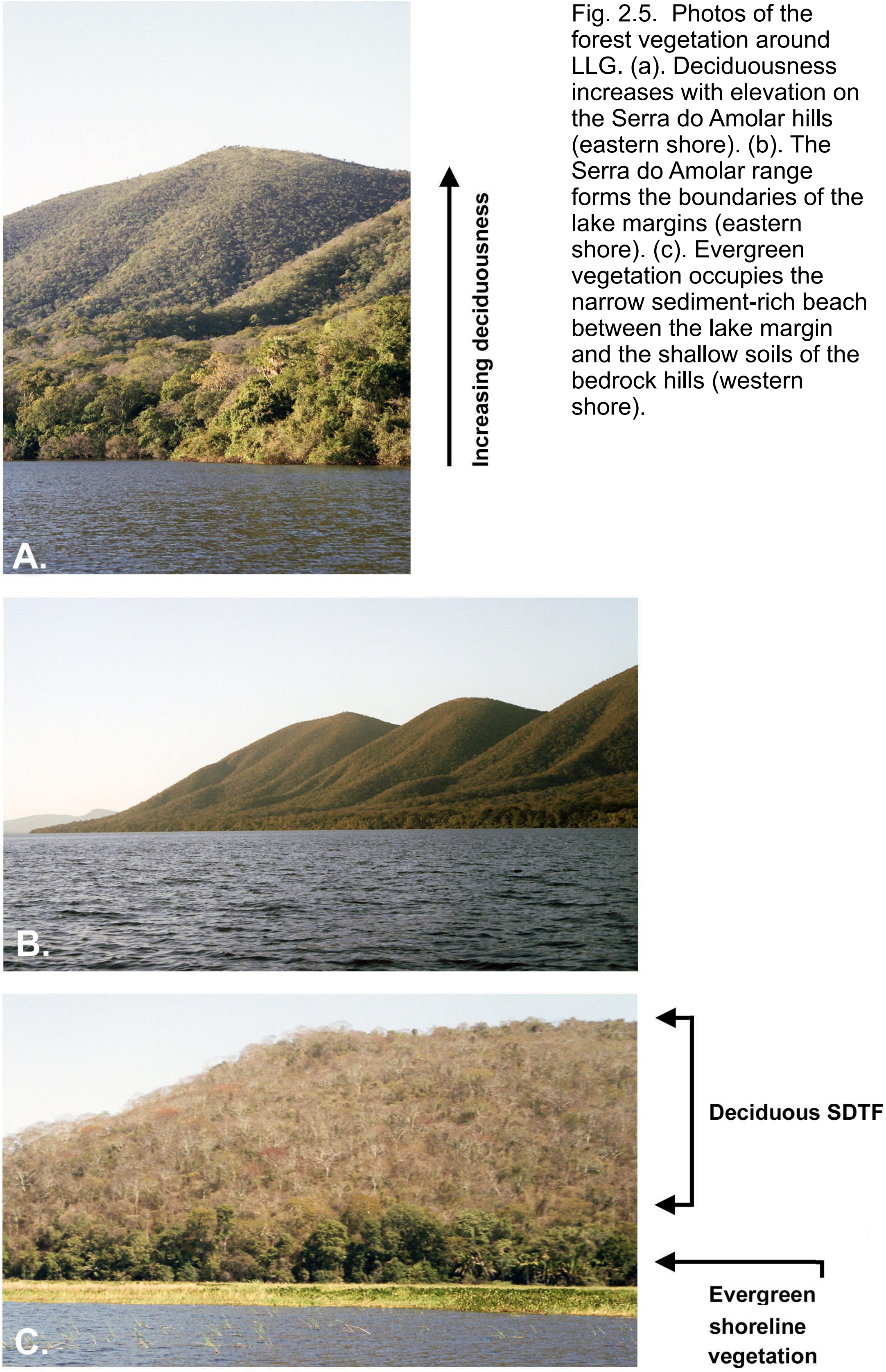

Fig. 2.5. Photos of the forest vegetation around LLG. (a). Deciduousness increases with elevation on the Serra do Amolar hills (eastern shore). (b). The Serra do Amolar range forms the boundaries of the lake margins (eastern shore). (c). Evergreen vegetation occupies the narrow sediment-rich beach between the lake margin and the shallow soils of the bedrock hills (western shore).

Table 2.2. Location and habitat of plant taxa recorded at LLG. Site no. refers to position on map. (Fig. 2.4)

	Habitat	**Site No.**	**Recorded taxa (*) denotes abundant** *t = tree, s = shrub, h = herb, p = palm, c = cactus, li = liana, hc = herbaceous climber, aq = aquatic*
	Floating mat	1	*Eichhornia crassipes** (aq), Poaceae* (h)
		2	*Eichhornia sp.** (aq), Poaceae* (h)
		7	Asteraceae (h), Cyperaceae (h), Poaceae (h)
		10	*Eichhornia sp.** (aq), Asteraceae (h), *Ludwigia sp.* (s), Poaceae (h)
	Swamp	1	*Copernicia alba** (p), *Ipomoea carnea** (s), Poaceae* (h)
	Inundated lake margin	2	*Aeschynomene sp.** (t), *Erythrina sp.* (t), *Ludwigia sp.* (s), *Tibouchina sp.* (s)
		3	*Albizia inundata* (t)
		5	Combretaceae (t), Myrtaceae (t)
	River margin	14	*Eichhornia sp.** (aq), Asteraceae (h), *Cissus sp.*, (hc), *Inga sp.* (t), *Ipomoea sp.* (hc), *Polygonum sp.* (aq), *Pterocarpus sp.* (t), Verbenaceae (t)
	Levée	12	*Albizia sp.** (t), Combretaceae (t), *Inga sp.* (t), Unk sp. 1 (t)
		13	*Albizia sp.* (t), *Inga sp.* (t), Unk sp. 2 (t)
Low elevation, terra firme	Lake shore	1	Acacia sp. (t), Combretum sp.1* (t)
		4	*Vitex sp.** (t), *Annona muricata* (t), *Anadenanthera colubrina* (t), *Arrabidaea sp.* (li), *Aspidosperma cylindrocarpon* (t), *Astronium fraxinifolium* (t), *Astronium urundeuva* (t), *Attalea sp.* (p), *Caesalpinia pluviosa* (t), *Cecropia concolor* (t), *Cordia sp.* (t), *Combretum sp.2* (t), *Ficus sp.* (t), *Guazuma ulmifolia* (t), *Inga sp.* (t), Olacaceae sp. (t), *Phyllostylon rhamnoides* (t), *Salacia sp.* (t), *Sapindus saponaria* (t), *Swartzia sp.* (t)
		6	*Samanea saman* (t), *Spondias mombin* (t)
		16	Sapotaceae* (t), *Astronium fraxinifolium* (t), Caesalpiniodeae (t), *Ficus sp.* (t), *Inga sp.* (t), *Lonchocarpus sp.* (t), Myrtaceae (t), *Salacia sp.* (t), *Vitex sp.* (t)
	Well-drained sediment-rich soils	6	*Anadenanthera colubrina** (t), *Acacia sp.* (t), *Albizia sp.* (t), *Cecropia concolor* (light-gaps) (t), *Combretum leprosum* (t), *Genipa americana* (t), *Guazuma ulmifolia* (t), *Guibourtia cf. chodatiana* (t), *Neea sp.* (t), *Piptadenia sp.* (t), *Tabebuia impetiginosa* (t)
Bedrock hill slopes	Calcareous bedrock	8	*Amburana cearensis* (t), *Amphilophium sandwithi* (li), *Calycophyllum sp.* (t), *Jacaratia hassleriana* (t), *Paullinia sp.* (li), *Smilax sp.* (li), *Spondias mombin* (t)
		9	*Anadenanthera colubrina* (t), *Acosmium cardenasii* (t), *Astronium fraxinifolium* (t), *Astronium urundeuva* (t), *Ceiba speciosa* (t), *Cereus sp.* (c), *Ruellea consanguinea* (s), *Swartzia sp.* (t)

Table 2.2 (continued)

Hill slopes (cont.)	Calcarous bedrock (ridge)	8	*Anadenanthera colubrina** (t), *Acacia sp.* (t), *Acosmium cardenasii* (t), *Bauhinia sp.* (t), *Capparis prisca* (t), *Capparis retusa* (s), *Ceiba speciosa* (t), *Cereus sp.* (c), *Cochlospermum sp.* (t), *Ficus sp.* (t), *Neea cf. hermaphrodita* (t), *Ruellea consanguinea* (s), *Urera baccifera* (t)
	Non-calcareous bedrock	11	Bignoniaceae* (li), *Ruellea consanguinea** (s), *Acacia sp.* (t), *Anadenanthera colubrina* (t), *Arrabidaea fagoides* (li), *Acosmium cardenasii* (t), *Aspidosperma sp.* (t), *Astronium fraxinifolium* (t), *Caesalpinia pluviosa* (t), *Capparis vertusa* (s), *Casearia sp.* (t), *Cereus sp.* (c), *Pouteria sp.* (t), *Salacia sp.* (t)
		15	*Astronium fraxinifolium** (t), *Dipteryx alata** (t), *Commiphora leptophloeos** (t), *Aspidosperma cf. rigidum* (t), *Caesalpinia sp.* (t), *Casearia cf. sylvestris* (t), *Cochlospermum cf. vitifolium* (t), *Dilodendron bipinnatum* (t), *Ficus sp.* (t), *Ouratea sp.* (t), Sapotaceae (t), *Simarouba sp.* (t), Vochysiaceae (t)
		16	*Anadenanthera colubrina** (t), *Acacia cf. praecox* (t), *Acosmium cardenasii* (t), *Alibertia sp.* (t), *Astronium fraxinifolium* (t), *Astronium urundeuva* (t), *Casearia sylvestris* (t), *Cereus sp.* (c), *Esenbeckia almawillia* (s), *Hymenaea stigonocarpa* (t), *Protium sp.* (t), *Salacia sp.* (t), *Smilax sp.* (li), *Tabebuia impetiginosa* (t)
		17	*Allophylus sp.* (hc), *Annona sp.* (t), *Arrabidaea fagoides* (li), *Bauhinia sp.* (li), *Dilodendron bipinnatum* (t), *Enterolobium contortisiliquum* (t), *Erthroxylum sp.* (t), *Setaria sp.* (h) (Poaceae), *Talisia cf. esculenta* (t)

aluminium tubes and extruded in the laboratory. Extruded cores were wrapped in plastic film, aluminium foil and thick plastic sleeves, and stored in a dark room at 4°C. The surface core, comprising the uppermost 110 cm of unconsolidated sediments and overlapping the Livingston core by 40 cm, was collected with a Perspex® tube and piston, and extruded in the field into air-tight plastic bags in consecutive 1 cm slices. Parallel cores were correlated by magnetic susceptibility and cross-checked through analysis of pollen at zonal boundaries, and the surface core was correlated to the consolidated Livingston cores through loss-on-ignition (550ºC) analysis (Dean 1974).

2.4.2. Chronology and Sedimentology

The entire age-model from LLG is based on 18 AMS ^{14}C dates analyzed by the NERC radiocarbon facility, East Kilbride, UK (Table 2.2); 16 of which were obtained from well-preserved terrestrial plant macrofossils and two from sediment. One outlying date was rejected; its anomalously young age possibly owing to contamination of the low carbon content of the sample material (12%). All AMS ^{14}C ages ($\pm 2\sigma$) were calibrated using the "Fairbanks0107" calibration curve (Fairbanks et al. 2005). The age-depth relationship was analyzed using mixed-effect regression, as described by Heegaard et al. (2005), and the age of each sample was calculated from a cubic spline fitted through the calibrated radiocarbon dates (Fig. 2.6). Unlike many lowland records (Ledru et al. 1998), sedimentation is constant across the LGM. Organic content estimated by loss-on-ignition analysis (Dean 1974) and sedimentological units are presented in Fig. 2.7.

2.4.3. Pollen Analysis

The entire record was sampled for pollen analysis at approximately 500-yr resolution, and 300-yr resolution across the glacial-Holocene transition where pollen assemblages demonstrate greater variability. Samples measuring 1 cm^3 were processed according to Fægri and Iversen (1989) and a known quantity of exotic *Lycopodium* spores was added during sample preparation to calculate concentration

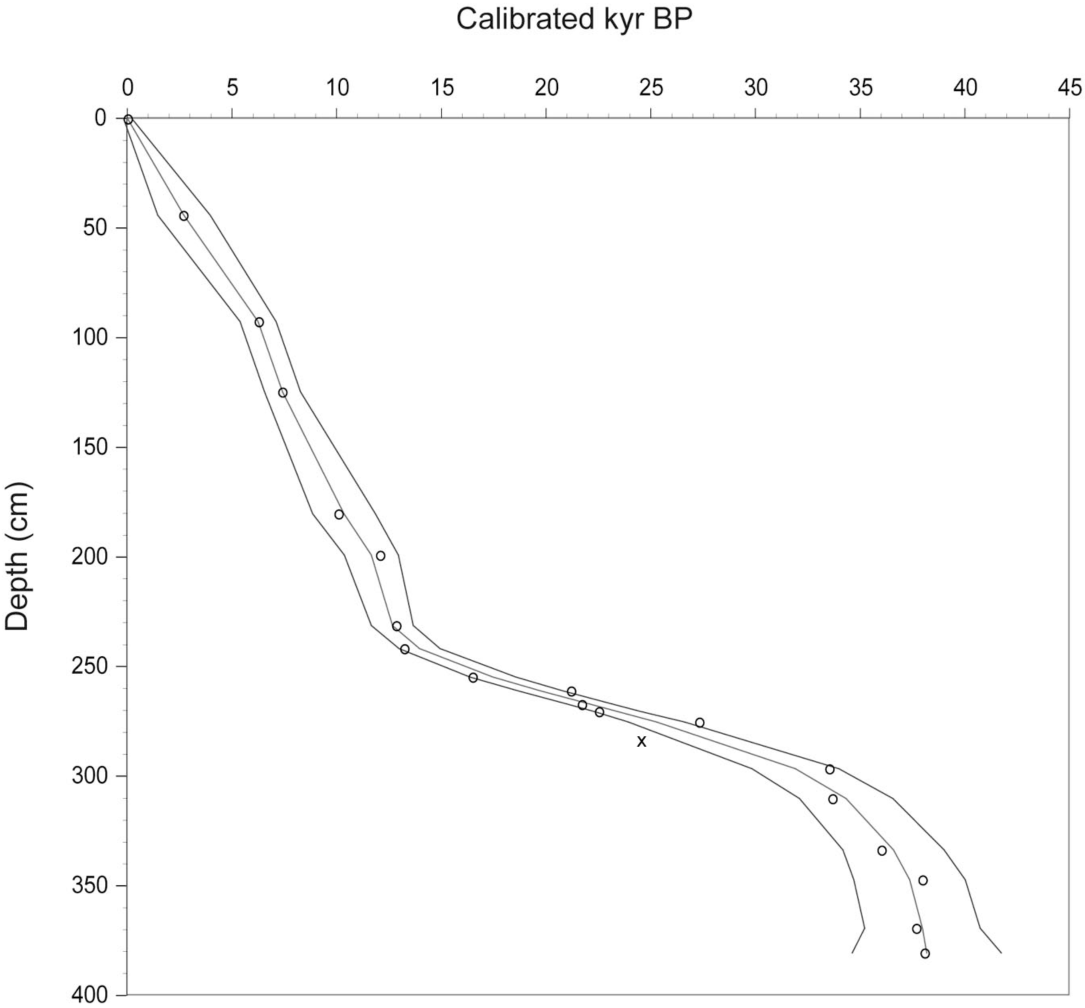

Fig. 2.6. The LLG age-model based on 18 AMS ^{14}C dates and an assumed modern date for the uppermost cm of sediment. The model built using a mixed-effect regression as described by Heegaard et al. (2005). Black (outer) lines represent 2σ error. Rejected date is denoted by ‘x’.

of pollen grains per cm^3. Fossil pollen identifications were made with reference to tropical pollen atlases (Roubik and Moreno 1991, Colinvaux et al. 1999), a digital pollen key (Bush and Weng 2007), and a modern pollen reference collection consisting of >1000 specimens representing > 850 taxa, located at the School of Geosciences, University of Edinburgh. Pollen counts totalled 300 terrestrial grains, and because of the proximity of the site to the Pantanal savannahs, Poaceae and

Table 2.3. Uncalibrated and calibrated AMS ^{14}C dates, their publication codes, corrected stratigraphic position, and carbon datat (see A.1 for core correlation details). †Denotes rejected date, and *denotes estimated value because of low carbon contest.

Publication Code	**Sampler Identifier**	**Material**	**Stratigraphic Position (cm)**	**^{14}C Enrichment (% modern)**	**Conventional ^{14}C Age (yrs BP ±1σ)**	**Carbon Content (% wt)**	**$\delta^{13}C_{VPDB}$ (‰ ±0.1)**	**Calibrated Age (yrs BP ±1σ)**
SUERC-11240	LLG surface: 49-50	Twig	44 - 45	72.79 ± 0.32	2552 ± 35	59	-26*	2701 ± 56
SUERC-16482	LLG1a: 92-94	Sediment	92 - 94	50.53 ± 0.24	5512 ± 38	10.5	-20.7	6298 ± 26
SUERC-16483	LLG1a: 124-126	Sediment	124 - 126	44.42 ± 0.22	6519 ± 40	8.9	-22.3	7431 ± 26
AA-51698	LG1: 175-176	Twig	180 - 181	32.86 ± 0.23	8939 ± 56	18	-26.2*	10116 ± 101
SUERC-11241	LLG1: 194-195	Twig/bark	199 - 200	27.68 ± 0.15	10317 ± 43	50	-26.6	12104 ± 77
SUERC-11242	LLG1: 226-227	Twig/bark	231 - 232	25.43 ± 0.14	10999 ± 46	56	-28.1	12874 ± 49
SUERC-16748	LLG1: 236-238	Twigs/seed	241 - 243	24.17 ± 0.15	11408 ± 48	61	-26.3	13258 ± 72
SUERC-11251	LLG1: 249-251	Twig/bark	254 - 256	17.24 ± 0.13	14121 + 60	47	-27.2	16519 ± 142
SUERC-11704	LLG1: 256-257	Twig/wood	260.8 - 261.8	10.78 ± 0.12	17892 ± 91	67	-27.5	21211 ± 157
SUERC-11703	LLG1: 264-265	Twig/wood	267.2 - 268	10.33 ± 0.12	18236 ± 94	36	-27.2	21742 ± 180
SUERC-16749	LLG1: 268-271	Leaf/twig	268.8 - 272.8	9.41 ± 0.12	18983 ± 104	52	-26.5*	22557 ± 126
SUERC-11243	LLG1: 274-275	Twig/bark	275.2 - 276	5.87 ± 0.12	22771 ± 164	27	-28.2	27348 ± 230
†SUERC-16750	LLG1: 280-282	Leaf/bark	281.6 - 283.9	7.80 ± 0.12	20489 ± 122	12	-26.7	24397 ± 152
SUERC-11244	LLG1: 293-294	Bark/wood	296.3 - 297.4	2.99 ± 0.12	28185 ± 320	51	-24.6	33559 ± 370
SUERC-11245	LLG1: 306	Twig/bark	310.2 - 310.8	2.94 ± 0.12	28320 ± 326	47	-25.0*	33700 ± 373
AA-51699	LG1a: 334	Twig	333.8 - 334.2	2.20 ± 0.11	30670 ± 390	36	-26.2	36042 ± 399
SUERC-16484	LLG1: 338	Twig	347 - 348.1	1.73 ± 0.12	32609 ± 556	56	-29.7	38002 ± 579
SUERC-16751	LLG1: 357-359	Leaf/twig	368.5 - 370.7	1.79 ± 0.12	32311 ± 535	43	-27.6	37701 ± 560
SUERC-11246	LLG1: 368	Wood	380 - 381.6	1.70 ± 0.13	32717 ± 564	47	-27.2	38110 ± 588

Cyperaceae were included in the terrestrial sum. Data are presented as relative percent abundance and concentration (Fig. 2.7 and Fig. 2.8, respectively), and stratigraphic plots were created with C^2 (Juggins 2003).

To capture the spatial variability of modern pollen deposition in LLG, six 1 cm^3 sediment samples taken from the surface-water interface were analyzed for pollen; four from the south basin (including the surface core top) and two from sites located in the north basin (Fig. 2.4). Percent abundance of key pollen types are presented in Fig. 2.9.

Twenty-five samples were examined to differentiate the pollen of Moraceae and Urticaceae into constituent genera. The horizons chosen for analysis were concentrated at pollen zonal boundaries, and the abundance of each Moraceae/ Urticaceae type was interpolated in the remaining samples. Moraceae/Urticaceae pollen was differentiated with reference to Burn and Mayle (2008), and grouped into seven types (total Urticaceae, *Brosimum* type, *Maquira* type, *Helicostylis* type, *Pourouma* type, *Pseudolmedia*/*Maclura* type and *Ficus*).

2.4.4. Statistics

Palynological richness was determined using rarefaction analysis, described by Birks and Line (1992), which standardizes pollen sums to control for the influence of count size on number of pollen types encountered. Sums were standardized to a count of 270 terrestrial pollen grains. Although the relationship between palynological richness and past plant diversity is complex and dependent on pollen dispersal method of individual taxa, production rates, and taphonomy, it has been shown to provide an approximate estimation of past diversity in the northern, temperate zone (Odgaard 1999). Zonation of percent abundance pollen data was achieved through optimal splitting by information content, and three statistically significant pollen zones were identified using the broken-stick model as described by Bennett (1996). Zonation calculations were performed using Psimpoll 4.26 (Bennett 2007).

2.5. Results

2.5.1. LG-I: 42.0 to 19.5 ka BP

Herbs dominate the glacial pollen assemblages, such as *Alternanthera* (20 – 55%), *Borreria/Spermacoce* (2 – 14%), Poaceae (10 – 45%), Cyperaceae (5 – 15%), and Asteraceae (2 – 10%) (Figs. 2.7, 2.8). Although there is negligible tree pollen, the abundance of woody plant macrofossils in the sediments demonstrates shrubs and/or trees were locally present, likely genera of the Fabaceae (Mimosoideae), because of the low, but continuous persistence of these taxa in the glacial pollen spectra. Pollen of Urticaceae, *Acalypha*, *Dalbergia/Machaerium*, Palmae, and Cactaceae are also present in low proportions (< 1%). Palynological richness of glacial assemblages is low.

The sediments of LG-1 consist of grey-brown clays interspersed with units of abundant fine sands and charcoal from 30.0 to 24.0 ka BP, and beginning at 21.0 ka BP near the top of the zone. Despite the abundance of terrestrial plant macrofossils, glacial sediments contain negligible concentrations of fine organic matter (< 5%).

2.5.2. LG-II: 19.5 to 12.2 ka BP

LG-II is characterized by pollen of *Symmeria paniculata* (10 – 15%), *Piranhea* (10 – 15%), and *Alchornea* (5 – 15%), species of which are inundation-tolerant and abundant in floodplain vegetation (Junk 1989, Worbes 1997). Species of Moraceae (1 – 5%), mostly represented by *Brosimum* and *Pseudolmedia/Maclura* types, Urticaceae (2 – 6%), *Acalypha* (1 – 4%), Myrtaceae (1 – 6%), and Combretaceae/Melastomataceae (1 – 6%) also appear after 19.5 ka BP. *Ficus*, *Ruprechtia*, *Triplaris*, are present, though in low abundance (< 1%). As in the glacial samples, pollen of *Dalbergia/Machaerium*, Cactaceae, and Palmae occur occasionally in these assemblages. The relative proportion of Asteraceae (2 – 6%) remains constant across the transition from LG-I to LG-II, but other herbaceous pollen types, *Borreria/Spermacoce* (2 – 4%) and *Alternanthera* (2 – 5%), much reduced from their high relative abundance in the glacial period, decline to negligible

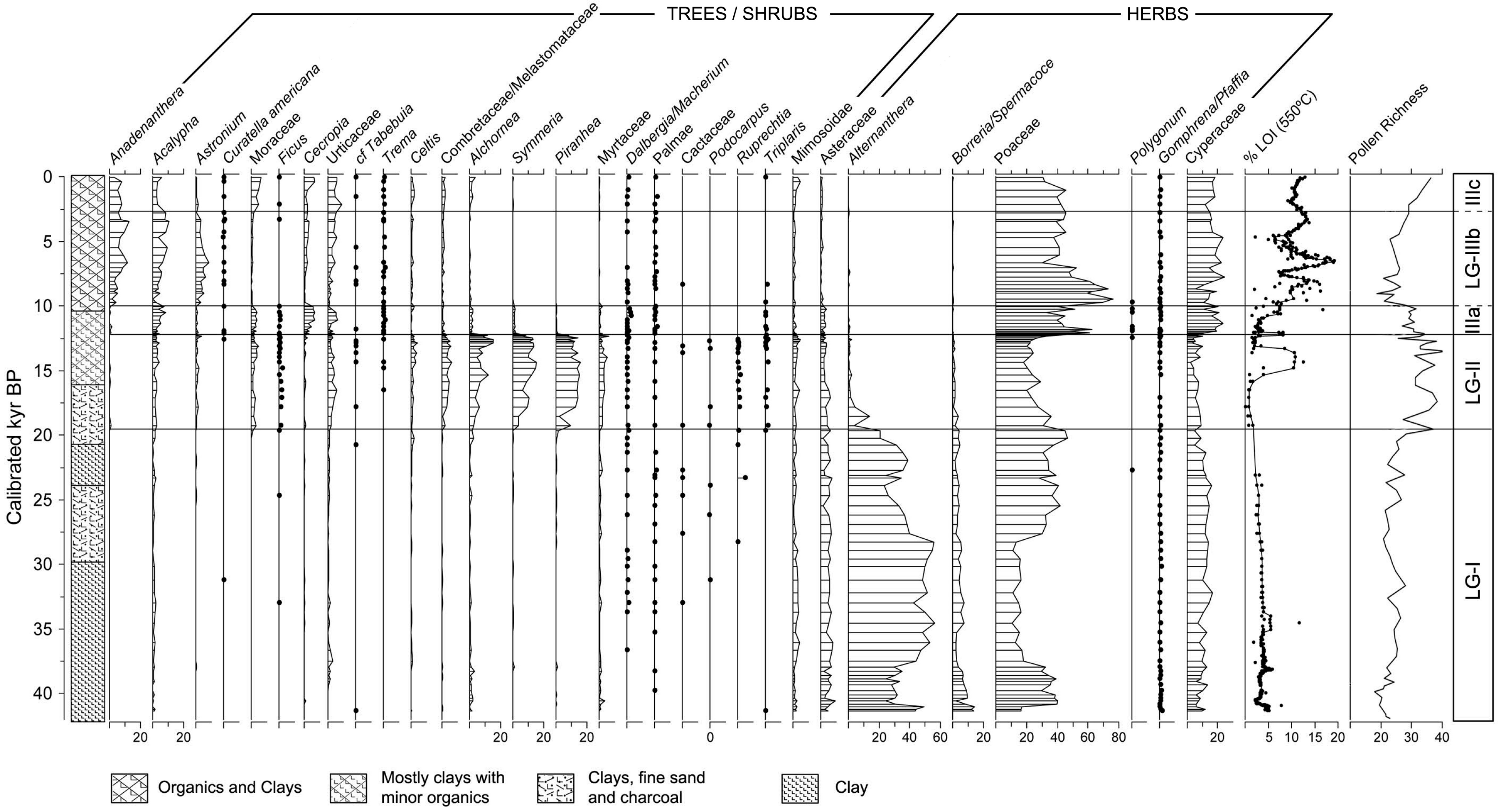

Fig. 2.7. LLG sediment stratigraphy, relative percent abundance of common fossil pollen types, percent loss-on-ignition of dried sediments (550ºC), and rarefied pollen diversity plotted against kyr BP.

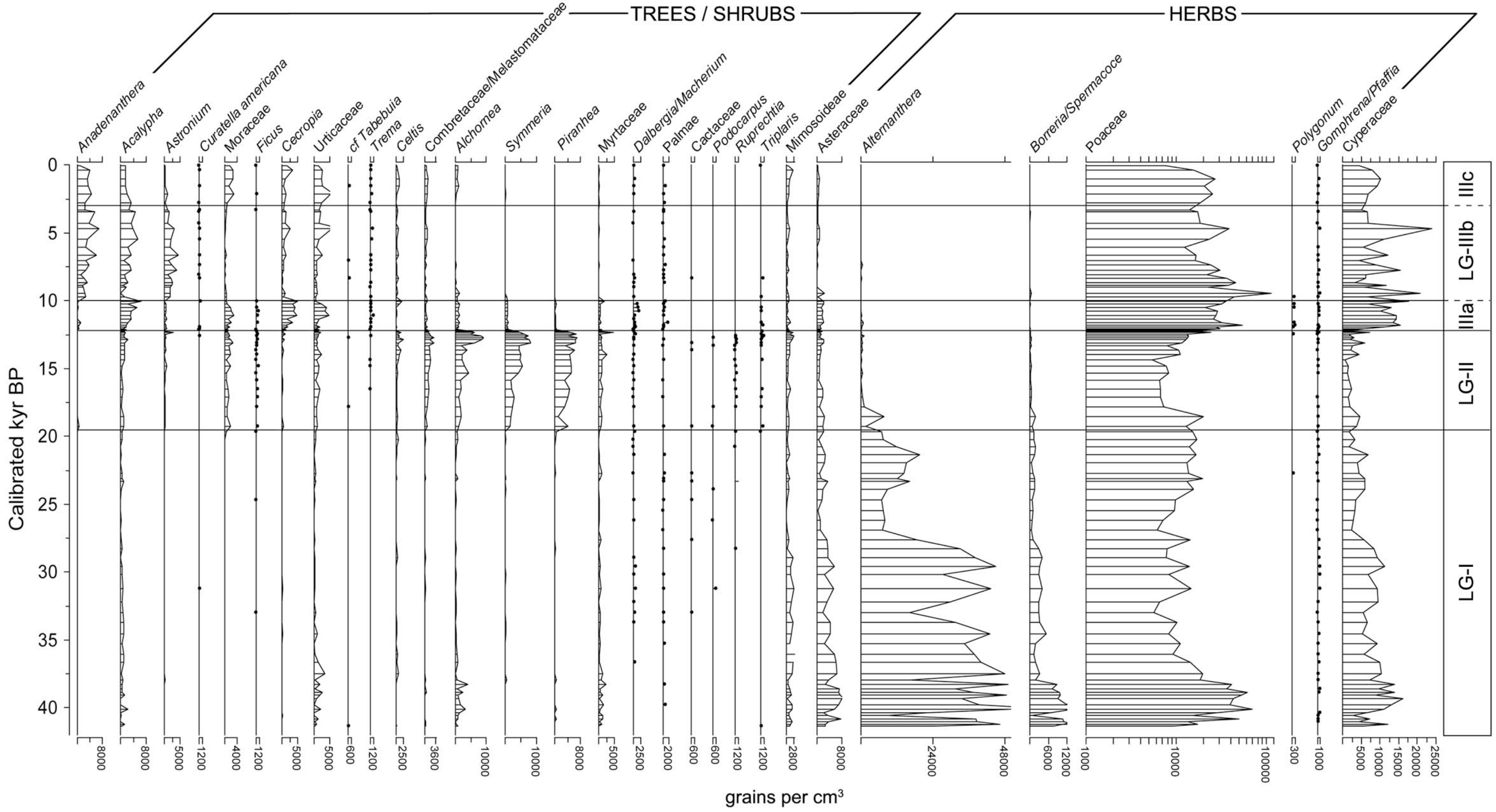

Fig. 2.8. Concentration of common fossil pollen types (grains per cm^3) plotted against kyr BP. (The Poaceae x-scale is logarithmic).

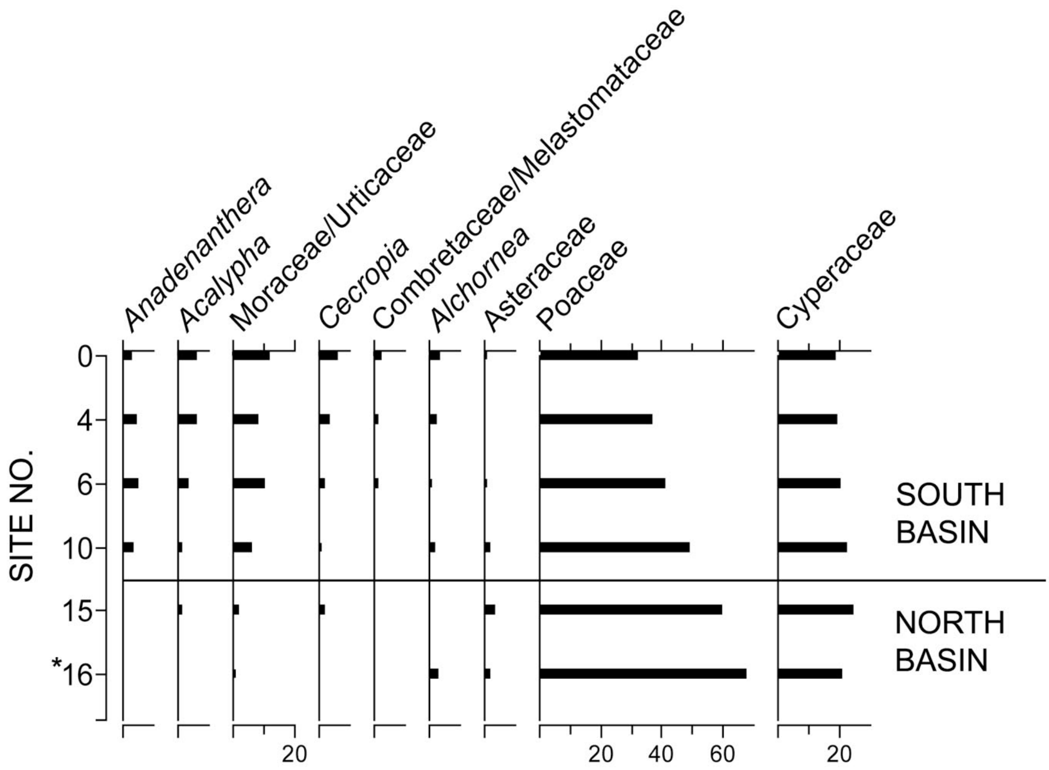

Fig. 2.9. Relative percent abundance of common pollen types encountered in the six surface samples analyzed from LLG, including the core top (0). Pollen assemblages from the aquatics-rich, shallow north basin (15, 16), and taken from near a river inflow (10), contain the high proportions of Poaceae and low tree pollen compared to those of the south basin. All pollen sums total 300 grains except site no. 16 (*).

proportions after 18.0 ka BP. Relative abundance of Poaceae and Cyperaceae varies from 20 – 40%, and 2 – 10%, respectively. With the exception of the late Holocene, palynological richness of samples in this zone is high compared to all other assemblages in the record.

As in the earlier glacial sediments of LG-I, the abundance of terrestrial plant macrofossils in sediments indicates that trees and shrubs were locally present. At the beginning of LG-II, sediments are characterized by clays interspersed with sands and abundant charcoal, and around 16.0 ka BP, the sediments shift to uniform grey-brown clay. Organic content is initially low (< 5%) for much of the zone, but rises to over 10% from 14.8 to 13.0 ka BP.

2.5.3. LG-III

Sub-zone IIIa: 12.2 to 10.0 ka BP

The transition from LG-II to LG-III is marked by a sharp reduction in *Symmeria*, *Alchornea*, and *Piranhea*. Combretaceae/Melastomataceae, Myrtaceae, and *Celtis* also decline in abundance. Though only occasionally present in the previous zone, *Ruprechtia* disappears from the record. The reduction in these pollen types is illustrated by a drop in pollen richness at the beginning of LG-III.

Poaceae increases three-fold at 12.2 ka BP, to a value of 60%, and subsequently declines to 40 – 50% after 11.8 ka BP. Cyperaceae rises in abundance to reach values of 20%. Also, *Cecropia* (5 – 10%), a pioneer tree genus, becomes more common in this zone than any other part of the record, with the exception of assemblages dating from the late Holocene. *Acalypha*, Moraceae, Urticaceae, Asteraceae, and undifferentiated Mimosoideae remain unchanged from the previous zone, and the pollen of *Ficus*, *Trema*, *Dalbergia/Machaerium*, *Curatella americana,* and Palmae occurs occasionally.

The sediments of LG-IIIa consist mostly of grey-brown clays. With the exception of a peak in organic matter at 12.2 ka BP, organic content is low (< 5%) and rises gradually towards the top of the zone. Although terrestrial plant macrofossils are uncommon in this zone, leaf fragments frequently occur in the sediments.

Sub-zone IIIb: 10.0 to 3.0 ka BP

The early Holocene at LLG is marked by the appearance of *Anadenanthera*, and an increase in *Astronium*, from < 1% to a maximum of 8%. The rise in these pollen types coincides with a decline in Asteraceae, *Acalypha*, total Moraceae (including *Ficus*), Urticaceae, and *Cecropia*. Continuing from the previous zone, *Dalbergia/Machaerium*, *Trema*, and Palmae are occasionally present. Poaceae abundances nearly double, rising from 30% to a value of 60% in the early half of LG-IIIb, but decline to 30 – 45% after 6.7 ka BP. Cyperaceae values remain relatively high at 5 – 25%. *Curatella americana*, occurring infrequently in previous assemblages, is present in most of the assemblages. Pollen diversity remains low in the early Holocene.

Similar to the previous zone, sediments consist mainly of grey-brown clays. Percent LOI varies across this zone; initial values of 6% rise to 20% at 6.5 ka BP, interrupted by a drop in organic matter centred at 7.5 ka BP. After 6.5 ka BP, organic content declines to around 10% and demonstrate a slight increase toward the top of the zone.

Sub-zone IIIc: 3.0 ka BP to present

Rising Moraceae (including the reappearance of *Ficus*), *Alchornea*, and *Cecropia* characterizes the last 3.0 kyr at LLG. Pollen of *Astronium* declines to < 1%, and relative proportions of *Anadenanthera* and *Acalypha* also fall slightly. Occurring in low abundance, *Dalbergia/Machaerium*, *Trema*, *Curatella americana*, and Palmae demonstrate little change from the previous sub-zone. Poaceae and Cyperaceae values demonstrate little variability, averaging 39% and 16%, respectively. Palynological richness demonstrates an increase at the beginning of LG-IIIc and continues to rise until present. Late Holocene sediments consist of mainly of clays and organics (10%).

2.6. Discussion

2.6.1. The glacial environment and the Pleistocene Dry Forest Arc

The negligible tree pollen concentrations in the glacial assemblages prior to 19.5 ka BP indicate SDTF was not present in the Chiquitanía-Pantanal region at the height of the last glacial period, instead climatic conditions were unfavourable for forest development. However, what aspect of the environment (temperature, precipitation, CO_2 concentrations) limited the growth of tropical forest prior to 19.5 ka BP is not immediately apparent. To simplify the problem, we will instead invert the question and ask: What environmental parameter allowed for the expansion of forest at 19.5 ka BP?

Large woody plant macrofossils frequently occur in sediment both prior to and following the expansion of floodplain taxa at 19.5 ka BP. Currently, under deeply-flooded conditions, the broad, flat south basin (25 $\mathrm{cm \cdot km^{-1}}$) prevents the transport of plant macrofossils into the centre of the lake, although the immediate catchment is covered in closed-canopy forest on steep hillslopes, and in low-lying areas, right up to the lake margin. Therefore, the woody vegetation was likely growing closer to the core site under conditions of lower lake level. The low concentrations of tree pollen in the glacial sediments implies this was a small, shrubby community that fringed the lake (Fig. 2.5b).

As well as the abundance of terrestrial plant macrofossils preserved in sediments, the ecology of the early forest community at LLG indicates that lake levels remained low after 19.5 ka BP. Typical of Amazonian floodplains, *Symmeria paniculata* and a species of *Piranhea* (*P. trifoliata*) are tolerant of inundation and drought, but favour sediment-rich soils (Junk 1989, Worbes 1997). The shallow soils of the bedrock hillslopes that constrict the margins of LLG are unsuitable for floodplain communities, therefore only under conditions of low lake levels would there be a greater expanse of the habitat preferred by seasonally-inundated forest. We hypothesize that fluctuating lake levels in the south basin maintained inundation-tolerant forest through an annual flooding/drought cycle in areas that are now permanently inundated. The ecology of inundation-tolerant forest, and the climatic implications of changes in this community are discussed in detail by Whitney et al. (Chapter 3).

That lake levels were lower-than-present prior to and after 19.5 ka BP suggests there was little or no increase in precipitation associated with the expansion of inundation-tolerant forest. Equally, the establishment of forest occurs despite glacial-level atmospheric CO_2 concentrations, thereby precluding the CO_2 fertilization effect as a potential trigger for vegetation change (Cowling and Sykes 1999). By eliminating the potential influence of precipitation and CO_2 concentrations, we infer that rising temperature is the driver of forest expansion at

LLG. Post-LGM warming in tropical South America is also demonstrated to occur between 22.0 - 19.5 ka BP in tropical Andean records (Seltzer et al. 2002, Hillyer et al. 2008), several thousand years prior to deglaciation in the northern high latitudes, but the well-dated temperature rise shown here is the first evidence of early warming in the tropical lowlands contemporaneous with Andean regions.

That cold temperatures prevented the growth of tropical forest around LLG is not surprising given that at present, occasional winter incursions of polar air masses can drop temperatures to near freezing in the Chiquitanía region and adjacent Pantanal wetlands (Jardim et al. 2003, Alho 2005), and frosts are rare, but known to occur (Alho 2005). During the glacial period, depressed annual temperatures, combined with more frequent incursions of cold polar air masses, would have produced sub-zero minimum winter temperatures and prevented the establishment of frost-intolerant tropical forest at southerly tropical latitudes. The abundance of Myrtaceae pollen in glacial-aged sediments extracted from Laguna Salitre (Ledru 1993), also located at a southerly tropical latitude in the Brazilian cerrados (19ºS, 46ºW), is suggestive of colder glacial temperatures. Although previously interpreted as reflecting tropical riparian forest, these assemblages could equally be representative of frost-adapted temperate forest.

However, temperate forest is noticeably absent from the glacial landscape at LLG. A cool, dry climate, possibly in combination with lower CO_2 concentrations, may have favoured the establishment of open, herbaceous vegetation in lowland Bolivia, perhaps analogous to the Argentine pampas. Our palaeodata corroborate the results from modelled dynamic vegetation for tropical South America indicating much of the southern hemisphere tropics of South America, including lowland Bolivia, were dominated by C_4 vegetation at the LGM (Mayle 2004, Mayle and Beerling 2004).

If tropical forest growth was limited in the southerly tropical latitudes, what of the biogeographic evidence in favour of past linkages between the Caatinga, Misiones, and Chiquitano regions? Although the glacial temperatures were low, a warmer and dry climate after 19.5 ka BP allowed for the establishment of inundation-tolerant forest on seasonally-flooded sediment-rich habitat of the lake basin. The hydrology of the Rio Paraguay and its associated lakes (including LLG), is coupled to yearly flooding in low-lying areas of the Pantanal (Chapter 3); therefore, we can extrapolate beyond the immediate catchment to hypothesize flooding was reduced in the entire basin, thereby allowing for widespread establishment of forest in the Pantanal.

The scenario is analogous to the recent prolonged drought in the Pantanal (1960 – 1973), when the maximum flooded area was half that of following decades (40,000 km^2 compared to > 80,000 km^2 from 1979 - 1987), allowing forest to encroach on the floodplains (Hamilton 2002). This description of a greater forested landscape in the Pantanal region during the glacial-Holocene transition is also not unlike the glacial-aged forest migration corridors of the Brazilian cerrados proposed by Ratter et al. (1988), and a similar warm and arid climate after 19.5 ka BP may have encouraged the growth of SDTF in the cerrados. Therefore, although the palaeoecological data indicate that minimum temperatures at the height of the last glaciation were too cold for tropical forest development, a post-LGM expansion of tropical forest in the Pantanal, and in fertile soils in the cerrado, agrees with both our pollen-inferred climate reconstruction and the biogeographic affinities among these regions (Ratter et al. 1988, Prado and Gibbs 1993, Oliveira-Filho and Ratter 1995, Pennington et al. 2000). The low-lying forest persists in the Pantanal until 12.2 ka BP when continuously high flooding causes permanent inundation of the habitats preferred by this community (discussed further by Whitney et al., Chapter 3), and flooding and precipitation remain high until 10.0 ka BP.

2.6.2. The Chiquitano SDTF: A Holocene-aged assemblage

An early dry forest community, composed of a depauperate set of the Chiquitano flora, begins to develop on the steep-sided hills after 18 ka BP, indicated by a decrease in herbaceous taxa and higher relative proportions of *Acalypha*, Urticaceae, Moraceae (characterized by *Maclura/Pseudolmedia* and *Brosimum* types), and occasionally occurring *Astronium* pollen (Figs. 2.7, 2.8). The low abundance of *Astronium* prior to 10.0 ka BP is analogous to that of the modern pollen assemblages at LLG, where species of *Astronium* are common in the catchment. *Astronium* is also found to be under-represented in modern pollen rain studies (Gosling et al. 2009), therefore, although *Astronium* pollen is of low abundance, it is likely that species of *Astronium* formed a part of this early forest community.

The early *terra firme* forest demonstrates little change across the glacial-Holocene transition until 10.0 ka BP, when *Astronium* pollen becomes abundant, and *Anadenanthera* appears in the record, species of which are common in the Chiquitano SDTF. Although, *Anadenanthera* pollen is not resolved to species, it almost certainly belongs to *A. colubrina*, the most abundant species of this genus in the modern catchment vegetation (Table 2.1). *A. colubrina* has been shown to be a reliable indicator of dry forest in lowland, tropical South America (Prado and Gibbs 1993, Mayle 2006, Gosling et al. 2009), thus its appearance at 10.0 ka BP provides strong evidence for the development of the Chiquitano SDTF on the hillslopes around LLG in the early Holocene.

The expansion of this community is coincident with a near absence in Moraceae, species of which are characteristic of moisture-dependent, evergreen formations. Although some Moraceae taxa can withstand arid conditions, changes in the relative abundance of Moraceae pollen is shown to broadly reflect past changes in moisture availability (see Mayle et al. 2000, Gosling et al. 2009). Also indicative of aridity in the early Holocene, the decline in Moraceae is accompanied by higher Poaceae abundance. The Chiquitano SDTF on the hillslopes surrounding LLG features low grass coverage in the understorey (Prance and Schaller 1982), also observed during the qualitative vegetation survey, therefore the source of this increase in Poaceae is not likely to be terrestrial. Rather, the early Holocene assemblages that exhibit a high proportion of grass pollen (60 – 70%) are analogous to the surface samples in the shallow, aquatics-rich north basin of LLG (Fig. 2.4, 2.9). Here, low water levels allow for the colonization of large swathes of emergent aquatic vegetation, including grasses. Lowering lake levels in the south basin beginning in the early Holocene would allow for rooted aquatic vegetation to encroach into the basin; a signal consistent with lower annual precipitation inferred from the arrival of dry forest indicators, and a reduction in Moraceae pollen.

Corroborating evidence of the Holocene expansion of SDTF and the onset of drier conditions is the appearance of *Anadenanthera* and *Astronium* pollen in the record from Laguna Chaplin (Mayle et al. 2000, Burbridge et al. 2004), concurrent with the arrival of *Anadenanthera,* and the rise in *Astronium* abundance at LLG (e.g., within the dating uncertainty). Abundant macroscopic charcoal in sediments from Laguna Chaplin indicates the development of SDTF is accompanied by a relatively arid climate; an interpretation mirrored by the reconstruction at LLG. Therefore, the expansion of SDTF in lowland Bolivia occurred under conditions of lower-than-present precipitation, or lengthened dry season, beginning in the early Holocene.

Clearly, the distribution of *Anadenanthera colubrina* in lowland Bolivia is the result of migration rather than vicariance, but the cause of the late development of the Chiquitano SDTF remains less clear. Despite relatively warmer temperatures and low precipitation from 19.5 to 12.2 ka BP, the early dry forest assemblage on the hills around LLG is composed of a subset of the Chiquitano flora until 10.0 ka BP; *Anadenanthera* is noticeably absent prior to this date. Biotic or geographic barriers may have hindered the migration *Anadenanthera colubrina* into this region until the early Holocene, but it is likely that climatic conditions were still unfavourable for SDTF prior to 10.0 ka BP.

The pollen of cool-adapted *Podocarpus*, typical of higher elevation forests, occurred prior to 10.0 ka BP at sites situated in the central Amazon basin (Colinvaux et al. 1996, Behling 2001), in coastal, equatorial Amazonia (Ledru et al. 2001), the southern margin the Amazon basin (14ºS) (Burbridge et al. 2004), and this site (Fig. 2.7), implying that temperatures across much of the tropical lowlands were cooler-than-present. These records suggest the beginning of the Holocene in the tropical lowlands was marked by a final increase in temperature, and in the Chiquitanía-

Pantanal region, warming and the onset of aridity may have allowed for the development of the modern Chiquitano flora.

2.6.3. Holocene precipitation changes and the Chiquitano SDTF

A reduction in moisture availability marks the onset of the Holocene at LLG, but falling precipitation and/or a lengthening dry season progresses from the early to mid-Holocene, as shown by steadily increasing relative abundance of *Anadenanthera* and *Astronium* pollen from 10.0 to 6.7 ka BP. The fossil *Astronium* pollen most closely resembles that of the drought-tolerant species *A. fraxinifolium* (Jardim et al. 2003), and although present in the modern catchment vegetation, the relatively high percent abundance of *Astronium* pollen suggests this taxon was prolific in the mid-Holocene. Furthermore, inferred aridity at LLG is consistent with widespread, coherent pattern of mid-Holocene aridity in tropical South America in both Andean and lowland records. Mayle and Power (2008) give a comprehensive overview of the palaeoclimatic evidence and the response of vegetation to this event. However, it can be best summarized by the lake level reconstruction from Titicaca, where the lake experienced a depth reduction as much as 100 m from 6.0 to 5.0 ka BP; its lowest stand over the past 25,000 years (Baker et al. 2001b).

At LLG, we infer greatest aridity occurred between 7.0 and 6.0 ka BP, approximately the timing of the lowstand at Lake Titicaca (Baker et al. 2001b), and arid conditions persist until 3.5 ka BP, when reduced *Astronium* and higher Moraceae abundance signals the onset of a moister, late Holocene climate. Moraceae values steadily increase from the late Holocene until present, consistent with the pattern of a strengthening of the summer monsoon in the southern hemisphere tropics of South America (Baker et al. 2001a, Cruz et al. 2005, Mayle and Power 2008). The effects of Holocene climate change on lake levels at LLG are discussed in greater detail by Whitney and Mayle (Chapter 4).

Quantitative climate estimates inferred from fossil pollen at Laguna Bella Vista, located 610 km northwest of LLG, suggest that mean annual precipitation may have been as much as 500 mm lower than present in the mid-Holocene (Mayle et al.

2000, Burbridge et al. 2004, Punyasena et al. 2008). These inferred estimates, combined with the lowstand in Titicaca, implies impact of aridity was severe in the southern hemisphere tropics. Despite this pronounced aridity, the response of SDTF is marked by changing relative abundance of composite taxa, rather than a broad-scale change in floristic composition, suggesting that at the ecosystem-level, the Chiquitano is adaptable to drought.

Although compositionally stable, palynological richness, a proxy for plant diversity, declines in the mid-Holocene, implying that enhanced aridity negatively influenced plant diversity in the Chiquitano SDTF. Using the relative abundance of Moraceae pollen as broadly representative of regional moisture availability, we can infer the positive correlation between Moraceae abundance and palynological richness ($R^2 = 0.6$) implies that varying Holocene precipitation directly influenced diversity in the Chiquitano SDTF. Furthermore, increasing palynological richness over the last 3,500 yrs implies that the relatively high α-diversity in the Chiquitano SDTF is of recent origin.

The evidence for recent changes in diversity, the Holocene variation in relative abundance of key SDTF pollen types, and the young age of the SDTF indicate the Chiquitanía-Pantanal region has experienced a high degree of vegetation dynamism, reflecting its ecotonal position at the intersection of humid evergreen forest, cerrado and Chaco vegetation. Rather than reflecting glacial-aged distribution of SDTF, the current ‘arc’ of taxa such as *Anadenanthera colubrina* in southerly tropical latitudes resulted from recent migration (early Holocene) as these latitudes warmed, and the current composition and diversity in the Chiquitano are the products of recent (late Holocene) rising precipitation.

2.7. Conclusions

The Chiquitanía-Pantanal region experienced aridity during the last glacial period, lasting until 12.2 ka BP. Glacial aridity inferred from LLG implies that relict dune fields in the Pantanal, now fixed by overlaying vegetation, may have been formed during the last glacial period (prior to 19.5 ka BP) as previously suggested (Clapperton 1993, Assine and Soares 2004). Evidence from this site adds to the growing body of palaeoenvironmental (van der Hammen and Absy 1994, Ledru et al. 1998, Burbridge et al. 2004) and modelled (Hostetler and Mix 1999) data that demonstrate the precipitation regimes of the tropical Andes and lowlands were decoupled during the last glacial maximum.

Although the precipitation regime was lower than modern, the Chiquitanía-Pantanal region did not support SDTF during the last glacial period (45.0 to 19.5 ka BP), as previously hypothesized. Rather, cold temperatures combined with polar air fronts prevented the establishment of tropical forest in the Chiquitanía-Pantanal region, and likely elsewhere in the southerly tropical latitudes, such as the cerrados of central Brazil. However, warming beginning as early as 19.5 ka BP allowed for the establishment of forested vegetation under conditions of reduced flooding in the Pantanal basin. Although compositionally dissimilar to SDTF, this ecosystem could have functioned as a ‘migration corridor’ as envisioned by Ratter et al. (1988) and Oliveira-Filho and Ratter (1995).

Despite early warming, conditions favouring the establishment of the modern Chiquitano flora did not occur until 10.0 ka BP. Rising temperature at the onset of the Holocene was the probable driver of the arrival of *Anadenanthera*, and once established, the Chiquitano SDTF exhibits compositional stability despite enhanced aridity in the early- to mid-Holocene. Instead, relative abundance in key dry forest taxa and diversity (palynological richness) varies in response to the changing precipitation regime throughout the Holocene. Declining drought-tolerant taxa, and a shift towards moisture-dependent vegetation from the late Holocene to present corresponds with the widely demonstrated late Holocene strengthening of the summer monsoon in the southern hemisphere.

Although there is strong evidence for a changing precipitation regime from the last glacial period through to the early Holocene, temperature is the climatic variable that shaped the ecosystems in lowland Bolivia; cold temperatures and frequents frosts limited the growth of tropical trees in the glacial environment, and early Holocene warming allowed for the development of the modern Chiquitano flora. In contrast, varying precipitation in the Holocene affected the diversity and relative abundance of dry forest taxa, rather than forcing broadscale ecosystem turnover. Closed-canopy forest was maintained under conditions of enhanced aridity of the mid-Holocene. The differing effects of precipitation and temperature on tropical ecosystems highlight the need to exercise caution when inferring palaeoclimate from fossil pollen data. In particular, the presence of closed-canopy forest cannot be used as evidence for 'lack of aridity', as both forested and non-forested ecosystems existed under drier climates in the Chiquitanía-Pantanal region.

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III. The Glacial-Holocene transition in the Bolivian Pantanal: Rapid flooding and vegetation change at 12.2 cal. ka BP

Bronwen S. Whitney, Francis E. Mayle, R. Toby Pennington, Michael J. Burn, Neil J. Loader, Ezequiel Chavez, and René Guillén

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3.1. Abstract

Weakened Atlantic meridional overturning circulation (AMOC) during the Younger Dryas event (12.9 – 11.6 cal. ka BP) is hypothesized to have altered the precipitation regime of tropical South America through a southward extension of the Intertropical Convergence Zone (ITCZ), intensifying the monsoon in the southern tropics, and inducing aridity in northern tropical regions. Although Andean and coastal sites demonstrate a precipitation anomaly during the YD chronozone, it is unknown whether this event is manifested in the continental interior due to the coarse temporal resolution of most lowland, lacustrine records. Here we present a well-dated, high-resolution palaeoenvironmental reconstruction from a site in eastern, lowland Bolivia spanning the glacial-Holocene transition (24.0 to 8.0 cal. ka BP). Fossil pollen, carbon ($\delta^{13}C$, C:N, %TOC) and XRF analyses were performed on sediments extracted from Laguna La Gaiba (LLG) (17°45'S, 57°40'W), a large (55 km^2), shallow lake located in the western Pantanal, the world's largest tropical wetland (140,000 km^2). LLG is located along the course of the Rio Paraguay that drains the seasonally-inundated savannahs of the Pantanal, therefore changing hydrological conditions in the lake are likely reflective of a regional signal. Two climatic shifts mark the glacial-Holocene transition. Firstly, the replacement of open, shrubby vegetation by inundation-tolerant forest at 19.5 cal. ka BP signals warming at the end of the last glacial period. This community persists until 12.2 cal. ka BP when higher precipitation in the Pantanal caused permanent flooding of shallow portions of the basin, resulting in a reduction of the seasonally-inundated forest community. Although this inferred hydrological change occurs during the YD chronozone, this

shift is unidirectional; lake levels remain high after 12.2 cal. ka BP, marking the onset of a wetter interglacial climate, a trend inconsistent with Altiplano and coastal reconstructions from the southern hemisphere tropics of South America (SHTSA) where more arid conditions return after the YD chronozone. Instead, the inception of Holocene climate at LLG coincides with the final stage of deglaciation in the southern high latitudes, implying a Southern Hemisphere influence over the continental interior of SHTSA.

3.2. Introduction

High frequency climate fluctuations characteristic of the glacial-Holocene transition in the North Atlantic region, such as the Younger Dryas cold event (GS-1 stadial = 12.9 to 11.6 cal. ka BP, terminology of Björck et al. 1998), are demonstrated to influence the precipitation regimes of tropical Asia, Africa, and South and Central America (Yuan et al. 2004, Garcin et al. 2007, Wang et al. 2007). Cooling in the North Atlantic during the Younger Dryas event is hypothesized to have caused a southward shift of mean position of the Intertropical Convergence Zone (ITCZ) (Dahl et al. 2005), resulting in an intensified monsoon in the southern hemisphere tropics of South America (SHTSA), and inducing aridity in northern tropical regions.

Although the distribution of high-resolution proxy records in tropical South America is patchy, there is evidence of a precipitation anomaly during the YD chronozone (hereafter referred to as YD) among high-resolution records concentrated in Andean and coastal regions (Fig. 3.1 and Table 3.1). Sites located in the northern hemisphere tropics and within 10°S of the equator generally experienced lower moisture availability, as demonstrated by: reduced input of terrigenous sediment in the Cariaco basin (site 4, Fig. 3.1) and off the coast of northern Brazil (site 1, Fig. 3.1) Arz et al. 1998, Peterson and Haug 2006), isotopic evidence of increased coverage of C_4 vegetation in coastal Venezuela (site 4, Fig. 3.1) (Peterson et al. 2000, Hughen et al. 2004), a reduction in available moisture and forest regression in coastal Brazil (site 2, Fig. 3.1) (Ledru et al. 2006, Jacob et al. 2007), and reduced outflow from the Amazon River (site 3, Fig. 3.1) (Maslin and Burns 2000). At higher altitudes, there is evidence of glacial retreat in the Ecuadorian Andes (site 6, Fig. 3.1) (Heine and Heine 1996), and the record from Lake Junin located at 11ºS in the central Peruvian Andes (site 8, Fig. 3.1) (Seltzer et al. 2000), demonstrates higher evaporation compared to the periods prior to and after the YD. Montane forest taxa were replaced by cold- and drought-tolerant taxa on the Bogotá plain, Colombia (site 5, Fig. 3.1) (Van ‘t Veer et al. 2000), and northern Peru experienced increased fire

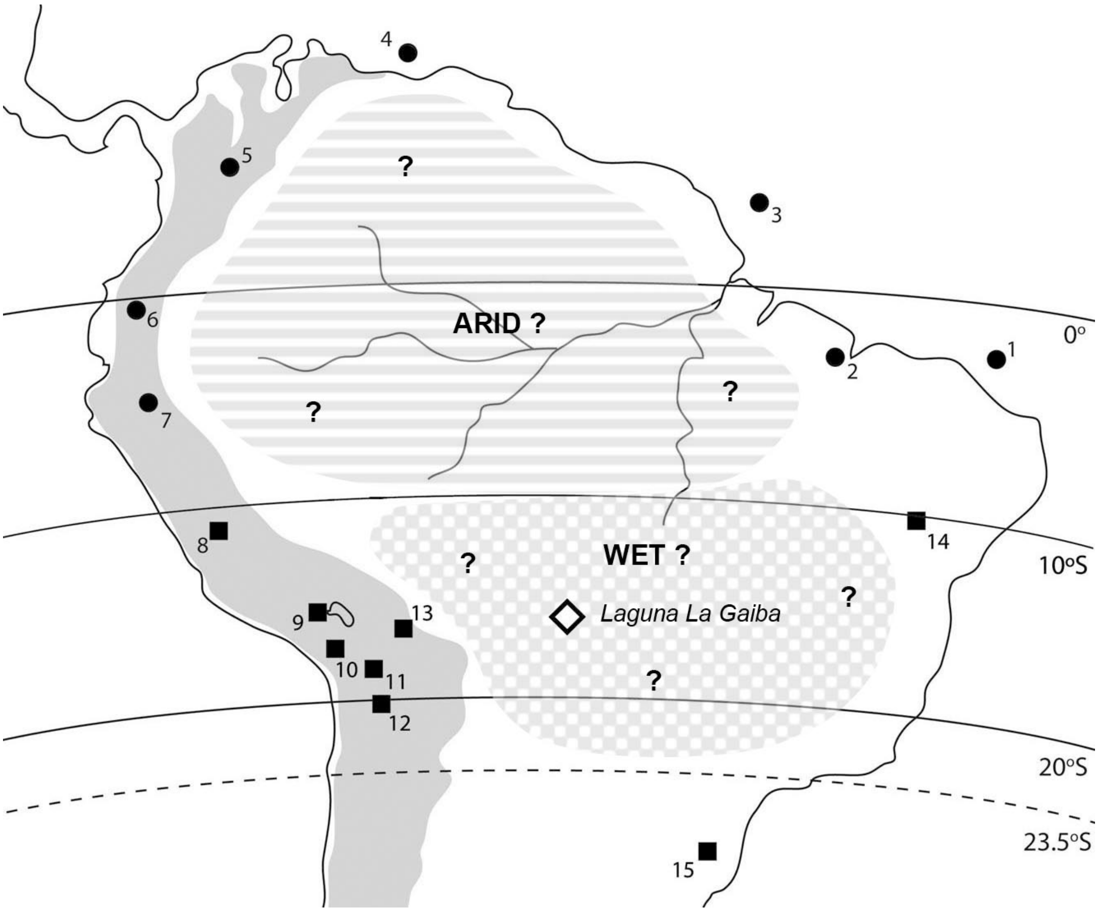

Fig. 3.1. Proposed model of YD climate change in tropical South America, based on data limited to Andean and coastal regions (see below). The open diamond marks the position of LLG (this study), located in a region for which there are no data, ideally situated to test if the interior SHTSA experienced a YD-like climate anomaly, or not (a), and if so, whether the precipitation anomaly was (b) positive (wet) as outlined by this model, or (c) negative (dry).

Symbols mark the position of palaeoenvironmental records that exhibit a precipitation anomaly during the YD (Circles = Arid, Squares = Wet). Sites included are well-dated and display sufficiently high temporal resolution for analysis of climate and/or vegetation change across the YD. See Table 3.1 for site data.

frequency and higher abundance of paramo taxa (site 7, Fig. 3.1) (Hansen 1995), agreeing with hypothesized aridity in this region.

Although there are fewer records in the Southern Hemisphere tropics of South America (SHTSA), there is an emerging pattern of higher precipitation associated with the YD at sites located south of 10°S. Travertine growth in the currently moisture-deficient region of central, NE Brazil indicates precipitation was

No.	Site	Country	Proxy	References
1	GeoB 3104-1	Brazil	Geochemistry, Isotopes	Arz et al. 1998, Behling et al. 2000
2	L. Caco	Brazil	Pollen	Ledru et al. 2006, Jacobs et al. 2007
3	Amazon Fan ODP 942	Brazil	Isotopes	Maslin and Burns 2000
4	Cariaco ODP 1002	Venezuela	Geochemistry, Reflectance, Pollen	Peterson et al. 2000, Hughen et al. 2004, Peterson and Haug 2006
5	Lake Fuquene, El Abra	Colombia	Pollen	Van 't Veer et al. 2000
6	Rucu Pichincha, Papallacta Pass	Ecuador	Moraines	Heine and Heine 1996
7	L. Baja	Peru	Pollen, Charcoal	Hansen 1995
8	L. Junin	Peru	Pollen, Isotopes	Seltzer et al. 2000
9	L. Titicaca	Bolivia	Isotopes, Diatoms, Palaeoshorelines	Baker et al. 2001b, Baker et al. 2005, Placzek et al. 2006
10	Sajama	Bolivia	Dust	Thompson et al. 1998
11	Altiplano rivers/wetlands	Bolivia	Geomorphology, Sedimentology	Rigsby et al. 2005
12	Salar de Uyuni	Bolivia	Gamma Radiation	Baker et al. 2001a
13	Valles San Francisco, de Rio Suturi, and Huara Loma	Bolivia	Moraines	Zech et al. 2007
14	Salitre and Jacare valleys	Brazil	Travertines	Auler et al. 2004, Wang et al. 2004
15	Botuvera cave	Brazil	Speleothems, Isotopes	Cruz et al. 2005, Wang et al. 2006, 2007

Table 3.1. Sites featured in Fig. 3.1 and discussed in the text

higher during the YD (site 14, Fig. 3.1) (Auler et al. 2004, Wang et al. 2004), also shown by oxygen isotope ratios in speleothems in subtropical Brazil (site 15, Fig. 3.1) (Cruz et al. 2005, Wang et al. 2006, 2007). On the Bolivian Altiplano, high palaeoshorelines representing the "Coipasa" lake phase (sites 9 and 11, Fig. 3.1) (Rigsby et al 2005, Placzek et al. 2006) and organic lacustrine sediment deposition in the Salar de Uyuni (site 12, Fig. 3.1) (currently a salt-flat) (Baker et al. 2001a) indicate the region experienced increased wetness during the YD. This trend of higher moisture availability is further demonstrated by glacial advance in the Cochabamba region of Bolivia (site 13, Fig. 3.1) (Zech et al. 2007), and higher snow accumulation on the Sajama ice cap compared to accretion rates prior to and after the YD (site 10, Fig. 3.1) (Thompson et al. 1998).

Although there is evidence of decreased (northern) and increased (southern) precipitation anomalies, in agreement with palaeoclimate model predictions (Dahl et al. 2005), the palaeoenvironmental reconstructions are concentrated in coastal and Andean regions. Whether the YD event influenced the climate and vegetation of the continental interior of South America is entirely unknown due to the poor chronological control, relatively young basal ages, and coarse temporal resolution of most lowland lacustrine records, a trend partly owing to low sedimentation rates.

The aim of this study is to reconstruct vegetation and climate from the glacial-Holocene transition for a site in the continental interior of SHTSA. Through high resolution pollen and geochemical analyses, we aim to determine if there is any evidence for precipitation anomaly associated with the YD chronozone, and if so, the sign of this precipitation change.

3.3. Site Description

The Pantanal, the world's largest tropical wetland (~140,000 km^2), is located in the lowland, continental interior of the SHTSA. It is centrally situated between the Altiplano and NE Brazil, both of which experienced increased precipitation during the YD chronozone (Figs. 3.1, 3.2), thus we hypothesize the Pantanal also

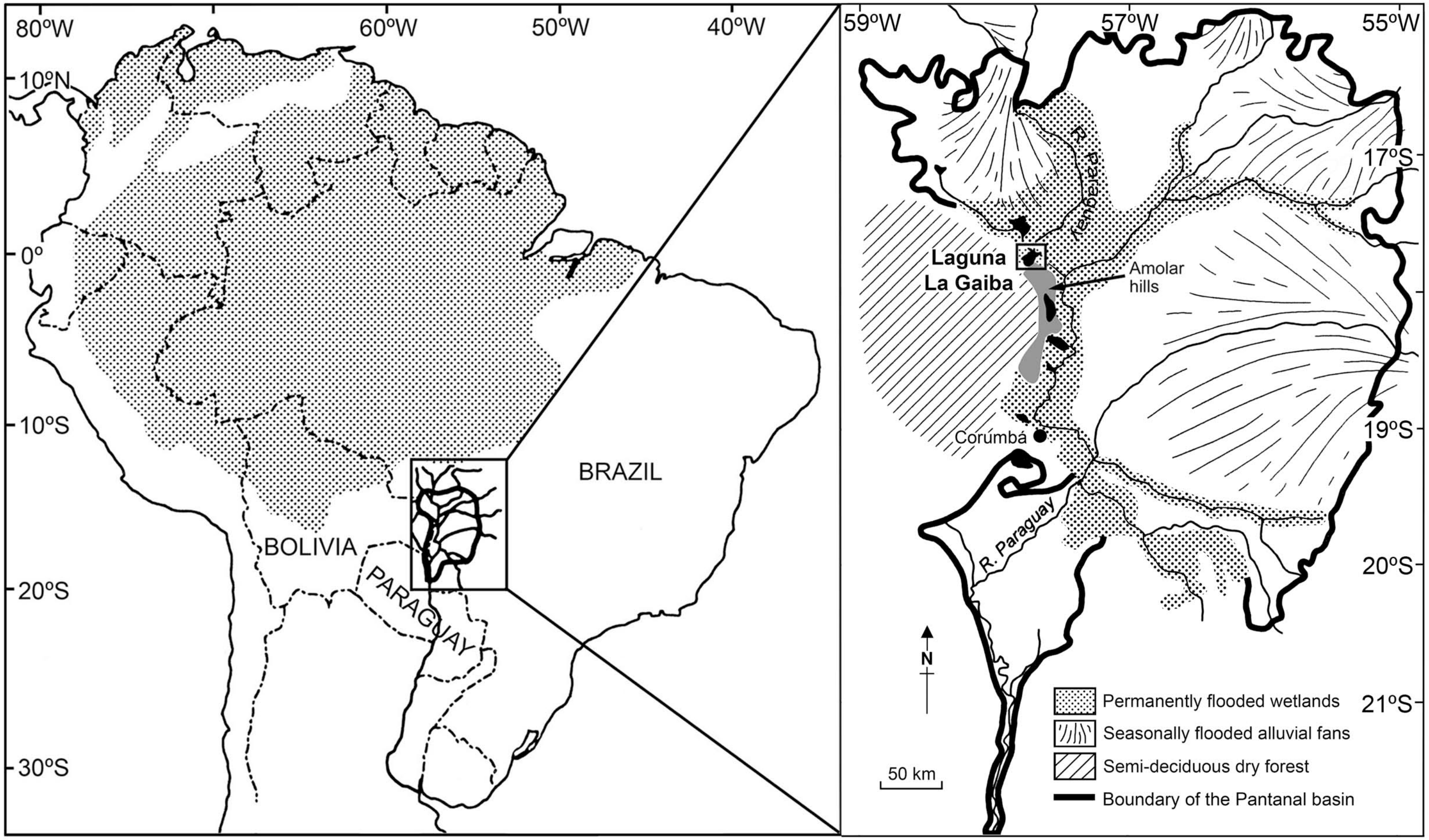

Fig. 3.2. (a) Location of the Pantanal basin relative to the Amazon rainforest (stippled). (b) The study site, Laguna La Gaiba, is situated along the Rio Paraguay and lies between the permanently flooded wetlands and gallery forests of the Pantanal (stippled) and the Chiquitano SDTF (hashed). Seasonally-inundated savannahs overlay alluvial fans to the east of the Rio Paraguay (radiating lines).

experienced a positive precipitation anomaly during the YD chronozone. This wetland occupies a tectonic depression between the Brazilian shield and the Andean foreland (elevation 80 – 120 m asl) (Clapperton 1993) and, together with the western Brazilian highlands, forms the headwaters of the River Paraguay. Precipitation in the Pantanal is highly seasonal. Mean annual precipitation is 1000-1700 mm, the bulk of which falls in the austral summer from December to February and causes widespread flooding in the basin. The mosaic of ecosystems comprising the Pantanal is defined by this seasonal flooding (Fig. 3.3); natural levées alongside the rivers support inundation-tolerant gallery forests, and permanently-flooded wetlands occupy areas of lowest elevation immediately behind these levées. The dominant Pantanal ecosystems are the seasonally-inundated savannahs that occupy lower-lying areas to the east of the Rio Paraguay, often supporting SDTF on higher terrain, created by the shifting channels that drain these floodplains, or termite activity (Dubs 1992, Alho 2005). Floating mats of aquatic vegetation, dominated by *Eichhornia* spp. (Pontederiaceae), Asteraceae, and Poaceae are common on the margins of lakes and water courses. In addition, the eastern edge of the Bolivian Chiquitano SDTF, a

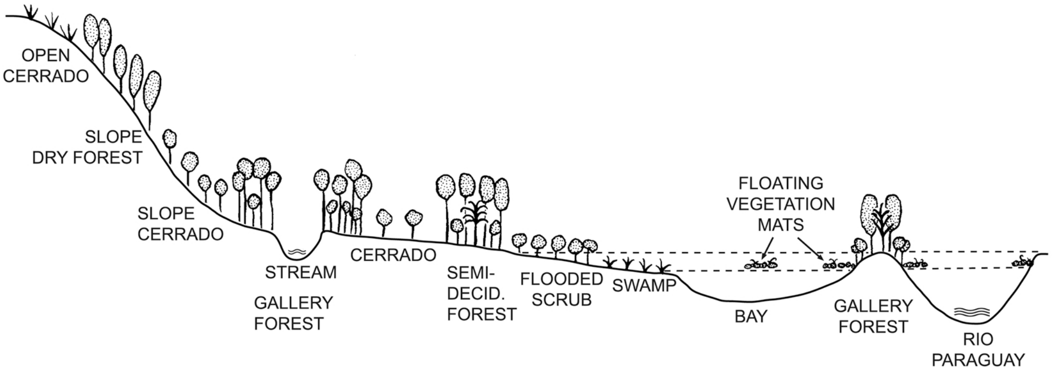

Fig. 3.3. An schematic illustration of the permanently- and seasonally-flooded, and upland (xeric) habitats of characteristic of the Pantanal. Adapted from Prance and Schaller (1982).

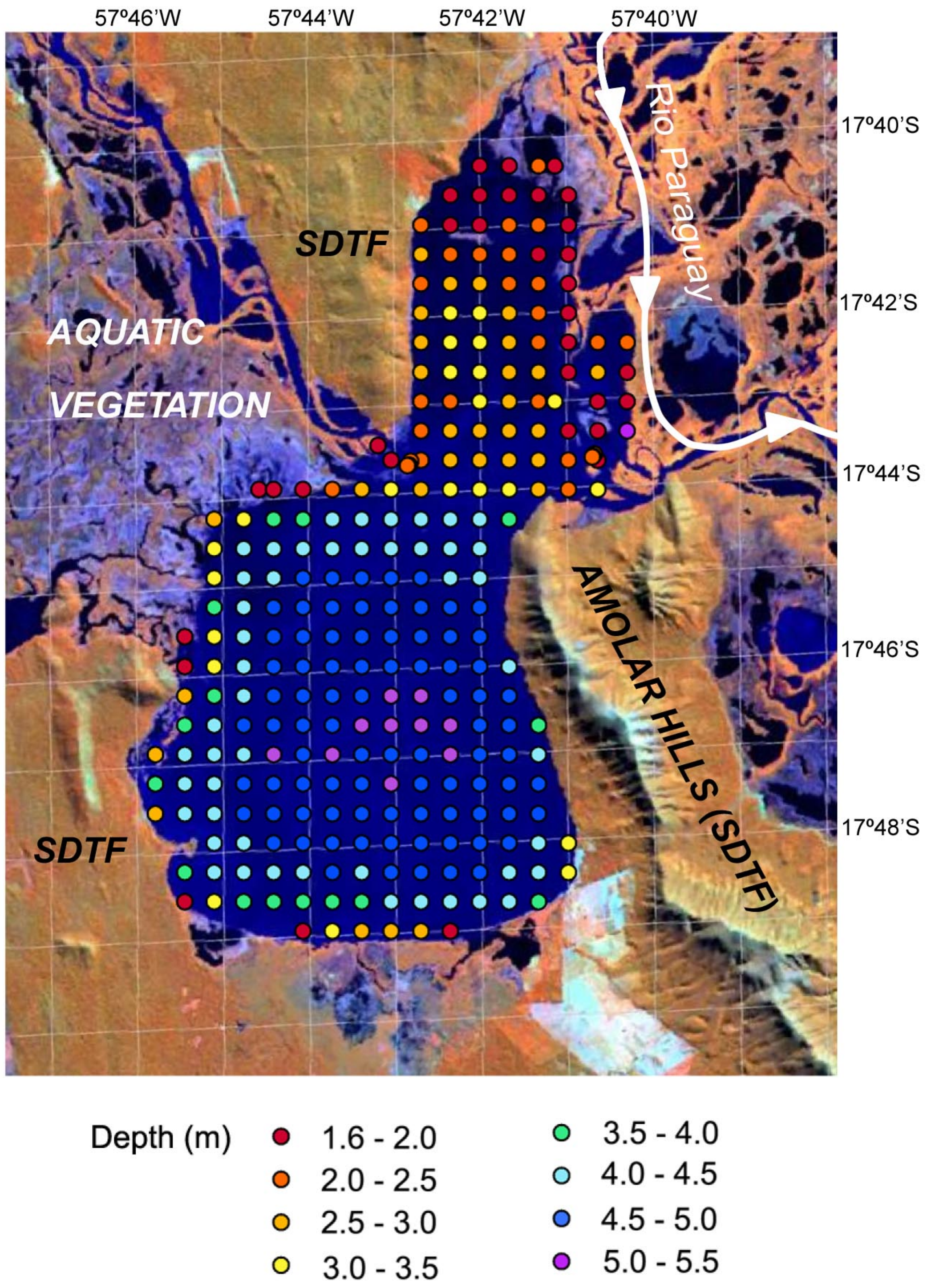

Fig. 3.4. Landsat image of the LLG and the surrounding terrain. Coloured circles correspond to water depth measured at 270 points across LLG (August 2008). The bathymetry is broad and flat, demonstrating < 1 m change across much of the south basin.

closed-canopy semi-deciduous forest, occupies steep-sided hills that rise above the flood level in the western Pantanal (Prance and Schaller 1982, Alho 2005, Nunes da Cunha et al. 2007).

Laguna La Gaiba (LLG) (17°45'S, 57°40'W) is a large, shallow lake located along the course of the Rio Paraguay in the western Pantanal. Lake levels peak when summer monsoon precipitation drains from the low-lying terrain in the Pantanal region and adjacent western Brazilian highlands, causing the river and its associated lakes to overflow (Alho et al. 1988, Alho 2005). Therefore, changing hydrological conditions at LLG are likely to reflect a broad pattern of precipitation change in the continental lowlands of SHTSA.

Maximum lake depth varies from around 4 m to 6 m, depending on the stage of the Rio Paraguay, and LLG has a dry season surface area of 55 km^2 that increases to 105 km^2 after the annual floods. The lake is comprised of two basins; the shallow northern basin (~ 3 m deep) merges with permanently flooded wetlands to the east, and its western margin is bounded by hills covered with SDTF. The south basin of LLG, although deeper and more clearly-defined than the north basin, is broad and flat. (Fig. 3.4). The south basin is almost entirely surrounded by upland SDTF, including the slopes of the Serra do Amolar range that rise steeply above the level of inundation, reaching an altitude of 550 to 1000 m asl. Narrow sediment-rich beaches of the southern margin are occupied by evergreen, floodplain communities, and palm swamp occupies the low-lying terrain to the southwest of the lake beyond the riparian vegetation. Aquatic grasses and water hyacinths (*Eichhornia* spp.) fringe the western margins (Fig. 3.5a).

3.4. Methodology

3.4.1. Coring

In 2001, two parallel, overlapping sediment cores were extracted from a floating platform in the centre of the south basin using a Colinvaux-Vohnout drop-hammer modified Livingston piston corer (Colinvaux et al. 1999). The cores,

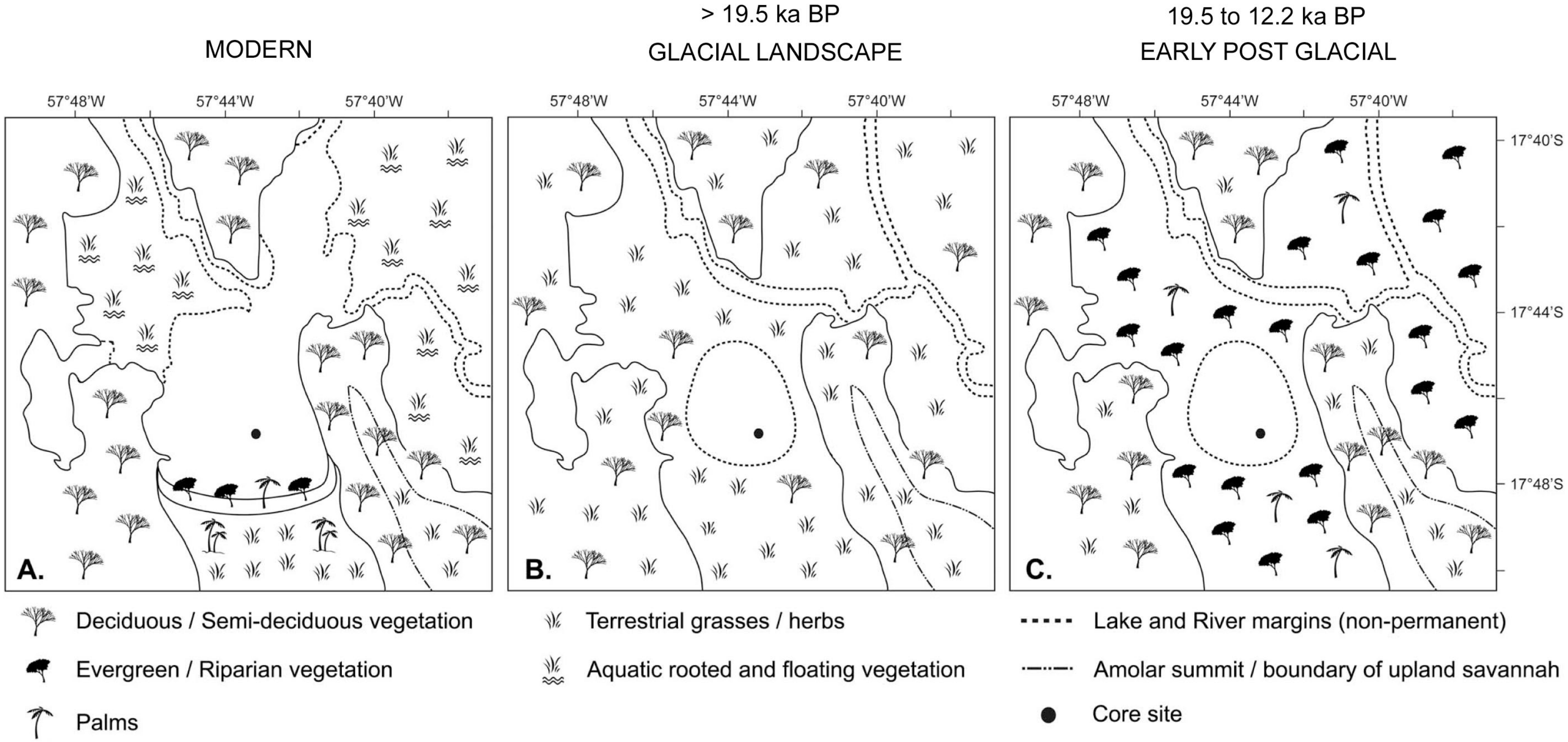

Fig. 3.5. Schematic representation of study site and key vegetation types at various time slices. Solid circle represents the core site. (a) The modern vegetation and lake margins. Semi-deciduous dry forest covers the steep slopes of the Serra do Amolar and upland savannah occupies the summit. Evergreen riparian vegetation covers the low-lying sediment-rich areas. The Rio Paraguay flows through the lake. Non-permanent lake margins (dashed lines) are defined by aquatic vegetation. (b) Open and shrubby vegetation dominates the glacial landscape. Lake levels are lower and the presence of terrestrial macrofossils indicates there is woody vegetation growing close to the core site. The Rio Paraguay may be only seasonally connected to the south basin. (c) Lower lake levels continue in the post-glacial environment, but extensive riparian vegetation occupies the sediment-rich lake bed and forest develops on the Serra do Amolar.

measuring 5.6 m and 4.8 m and extending to ~ 45 ka BP, were shipped in their aluminium tubes and extruded in the laboratory. Extruded cores were wrapped in plastic film, aluminium foil and thick plastic sleeves, and stored in a dark room at 4°C. The surface core, comprising the uppermost 110 cm of unconsolidated sediments and overlapping the Livingston core by 40 cm, was collected with a Perspex® tube and piston, and extruded in the field into air-tight plastic bags in consecutive 1 cm slices. Parallel cores were correlated by magnetic susceptibility and cross-checked through analysis of pollen at zonal boundaries, and the surface core was correlated to the consolidated sediments of the Livingston-extracted cores by loss-on-ignition at 550ºC (Dean 1974).

3.4.2. Chronology

The entire age-model from LLG is based on 18 AMS ^{14}C dates determined by the NERC radiocarbon facility, East Kilbride, UK (Table 3.2); 16 of which were obtained from well-preserved terrestrial plant macrofossils and two from non-calcareous bulk sediment. One outlying date was rejected; its anomalously young age possibly owing to contamination of the low carbon content of the sample material (12%). The glacial-Holocene transition is defined by five dates obtained from terrestrial plant macrofossils. All AMS ^{14}C ages ($\pm 2\sigma$) were calibrated using the "Fairbanks0107" calibration curve (Fairbanks et al. 2005). The age-depth relationship was analyzed using mixed-effect regression, as described by Heegaard et al. (2005), and the age of each sample was calculated from a cubic spline fitted through the calibrated radiocarbon dates (Fig. 3.6).

3.4.3. Vegetation data

The glacial-Holocene transition was sampled for pollen analysis at approximately 350-yr resolution from 24.0 to 13.0 ka BP and 11.0 to 8.0 ka BP, and 150-yr resolution across the Younger Dryas chronozone (13.0 to 11.0 ka BP). Samples measuring 1 cm^3 were processed according to Fægri and Iversen (1989) and a known quantity of exotic *Lycopodium* spores was added during sample preparation

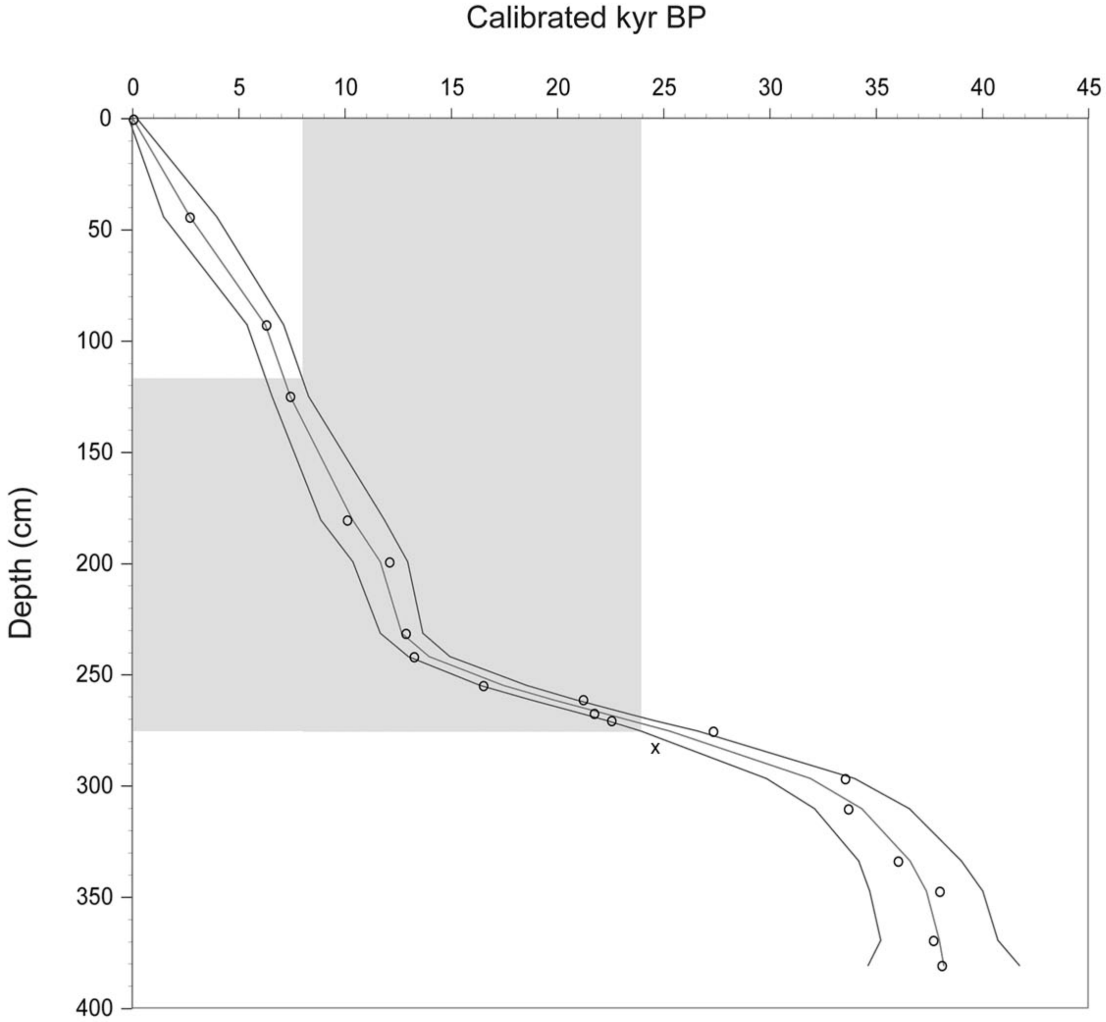

Fig. 3.6. The entire age-model for LLG based on 18 AMS ^{14}C dates and an assumed modern date for the uppermost cm of sediment. The model built using a mixed-effect regression as described by Heegaard et al. (2005). The section of core analyzed for this study is highlighted in grey. Black outer lines represent 2σ error.

to calculate concentration of pollen grains per cm^3. Fossil pollen identifications were made with reference to tropical pollen atlases (Roubik and Moreno 1991, Colinvaux et al. 1999), a digital pollen key (Bush and Weng 2007), and a modern pollen reference collection consisting of >1000 specimens representing > 850 taxa, located at the School of Geosciences, University of Edinburgh.

The terrestrial pollen sum was 300 grains, and because of the proximity of the site to the Pantanal savannahs, Poaceae and Cyperaceae were included in the

Publication Code	Sample Identifier (uncorrected depth)	Material	Stratigraphic position (cm) (Corrected depth)	Uncalibrated ^{14}C yr BP (± 1σ)
SUERC-11240	LLG surface: 49-50	Twig	44 - 45	2552 ± 35
SUERC-16482	LLG1a: 92-94	Sediment	92 - 94	5512 ± 38
SUERC-16483	LLG1a: 124-126	Sediment	124 - 126	6519 ± 40
AA-51698	**LG1: 175-176**	**Twig**	**180 - 181**	**8939 ± 56**
SUERC-11241	**LLG1: 194-195**	**Twig/bark**	**199 - 200**	**10317 ± 43**
SUERC-11242	**LLG1: 226-227**	**Twig/bark**	**231 - 232**	**10999 ± 46**
SUERC-16748	**LLG1: 236-238**	**Twigs/seed**	**241 - 243**	**11408 ± 48**
SUERC-11251	**LLG1: 249-251**	**Twig/bark**	**254 - 256**	**14121 ± 60**
SUERC-11704	LLG1: 256-257	Twig/wood	260.8 - 261.8	17892 ± 91
SUERC-11703	LLG1: 264-265	Twig/wood	267.2 - 268	18236 ± 94
SUERC-16749	LLG1: 268-271	Leaf/twig	268.8 - 272.8	18983 ± 104
SUERC-11243	LLG1: 274-275	Twig/bark	275.2 - 276	22771 ± 164
*SUERC-16750	LLG1: 280-282	Leaf/bark	281.6 - 283.9	20489 ± 122
SUERC-11244	LLG1: 293-294	Bark/wood	296.3 - 297.4	28185 ± 320
SUERC-11245	LLG1: 306	Twig/bark	310.2 - 310.8	28320 ± 326
AA-51699	LG1a: 334	Twig	333.8 - 334.2	30670 ± 390
SUERC-16484	LLG1: 338	Twig	347 - 348.1	32609 ± 556
SUERC-16751	LLG1: 357-359	Leaf/twig	368.5 - 370.7	32311 ± 535
SUERC-11246	LLG1: 368	Wood	380 - 381.6	32717 ± 564

Table 3.2. Uncalibrated AMS ^{14}C dates, their stratigraphic position and publication codes from the entire LLG record. Dates from the glacial-Holocene transition are in bold-face and * denotes the rejected date. See Table 2.3 for full details of ^{14}C results.

terrestrial sum. Data are presented as relative percent abundance (Fig. 3.7), and pollen concentrations (grain per cm^3) are also shown (Fig. 3.8) to test whether changes in pollen percentages are reflections of true changes in abundance, or if they are statistical artefacts resulting from changes in the catchment (e.g., local *versus* regional pollen signal). Stratigraphic plots were generated using C^2 (Juggins 2003). In addition, presence/absence of terrestrial plant macrofossils was recorded at 1 cm resolution and grouped into three categories; leaf fragments, seeds, and twigs/woody fragments (Fig. 3.7).

Twenty-five samples were examined to differentiate the pollen of Moraceae and Urticaceae into constituent genera, 14 of which were taken from the glacial-Holocene transition. The horizons chosen for analysis were concentrated at pollen zonal boundaries, and the abundance of each Moraceae/Urticaceae type was interpolated in the remaining samples. Moraceae/Urticaceae pollen was differentiated with reference to Burn and Mayle (2008), and grouped into seven types (total Urticaceae, *Brosimum* type, *Maquira* type, *Helicostylis* type, *Pourouma* type, *Pseudolmedia*/*Maclura* type and *Ficus*).

3.4.4. Geochemistry

High-resolution (2 mm) inorganic geochemical analysis was obtained using the Itrax® X-Ray Fluorescence core scanner facility, Aberystwyth University, UK. The Itrax® XRF scanner, described in detail by Croudace et al. (2006), produces rapid geochemical analysis through incrementally scanning split sediment cores, and the peak area of the spectral profiles generated for each detectable element is roughly proportional to elemental concentration (Fitton 1997, Thomson et al. 2006). Detrital clay (K, Ti, Rb) and coarse-grain (Zr) indicators (Sageman and Lyons 2004) in counts per second (cps) are plotted against age (Fig. 3.9). Geochemical data are presented as ratios of fine-to-coarse grain indicators to mitigate the ‘closed sum effect’(Rollinson 1993).

Percent total organic carbon (%TOC), C:N and $\delta^{13}C$ analyses were performed at Swansea University. An aliquot of the dried core material (*ca.*1 cm^3) was gently crushed and washed with an excess of 5% HCl to remove carbonates, were rinsed with distilled water to remove any residual HCl and dried at 60ºC for 48 hours. Stable carbon isotope analyses and C:N ratios were measured using a PDZ Europa ANCA GSL Elemental Analyser coupled with a 20/20 isotope ratio mass spectrometer. Samples of the dried sediment were weighed into tin foil capsules and combusted over chrome oxide in excess oxygen at 1000ºC. The resulting gases were reacted over hot copper (600ºC) to reduce oxides of nitrogen and the resulting CO_2 and N_2 resolved gas chromatographically. Elemental composition and C:N ratios were calculated based upon peak areas relative to standard reference materials acetanilide and atropine. For stable carbon isotope analysis samples equivalent to between 100-150 μm of carbon were weighed into tin capsules and combusted online as described above. The isotopic ratio of the resulting carbon dioxide gas was reported as per mille (‰) deviations from the VPDB standard. Replicate analyses of laboratory reference and standard materials yield the following precision data (n=12 σ_{n-1}) 0.10%, 0.65% and 0.09‰ for %N, %C and stable carbon isotopes respectively. %TOC, C:N and $\delta^{13}C$ results are presented in Fig. 3.9.

3.5. Results

3.5.1. GH-I: > 24.0 to 19.5 ka BP

The glacial pollen assemblages at LLG are dominated by *Alternanthera* (20 – 40%), *Borreria/Spermacoce* (2 – 4%), Asteraceae (2 – 7%), and Poaceae (30 – 40%), indicating the presence of an open, herbaceous community (Figs. 3.7, 3.8). Although these assemblages contain very little tree pollen, the abundance of woody plant macrofossils in the sediments demonstrates shrubs and/or trees were locally present, likely genera of the Fabaceae (Mimosoideae) and Urticaceae families because of the low, but continuous persistence of these taxa in the glacial pollen spectra. Glacial sediments consist of a heterogeneous mixture of fine sands and clays, and contain negligible organics (< 1%). Fine-to-coarse grain indicators (Ti/Zr, Rb/Zr, K/Zr) are highly variable near the top of the zone, reflecting the heterogeneity of glacial sediments.

3.5.2. GH-II: 19.5 to 12.2 ka BP

This zone is marked by the appearance of pollen typical of inundation-tolerant trees, particularly, *Symmeria* (10 – 15%), *Piranhea* (10 – 15%), and *Alchornea* (5 – 15%). Myrtaceae, Combretaceae/Melastomataceae, *Ficus*, *Ruprechtia*, *Triplaris* and *Dalbergia/Machaerium* are also present, though in low abundance. The relative proportion of Asteraceae (2 – 6%) remains constant across the transition from GH-I to GH-II, but other herbaceous pollen types, *Borreria/ Spermacoce* (2 – 4%) and *Alternanthera* (2 – 5%), much reduced from their high relative abundance in the glacial period, decline to negligible proportions after 18.0 ka BP. The decline of these taxa is followed by a minor rise in *Celtis* around 16.0 ka

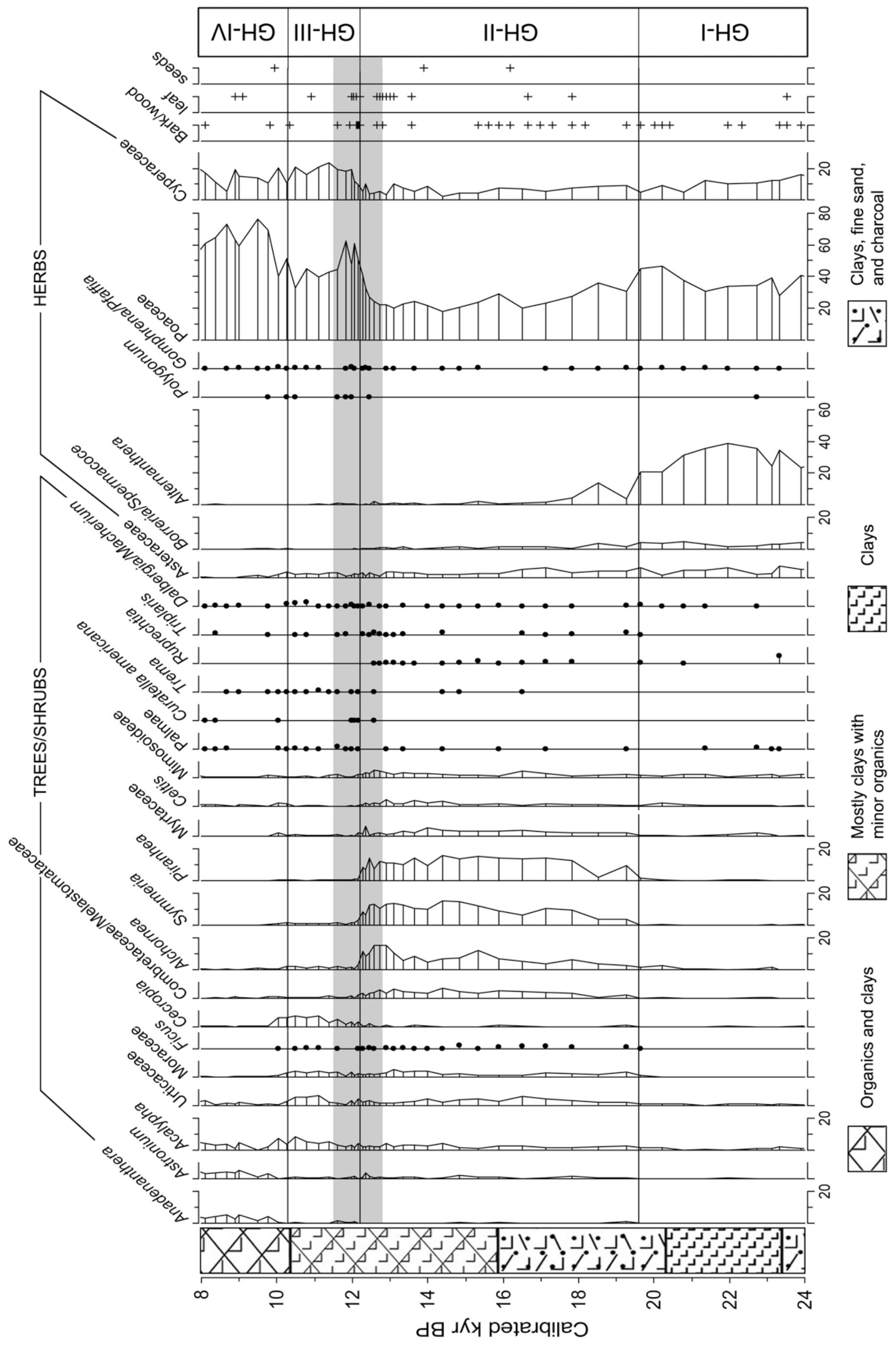

Fig. 3.7. Relative percent abundance of selected pollen types from LLG plotted against calibrated kyr BP. Troels-Smith lithology column, and presence/absence of terrestrial plant macrofossils are presented on the left and right of the pollen data, respectively. Shaded zone represents the YD chronozone.

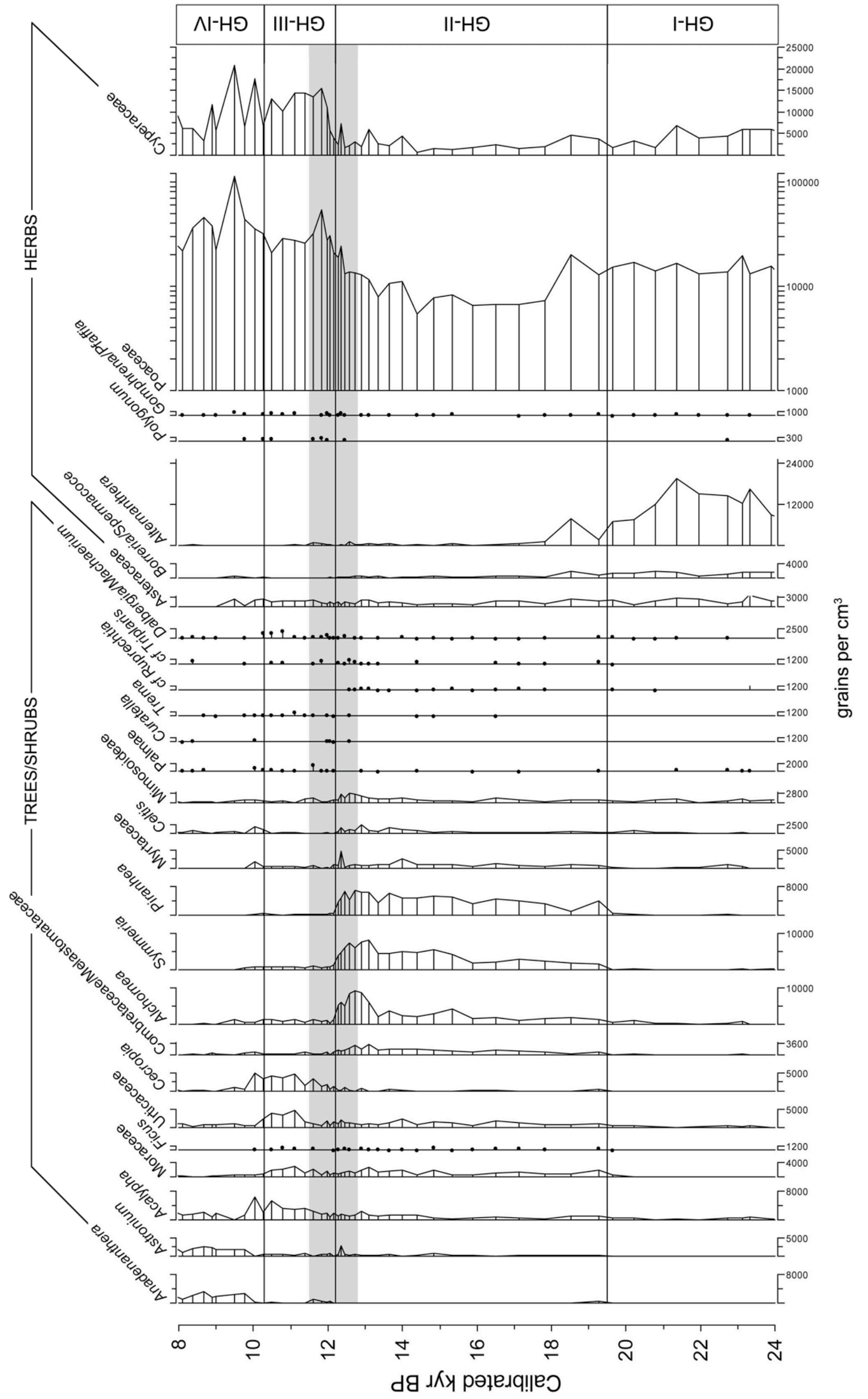

Fig. 3.8. Concentration (grains per cm^3) of selected pollen types from LLG plotted against calibrated kyr BP. Note the logarithmic scale for Poaceae abundance. Shaded zone represents the Younger Dryas chronozone.

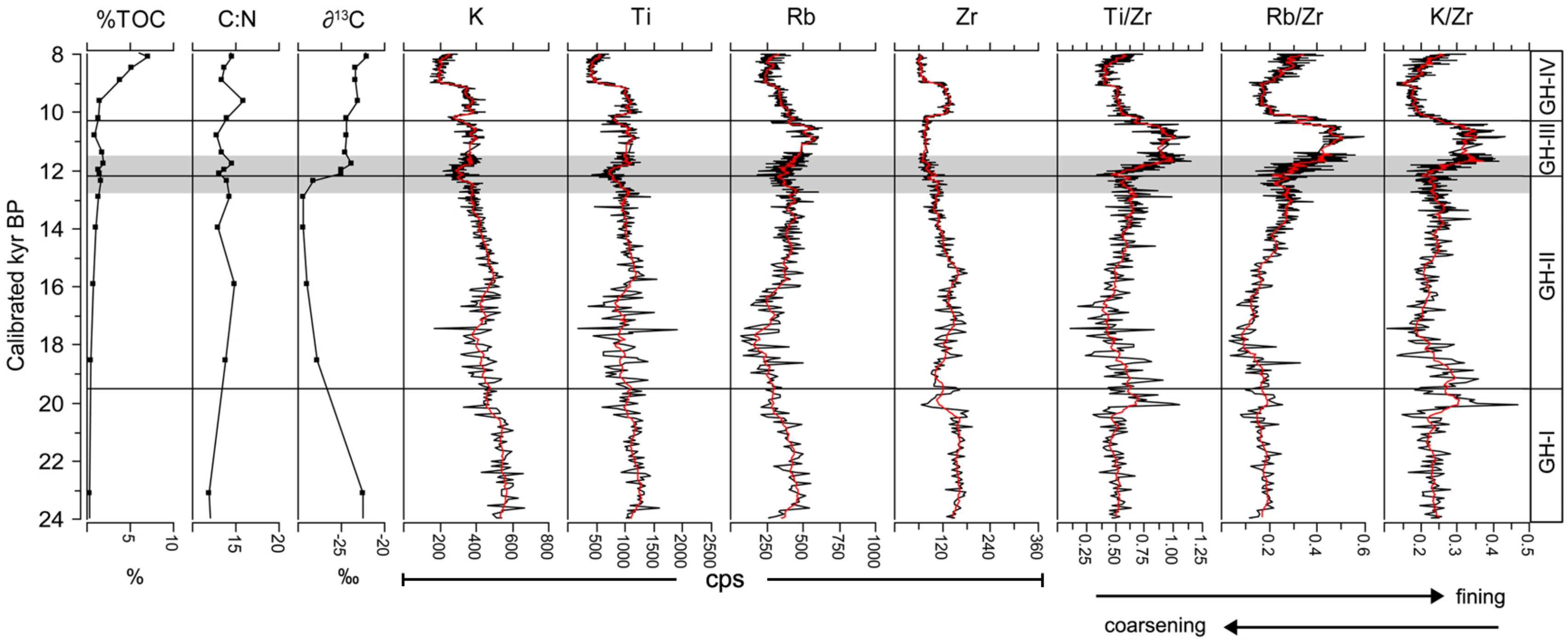

Fig. 3.9. Carbon analyses (% total organic carbon, C:N, $\partial^{13}C$ (‰)), selected elemental data from XRF analysis (counts per sec), and elemental ratios plotted against calibrated kyr BP. Red lines are 10-pt. moving averages. Shaded zone represents the Younger Dryas chronozone.

BP, and also a change in lithology and geochemistry. The sand content declines, and fine-to-coarse grain size indicators become higher and less variable after 16.0 ka BP. The clay content subsequently decreases at 12.6 ka BP, a trend particularly evident in the Ti/Zr and Rb/Zr curves. Percent TOC is low (<1%) and $\delta^{13}C$ values range from -29 to -27‰ throughout GH-II. Woody plant macrofossils are abundant in sediments throughout this zone, and leaf fragments become frequent after 14.0 ka BP.

3.5.3. GH-III: 12.2 to 10.0 ka BP

The transition from GH-II to GH-III is marked by a reduction in *Symmeria*, *Piranhea*, *Alchornea* pollen. Though only present in low abundance in the previous zone, *Ruprechtia* also disappears from the record. GH-III is the only zone across the glacial-Holocene transition characterized by the presence of *Cecropia* (5 – 10%), a tree genus of weedy generalists. Pollen of *Ficus*, *Trema*, *Dalbergia/Machaerium* and Palmae is present in low abundance. Pollen assemblages in this zone also contain high abundance of Poaceae (25 – 60%), and Cyperaceae (15%), and the rise in these taxa is parallelled by an increase in $\delta^{13}C$ (-24 to -22‰) at 12.2 ka BP. Although fine-to-coarse grain ratios are initially low, they rapidly increase around 11.8 ka BP to reach their highest value across the glacial-Holocene transition.

3.5.4. GH-IV: 10.0 to 8.0 ka BP

The early Holocene at LLG is marked by the appearance of *Anadenanthera* (5%) and a rise in *Astronium* (5%) pollen, species of which are common in SDTF and on the hillslopes around LLG. The appearance of these pollen types coincides with a decline in Asteraceae, *Acalypha*, total Moraceae (including *Ficus*), Urticaceae, and *Cecropia*. Poaceae abundances increase by 20%. These shifts in vegetation are parallelled by a coarsening of sediments, shown by an abrupt and simultaneous reduction in Ti/Zr, Rb/Zr and K/Zr. $\delta^{13}C$ values range from -23 to -22‰, and total organic content begins to rise around 9.5 ka BP.

3.6. Discussion

3.6.1. Riparian community change across the glacial-Holocene transition

The landscape surrounding LLG is characterized by two broad classes of habitats: shallow-soil hillslopes and seasonally-flooded low-lying areas. Our discussion is largely confined to development and change in the riparian communities located along river courses and the margins of LLG. Although "riparian" often refers specifically to riverine vegetation, in this case, we are using the term to refer to the seasonally-inundated shoreline forest around LLG.

In the glacial period, prior to 19.5 ka BP, both upland and low-lying areas were dominated by an open, herbaceous vegetation, but the abundance of woody terrestrial plant macrofossils in the glacial sediments indicates shrubs and/or trees were locally present. The south basin of LLG is currently surrounded by closed-canopy forest, but few terrestrial macrofossils are transported into the centre of the lake due to the large breadth of the lake (8 x 8 km) and shallow gradient of the basin (25 $cm \cdot km^{-1}$) (Fig. 3.4). Therefore, high abundance of woody macrofossils in the glacial sections implies the shrubby community was growing close to the core site on seasonally-inundated sediment-rich habitat under conditions of lower-than-present lake levels (Fig. 3.5b).

At 19.5 ka BP, the composition of this local community altered as riparian forest, characterized by species of *Symmeria*, *Piranhea* and *Alchornea*, invaded the seasonally-flooded habitat around the lake. The genus *Symmeria* contains a single species (*S. paniculata*) found only in periodically flooded forest that tolerates six to eight months inundation (Junk and Piedade 1997, Waldhoff et al. 2002), and has been found to be a palynological indicator of seasonally-inundated riparian forest (Burn 2008). Also indicative of inundation-tolerant forest is *Piranhea*, a species of which (*P. trifoliata*) frequently occurs in Amazonian floodplains where it occupies higher terrain (Worbes et al. 1992). *Alchornea* contains c.50 species that grow in a range of ecosystems, but this pollen type likely represents *A. discolor* and *A. castaneifolia,* common constituents of inundation-tolerant riparian forest in the Pantanal (Worbes

1997, Sanjiné and Beck 2004, Damasceno-Junior et al. 2005). Also present in the pollen assemblages is Combretaceae/Melastomataceae, genera of which are currently found on the narrow southern beach of LLG (*Combretum*), and *Ruprechtia*, also present in low abundance, includes a species found in riparian forest, *R. brachysepala,* recorded in eastern Bolivia (Worbes 1997, Jardim et al. 2003, Damasceno-Junior et al. 2005).

Riparian forest taxa are tolerant of flooding and drought, but they favour sediment-rich soils. The surface area of the south basin is constricted by steep hillslopes overlain by shallow soils, an unsuitable habitat for this community. Therefore only under conditions of lower lake levels would there be a greater expanse of sediment-rich habitat favoured by inundated riparian forest. Riparian communities are maintained by a strongly seasonal hydrological cycle (Junk 1989), and would have occupied seasonally-exposed lake bed of the south basin which experienced flooding and drought in areas that are now permanently-inundated. Therefore, mean lake level in the south basin remained low towards the end of the glacial period, and warming at 19.5 ka BP allowed for the establishment of extensive riparian forest (Fig. 3.5c).

As in GH-I, the abundance of woody macrofossils in GH-II (19.5 to 12.2 ka BP) provides corroborating evidence that riparian forest occupied seasonally-inundated lake bed close to the core site under conditions of lower mean lake level compared to present. In addition, the relative proportion of riparian pollen types is higher here than in the modern pollen spectrum (see Chapter 2, Fig. 2.9), despite the presence of inundation-tolerant vegetation currently occupying the narrow margin between the lake shore and bedrock hills, thereby bolstering our interpretation that riparian forest dominated the local catchment. The carbon isotope data point to a strong influence of C_3 vegetation (-27 to -29 ‰), further supporting the presence of an extensive, local riparian community from 19.5 to 12.2 ka BP. The minor relative contribution of savannah pollen to the fossil assemblages, particularly Poaceae, suggests the south basin was at least seasonally-isolated from the Rio Paraguay, inhibiting the delivery of pollen from the Pantanal grasslands to LLG (Fig. 3.5c).

The broad riparian community at LLG persists until 12.2 ka BP, when it declines within several decades. Although inundation-tolerant taxa are generally adapted to the poor growing conditions of flooding and drought, permanent flooding is known to cause widespread mortality of riparian shrubs within several years (Junk 1989, Damasceno et al. 2004). In particular, *Symmeria paniculata* is well-adapted to deep-flooding conditions, surviving up to 270 days inundation at several metres depth without dropping its leaves (Waldhoff et al. 2002), but *S. paniculata* seedling establishment is dependent on the terrestrial phase of the annual flooding cycle, thus prolonged inundation of lake margins will prevent its regeneration (Waldhoff et al. 2002). Typically occupying areas 1-2 m above the mean water level (Junk 1989, Worbes 1997), less inundation-tolerant species of *Piranhea* and *Alchornea* also experience an abrupt and contemporaneous decline. The disappearance of these taxa is most likely due to habitat loss as the once seasonally-inundated habitat (lake bed) was flooded at 12.2 ka BP, and remained permanently flooded from this point onwards.

Additional evidence of rising lake levels includes the decline in woody macrofossils as the lake margins expanded to reach their maximum extent at the base of the Amolar hills, thereby eliminating the forested vegetation previously occupying the seasonally-inundated lake bed in close proximity to the core site. Rising $\delta^{13}C$ values (Fig. 3.9) demonstrate greater isotopic contribution from C_4-dominated (sedge and grass) Pantanal communities, also corroborated by steeply rising Poaceae abundance, and reflective of a broadening of the catchment as higher lake levels connect LLG to the Pantanal through the Rio Paraguay. Higher temporal resolution of the pollen data demonstrates that Poaceae began to rise at 12.5 ka BP, 300-yrs prior to the elimination of the riparian forest, suggesting the rapid disappearance of this community represents the crossing of a threshold, by which steadily increasing precipitation in the Pantanal eventually led to permanent flooding of the south basin, and an irrevocable change in the riparian community.

The pollen signature representative of the succeeding shoreline community (GH-III) is characterized by *Cecropia*, a genus of weedy trees, the relative percent abundance of which is analogous to the modern pollen signature at LLG (5 – 10%). At present, the only species of this genus present at LLG, C. *concolor* (see Chapter 2, Table 2.1), occurs infrequently in the light-gaps in the narrow, swampy habitat between the lake margin and dry forest, thus the abundance of *Cecropia* pollen is also suggestive of high lake levels, possibly comparable to modern levels. The high detrital clay to coarse material ratios (Fig. 3.9) also implies that LLG was a deeply flooded, low-energy environment, allowing for clays to accumulate.

At 10.0 ka BP *Cecropia* declines, accompanied by the highest abundance of Poaceae in the record, and the occurrence of *Anadenanthera* and *Astronium* pollen. Although *Anadenanthera* is not resolved to species, it is likely *A. colubrina,* the most abundant species of *Anadenanthera* in the catchment, shown to be a reliable indicator of dry forest (Prado and Gibbs 1993, Mayle 2006, Gosling et al. 2009). In particular, *Astronium fraxinifolium*, *A. urundeuva* and *Anadenanthera colubrina* are commonly found in SDTF of Chiquitanía and the western Pantanal, including the steep hillslopes around LLG where these taxa abound (see Chapter 2) (Killeen et al. 1998, Jardim et al. 2003, Nunes da Cunha et al. 2007).

Dry forest communities of the Chiquitano and the western Pantanal have a negligible abundance of grasses in the understorey (Prance and Schaller 1982), so likely sources of this grass pollen are the Pantanal savannahs and marginal aquatic communities. These pollen assemblages are analogous to modern pollen spectra (Chapter 2) from the shallow, aquatics-rich north basin of LLG that merges with the Pantanal wetlands, where Poaceae comprises 60 – 70% of the pollen sum. In the north basin, rooted aquatic grasses occupy a large surface area, but the shallow, permanent water-body prevents the establishment of a riparian forest. Similar conditions may have occurred in the south basin beginning at 10.0 ka BP. Lower

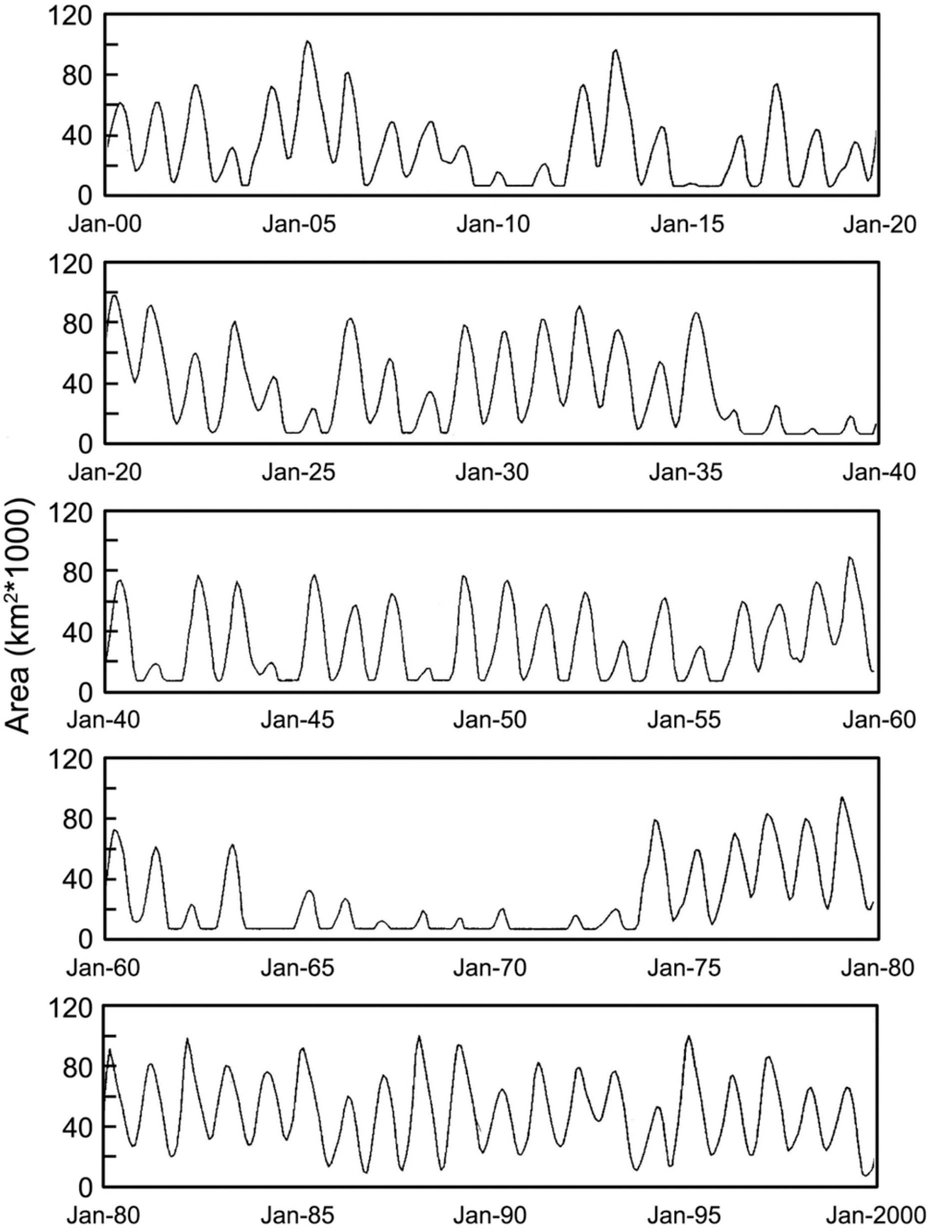

Fig. 3.10. Inundated area in the Pantanal extrapolated from river stage measurements (at Corumbá) for the last century, as calculated by Hamilton et al. (1996). Data were produced using a predictive relationship between river stage and inundated area during the periods when remote sensing data were available (1979 – 1987). Figure adapted from Hamilton (2002). Less inundation in the Pantanal for the years 1960 – 1973 resulted in an expansion of forest in lower-lying areas.

lake levels in the south basin may have also reduced the available swampy habitat and allowed dry forest to close in on the narrow margin between the lake shore and bedrock outcrops, reducing the abundance of *Cecropia*. Although these shifts suggest a lowering of water levels beginning at 10.0 ka BP, the margins of the south basin remained permanently flooded because extensive riparian forest does not regain dominance in the local catchment.

3.6.2. Climatic implications of hydrological change

The hydrology of the Rio Paraguay, and its tributaries and associated lakes, is controlled by (austral) summer precipitation in the Pantanal region (Hamilton 2002). Precipitation accumulating on the savannahs of the eastern Pantanal basin and western Brazilian highlands flows westward across the low gradient of the floodplains toward the Rio Paraguay. The passage of rain water is aided by shifting and seasonal channels, *corixos* and *vazantes*, the latter often seasonally dry (Hamilton 2002). Several months after the summer monsoon, water levels peak in the Rio Paraguay and associated lakes, including LLG. The lag between the rainy season and high water varies depending on location, but at Corumbá, located 135 km south of LLG (Fig. 3.2), the offset is approximately three months (Hamilton 2002, Damasceno-Junior et al. 2005). High water levels in the Rio Paraguay reverses the flow of the tributaries, causing widespread flooding on adjacent floodplains, and fills the backswamps situated behind the gallery forests bordering the river. Therefore, flooding in the region adjacent to the Rio Paraguay is indirectly related to annual precipitation, and the height of the river stage determines the extent of inundation in floodplains of the Rio Paraguay and associated lakes (Alho 2005).

Annual flooding in the Rio Paraguay follows a predictable pattern; the yearly hydrograph is unimodal, and on average, total inundated area ranges from 10,000 km^2 (low stage) to 110,000 km^2 (high stage) throughout the year (Hamilton 2002). However, precipitation in the Pantanal demonstrates a high degree of interannual variability (Hamilton et al. 1996, Hamilton 2002), which indirectly influences the extent of flooding in low-lying areas around the Rio Paraguay. In the years 1960 to

1973, low precipitation in the Pantanal resulted in a maximum river stage of 3 m lower than the succeeding decades. This in turn is estimated to have halved the maximum inundated area in the Paraguay region (Fig. 3.10) of the Pantanal (40,000 km^2) compared to the following decade (> 80,000 km^2) (Hamilton et al. 1996, Hamilton 2002).

Not surprisingly, interannual variability in the flooding regime directly influences the low-lying vegetation communities. In particular, the drought of the 1960s allowed for forested vegetation to encroach on the floodplains of the Rio Paraguay. In the following decades, higher precipitation resulting in greater inundation of low-lying areas caused these forests to die back, the dead stumps of which are still visible in water-logged areas (Hamilton 2002). Therefore, the precipitation regime of the Pantanal indirectly influences the extent of low-lying forest, mediated through the yearly flood pulse.

The abundance of pollen characteristic of inundation-tolerant forest from 19.5 to 12.2 ka BP reflects local riparian forest in the immediate catchment at LLG. However, due to the links between the hydrology of LLG, the Rio Paraguay, and mean annual precipitation, the abundance of riparian forest at this site is representative of lower precipitation in the Pantanal basin and the western Brazilian highlands. The *Symmeria-Piranhea* community abruptly declines at 12.2 ka BP, and a similar forested riparian community does not reappear in the Holocene, marking the onset of a wetter interglacial climate in the Pantanal and adjacent regions.

Although in recent decades, pronounced interannual variability in mean annual precipitation is known to have caused broad-scale alterations in the abundance of low-lying forest in the Pantanal (Hamilton 2002, Alho 2005), the comparative droughts and flooding have lasted for no more than a couple of decades. Sub-centennial scale fluctuations in the Pantanal flood regime that influenced the extent of seasonally-inundated forest may have occurred after 12.2 ka BP, but the temporal resolution of the pollen analysis at LLG is too coarse to pick out any such variability. However, the negligible abundance of riparian types after 12.2 ka BP demonstrates that on average, the climate of the early Holocene is characterized by higher precipitation than the last glacial period and the glacial-Holocene transition.

3.6.3. Was there a climatic event in the continental interior of SHTSA during the YD chronozone?

Four hundred years prior to the reduction of the riparian community at 12.2 ka BP, the Rio Paraguay increases sediment and pollen transport into the south basin, as shown by a threefold increase in Poaceae concentration from the Pantanal savannahs (Fig. 3.8), and the deposition of coarser sediments beginning at 12.6 ka BP (Fig. 3.9). Although indicative of higher precipitation in the Pantanal basin around the beginning of the YD chronozone in accordance with palaeoclimate model predictions (Dahl et al. 2005), this climatic shift is unidirectional and riparian forest does not regain dominance in the catchment after 12.2 ka BP.

The precipitation rise beginning at 12.6 ka BP is consistent with diatom- and geochemically-inferred precipitation change on the Altiplano (Baker et al. 2001a,b), and travertine growth in NE Brazil (Auler et al. 2004, Wang et al. 2004), but the overall pattern observed at LLG is contrary to these records because precipitation in the Pantanal remains high at the end of the YD chronozone. On the other hand, aridity returns to the Altiplano and NE Brazil around 11 ka BP, a trend attributed to the northward shift of the ITCZ, as resumed heat transport to the North Atlantic restored the interhemispheric thermal gradients after the YD. However, the continuation of relatively high precipitation in the Pantanal basin in the early Holocene contrasts with the predicted northward shift of the ITCZ, therefore North Atlantic climate forcing does not explain the observed changes at LLG.

Instead, the glacial-Holocene transition at LLG resembles the progressive and step-wise climate change observed in mid- and high latitudes of South America, reflected in the deglaciation of Patagonian ice fields (McCulloch et al. 2000, Turner et al. 2005), and clear transitions in the pollen records of these latitudes (McCulloch et al. 2000, Markgraf et al. 2007), argued to reflect an Antarctic climate signal. The similar pattern of post-LGM climate change hints at common forcing mechanism for the continental SHTSA, demonstrating asynchroneity between tropical latitudes of the continental interior of southern hemisphere and the North Atlantic. In particular, the inception of 'wet' interglacial climate at LLG in the middle of the YD chronozone implies the influence of Antarctic climate during the glacial-Holocene transition penetrated further north into South America than 40ºS as previously recorded (i.e., Sudgen et al. 2005).

3.7. Conclusions

The high temporal resolution of the record at LLG provides an unique insight into the pattern of deglaciation in the interior of SHTSA, the climate of which has been previously extrapolated from Andean records (e.g. Titicaca). We demonstrate that two major shifts in climate and vegetation define the glacial-Holocene transition in the Pantanal basin. Initially, warming at 19.5 ka BP allowed for the establishment of riparian forest around the lake shores of LLG, and likely elsewhere alongside sediment-rich rivers and water bodies in the Pantanal. However, the region was drier than present until the beginning of the YD chronozone, after which increased precipitation in the Pantanal basin caused permanent inundation of the LLG lake shores, thereby eliminating the riparian community. The riparian taxa do not become re-established at LLG, indicative of continued higher flooding, and therefore higher precipitation, in the Pantanal after the end of the YD chronozone.

The unidirectional nature of the inferred hydrological change at LLG suggests that unlike Andean and coastal sites, the Pantanal did not experience a YD precipitation anomaly. Rather, the timing of the Pleistocene-Holocene boundary at LLG (12.6 to 12.2 ka BP) coincides with that of southern South America and Antarctica, suggesting the climate of the continental interior of SHTSA was dominantly influenced by the higher latitudes of the southern hemisphere, inconsistent with hypothesized northern hemisphere forcing, as demonstrated in Andean and coastal sites of SHTSA.

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IV. The potential of *Pediastrum* species as indicators of lake level change in tropical South America

Bronwen S. Whitney and Francis E. Mayle

4.1. Abstract

Here we present a pilot study demonstrating the potential of *Pediastrum*, a green alga commonly reported from palaeoecological reconstructions, as a proxy for lake level change in tropical South America. The study site is Laguna La Gaiba (LLG) (17º45'S, 57º40'W), a broad, shallow lake located along the course of the Rio Paraguay in the Pantanal, a 140,000 km^2 tropical wetland located mostly in western Brazil, but extending into eastern Bolivia. Eleven surface samples, taken from the sediment-water interface across a range of lake depths (3 – 6 m) at LLG, are analyzed for *Pediastrum*. In total, seven species are reported, and *P. musteri*, *P. argentiniense*, and *P. angulosum* are identified as potential indicators of past lake levels. The results of the modern dataset are applied to thirty-one fossil *Pediastrum* assemblages spanning the early Holocene (12.0 ka BP) to present to qualitatively infer past lake level changes. The early Holocene (12.0 – 9.8 ka BP) assemblages do not show a clear signal, though the abundance of *P. simplex* suggests lake levels were relatively high. The absence of *P. musteri*, characteristic of deep, open water, and abundance of macrophyte-associated taxa indicates lake levels were lowest from 9.8 – 3.0 ka BP. A shift towards wetter conditions begins at 4.4 ka BP, indicated by the appearance of *P. musteri*, though LLG does not reach modern lake levels until 1.4 ka BP. The *Pediastrum*-inferred mid-Holocene lowstand is consistent with lower precipitation previously inferred through pollen analysis at this site, and also corresponds to widespread evidence of aridity in the South American tropics during the mid-Holocene. Steadily increasing lake levels from 4.4 ka BP to present is consistent with diatom-inferred lake level change at Lake Titicaca, and demonstrates

coherence with other records showing a strengthening of the southern hemisphere monsoon in the late Holocene.

4.2. Introduction

Pediastrum, a colonial green alga of the family Hydrodictyaceae, is a good candidate for a palaeoenvironmental proxy because: (1) it is abundant in freshwater lakes and wetlands, thus it is often found in high concentrations in sediment cores; (2) it is globally-distributed; (3) it survives the harsh chemical treatment of pollen preparations, thus it can be analyzed alongside pollen; (4) and it can be resolved to species, and often subspecies level, with the use of light microscopy (Komárek and Jankovská 2001, Van Geel 2001). However, despite these strengths, the full potential of *Pediastrum* as a palaeoenvironmental proxy has remained unexplored.

Of palaeoecologists who record the presence of *Pediastrum*, the majority do not differentiate between species, and *Pediastrum* is reported as total concentration alongside other non-pollen palynomorphs (NPP) (Van Geel 2001). The bulk of these studies are from the northern mid-latitudes, where fluctuations in *Pediastrum* concentration are typically thought to reflect changes in trophic state and erosion in the catchment (Komárek and Jankovská 2001, Van Geel 2001, and references therein). In tropical and subtropical regions, interpretation of the *Pediastrum* signal varies among studies. In tropical Andean lakes, high *Pediastrum* concentration has been interpreted as reflecting either colder temperatures (Rull et al. 2006), or lower lake levels (Sylvestre 2002, Gosling et al. 2008). The presence/absence of *Pediastrum* has also been used to differentiate between marine and freshwater environments in coastal lagoons of South America (Medeanic 2006, del Puerto et al. 2006). In addition, *Pediastrum* concentrations are found to be inversely correlated with macrophyte cover in semi-arid regions of Morocco (Lamb et al. 1999) and Mexico (Caballero et al. 1999), but the opposite trend is found in a macrophyte-dominated lake in Florida (Brenner 2006).

Since species of *Pediastrum* have varying ecological tolerances (Komárek and Jankovská 2001, Van Geel 2001), qualitative and/or quantitative estimates of past environmental change might be inferred from fossil *Pediastrum* community composition. However, there are few studies that resolve *Pediastrum* to species, and of those that do, the fossil assemblages are commonly used to qualitatively infer past nutrient availability, pH and water quality within a lake (Cohen et al. 2000, Jankovská and Pokorny 2002, Bradshaw et al. 2005). Attempts to draw regional climatic inferences from *Pediastrum* assemblages in the mid- to high latitudes have focused on the classic North Atlantic late-glacial climate sequence (Bølling-Allerød/ Younger Dryas), but no clear correlations have been drawn between changes in climate and *Pediastrum* communities (Nielsen and Sørensen 1992, Sarmaja-Korjonen et al. 2006). This is an unsurprising result given that broad landscape change characteristic of recently deglaciated environments, such as soil and vegetation development, are shown to directly influence lake chemistry (Engstrom et al. 2000), possibly overriding any effect of climate change on fossil *Pediastrum* assemblages. However, a palaeoclimate signal might be inferred from fossil *Pediastrum* at sites not recently influenced by glacial activity, and where the catchment has been relatively stable.

The aim of this study is to explore the potential of *Pediastrum* as a proxy for Holocene climate change at a site in lowland, tropical South America. Palaeoclimatology of South America is a nascent field. There are few reconstructions of past climate, the majority of which are located in Andean regions, and the palaeoclimate of tropical lowland regions is often extrapolated from these high elevation studies. In addition, the scarcity of palaeoclimate proxies in lowland regions has resulted in the inference of climate from pollen analysis, but the effects of precipitation, temperature and atmospheric CO_2 concentrations on tropical vegetation are not easily disentangled. *Pediastrum* has been reported in fossil pollen studies from lowland, tropical sites (i.e., Ledru et al. 2006), therefore these algae could provide an independent tool to be used in conjunction with pollen analysis.

Laguna La Gaiba, located on the western edge of the Pantanal in the lowland southern hemisphere tropics, is an ideal study site because previous fossil pollen analysis indicates the catchment was continuously forested throughout the Holocene, thereby eliminating the influence of ecosystem change on the lake chemistry. Also,

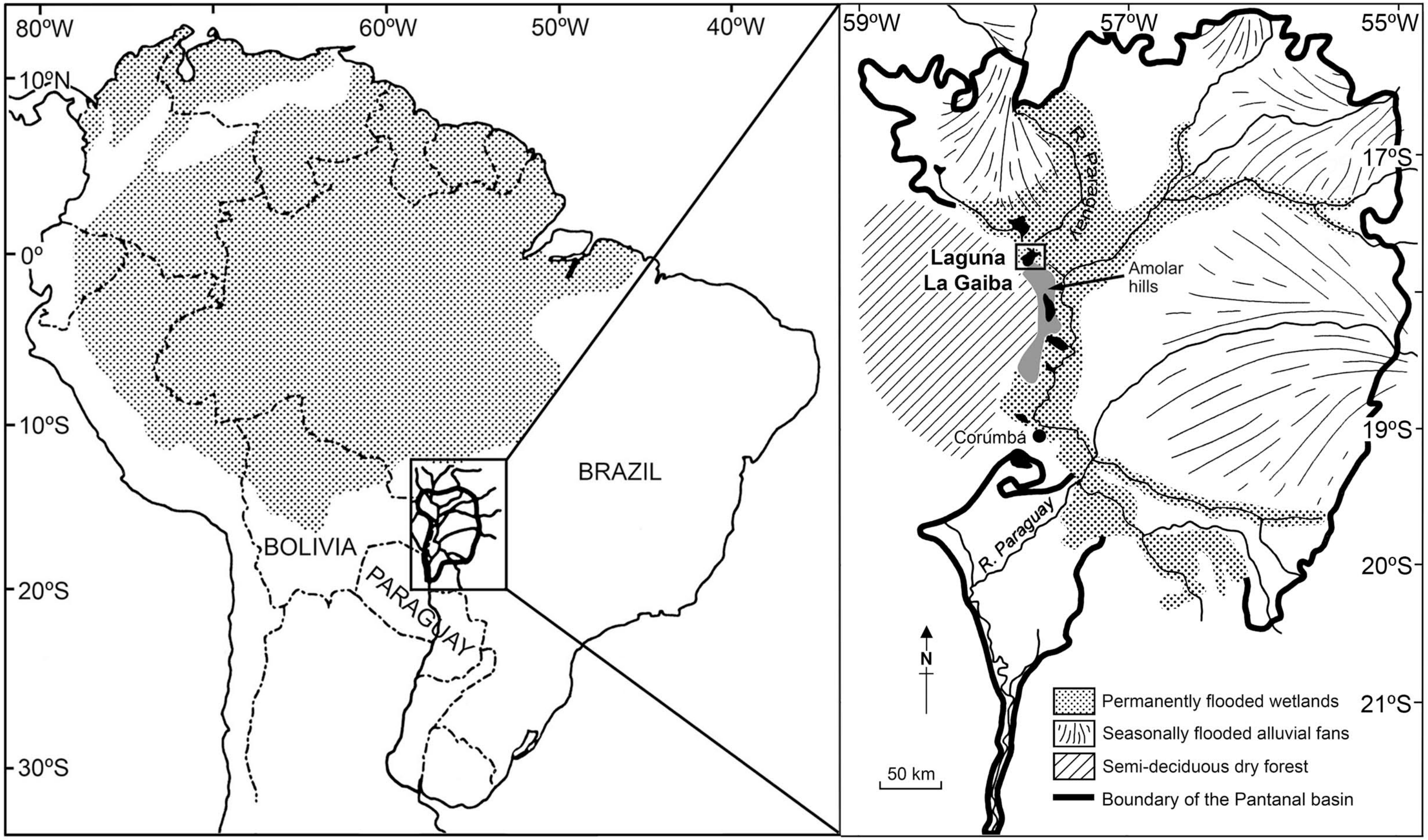

Fig. 4.1. (a) Location of the Pantanal basin relative to the Amazon rainforest (stippled). (b) The study site, Laguna La Gaiba, is situated along the Rio Paraguay and lies between the permanently flooded wetlands and gallery forests of the Pantanal (stippled) and the Chiquitano dry forest (hashed). Seasonally-inundated savannahs overlay alluvial fans to the east of the Rio Paraguay

there is evidence of changing precipitation at this site during the mid-Holocene, corresponding with the broader trend of Holocene climate change across tropical South America (Mayle and Power 2008), and therefore our results can be compared to a climatic pattern based on independent evidence.

4.3. Site Description

The Pantanal is the world's largest tropical wetland (~140,000 km^2), located predominantly in western Brazil, but extending into easternmost Bolivia (Fig. 4.1). This wetland occupies a tectonic depression between the Brazilian shield and the Andean foreland (Clapperton 1993), and together with the western Brazilian highlands, forms the headwaters of the Rio Paraguay. Climate of the Pantanal is tropical and highly seasonal. Mean annual precipitation is 1000-1700 mm, the bulk of which falls in the austral summer from December to February, and annual flooding occurs in the Pantanal basin when these seasonal rains cause the River Paraguay and its associated tributaries to overflow (Alho et al. 1988, Alho 2005). The mosaic of ecosystems comprising the Pantanal is defined by this seasonal flooding; river levées support inundation-tolerant gallery forests, permanently-flooded wetlands occupy areas of lowest elevation immediately behind these levees, and seasonally-inundated savannahs overlay higher ground east of the Rio Paraguay. Floating mats of aquatic vegetation, dominated by *Eichhornia* spp. (Pontederiaceae), Asteraceae, and Poaceae are common on the margins of lakes and water courses (Alho 2005, Chavez, *pers. comm.*). In addition, closed-canopy seasonally-dry tropical forest (SDTF) dominates the bedrock hills that rise steeply above the flood level in the western Pantanal (Prance and Schaller 1982, Alho 2005, Nunes da Cunha et al. 2007).

Laguna La Gaiba (LLG) (17°45'S, 57°40' W) is a large, shallow lake located along the course of the Rio Paraguay. Lake levels peak when summer monsoon precipitation drains from inundated Pantanal savannah wetlands into the Rio Paraguay, causing the river and its associated lakes to overflow (Alho et al. 1988, Alho 2005), thus changing hydrological conditions at LLG are reflective of regional precipitation change. Maximum lake depth varies from around 4 m to 6 m depending on the season, and LLG has a dry season surface area of 55 km^2 that increases to 105 km^2 after the annual floods. The lake is comprised of two basins; the shallow northern basin (~ 3 m deep) merges with permanently flooded wetlands to the east, and its western margin is bounded by steep-sided hills covered with SDTF (Fig. 4.2). The south basin of LLG is deeper and more clearly-defined, and its northern extent is flanked by the Rio Paraguay. The south basin is almost entirely surrounded by SDTF on the slopes of the Serra do Amolar range that rise steeply above the level of inundation. Basic analyses of lake water in July 2006 show the lake to be oligotrophic and slightly alkaline (Table 4.1).

4.4. Methodology

4.4.1. Field

In 2001, two parallel overlapping sediment cores were extracted from a floating platform in the centre of the south basin using a Colinvaux-Vohnout drop-hammer modified Livingston piston corer (Colinvaux et al. 1999). The cores, measuring 5.6 m and 4.8 m and extending to ~ 45 ka BP, were shipped in their aluminium core tubes and extruded in the laboratory. Extruded cores were wrapped in plastic film, aluminium foil and thick plastic sleeves, and stored in a dark room at 4°C. The surface core, comprising the uppermost 110 cm of unconsolidated sediments and overlapping the Livingston core by 40 cm, was collected with a Perspex® tube and piston, and extruded in the field into air-tight plastic bags in consecutive 1 cm slices. Parallel cores were correlated by magnetic susceptibility and cross-checked through analysis of pollen at zonal boundaries, and the surface core was correlated to the consolidated sediments of the Livingston-extracted cores by loss-on-ignition (550ºC) analysis.

In July 2006, the uppermost 1 cm of sediment was collected at 19 sites across LLG using a Perspex® tube and piston. Samples were extruded in the field and

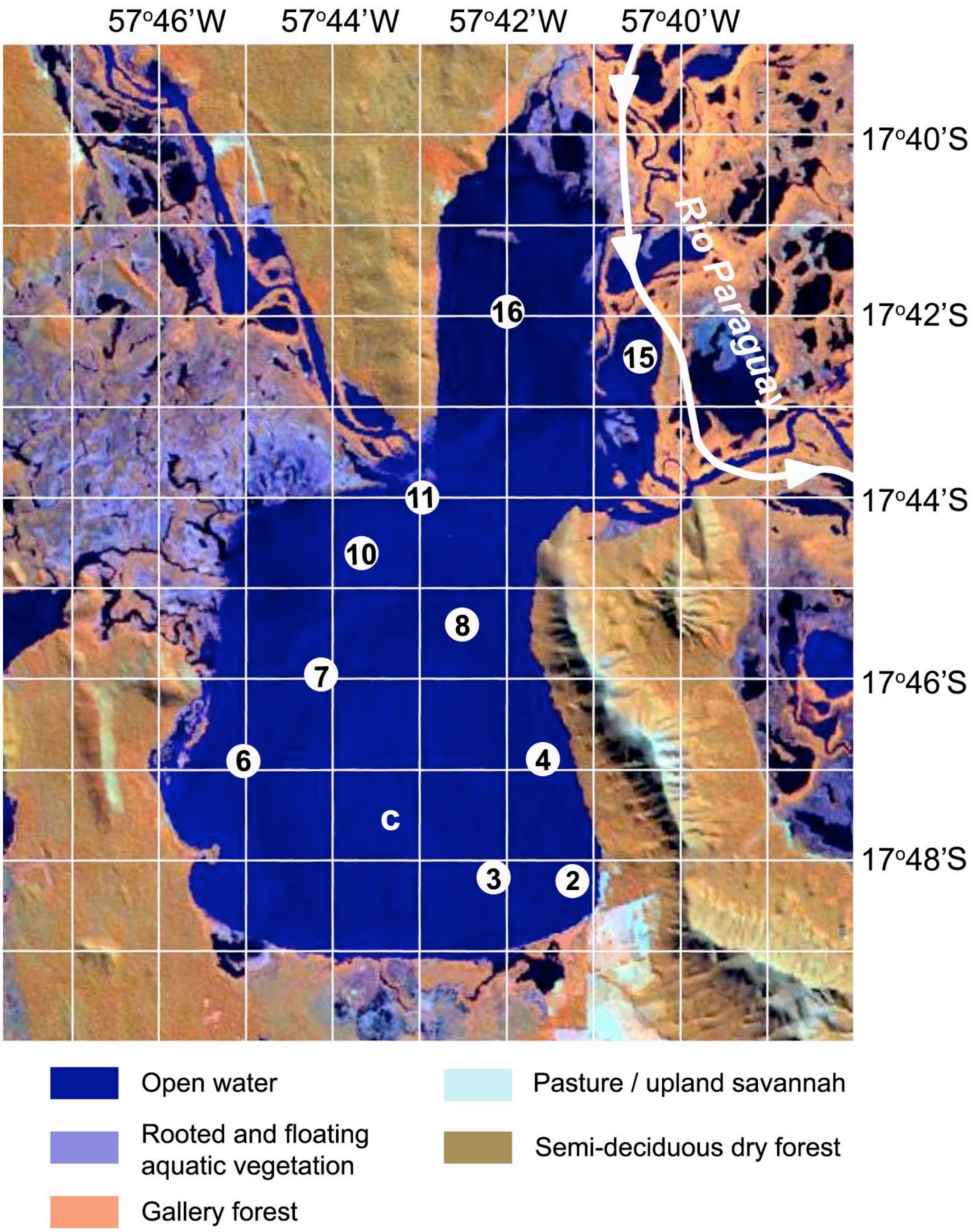

Fig. 4.2. Location of the 11 surface sediment samples analyzed for modern *Pediastrum*, including the core top (c), and their position relative to the approximate course of the river (white line), and rooted and floating aquatic vegetation.

Site	Depth (m)	Temp (°C)	Cond. (μS)	pH	PO_4 (mg/L)	NO_3/NO_2 (mg/L)	Secchi (m)
Lake Centre 1	5.10	26.4	74	7.99	<1	<1	1.04
Lake Centre 2	5.82	25.6	68	7.99	1.5	<1	-----
Lake Centre 3	3.12	25.2	62	7.28	2	<1	1.13
Macrophyte 1	0.62	26.9	80	7.68	<1	<1	-----
Macrophyte 2	2.70	25.4	70	7.24	1	<1	-----
Macrophyte 3	3.05	25.8	63	7.14	2	<1	-----
River outflow	3.54	24.8	77	7.26	2	<1	1.04
River inflow	5.00	25.2	66	7.12	1.5	<1	1.33

Table. 4.1: Physical and chemical parameters of LLG measured in July 2006. Lake Centre sites were located in open water; Macrophyte sites were sampled within floating mats of aquatic vegetation (dominated by *Eichhornia* spp.); River samples were located in the inflow and outflow at the western and eastern extent of LLG, respectively.

stored in airtight plastic jars. Eight 500 mL water samples were also collected from three different lake environments (shallow, macrophyte-dominated lake margins; deep, open water; river inflow/outflow), and basic water chemistry and lake parameters were measured at each site (Table 4.1). Due to the remoteness of the field site and the lack of appropriate storage for water samples in a hot climate, nitrite/nitrate and phosphate concentrations were measured in the field using a Hach® field testing kit.

The attempt to collect living *Pediastrum* communities at these sites failed, possibly due to the season in which the fieldwork was conducted. At the time of sampling, lake levels were high, and algal concentrations are inversely correlated to river stage in the Rio Paraguay and associated lakes (De-Lamonica-Freire et al. 1996, de Oliveira and Calheiros 2000).

4.4.2. Chronology

The entire LLG age-model is based on 18 AMS ^{14}C dates analyzed by the NERC radiocarbon facility, East Kilbride, UK (Table 2.2); 16 of which were obtained from well-preserved terrestrial plant macrofossils and two from sediment. The Holocene section of the core is constrained by five dates, including those obtained from bulk sediments. AMS ^{14}C ages (± 2σ) were calibrated using the

"Fairbanks0107" calibration curve (Fairbanks et al. 2005). The age-depth relationship was analyzed using mixed-effect regression, as described by Heegaard et al. (2005), and the age of each sample was calculated from a cubic spline fitted through the calibrated radiocarbon dates (Fig. 4.3).

4.4.3. Laboratory

The uppermost 2 m of core, representing the Holocene, was sampled for 1 cm^3 of sediment at approximately every 500-years, processed according to standard pollen preparation protocol (Fægri and Iversen 1989), and analyzed for *Pediastrum*. In addition, 1 cm^3 of sediment from the surface-water interface at 11 sites (including the core top) (Fig. 4.2) were analyzed for *Pediastrum* to further understanding of the species' modern distribution and deposition in the lake. The remaining nine samples, taken across river inflow/outflow or from very shallow water, contained negligible concentrations of *Pediastrum* coenobia and so were excluded from analysis. Modern and fossil *Pediastrum* identifications were made with reference to Komárek and Jankovská (2001), Pasztaleniec and Poniewozik (2004), and Zamaloa and Tell (2005). *Pediastrum* photographs (Fig. 4.6) were taken using a Canon® 350D SLR digital camera attached on a triocular Olympus® BX40 microscope using a 2.5 x Olympus® phototube.

4.4.4. Statistics and Presentation of Data

Pediastrum species' abundance was calculated as a proportion of the sum of all identified *Pediastrum* in each sample. Detrended correspondence analysis (DCA) was performed on the relative percent abundance of *Pediastrum* taxa in the eleven surface samples (Fig. 4.4), and the fossil *Pediastrum* assemblages (Fig. 4.8). Data were first square-root transformed to downweight the dominant taxa. *Pediastrum* taxa demonstrating high species scores for DCA axis 1 and commonly occurring in surface samples ($n \geq 5$) were regressed against water depth, the only lake parameter found to have varied across the sampled locations at LLG (Table 4.1), and the relative proportions were first arc-sine transformed to normalize the data (Crawley 2005) (Fig. 4.5). The fossil *Pediastrum* dataset was zoned using optimal splitting by

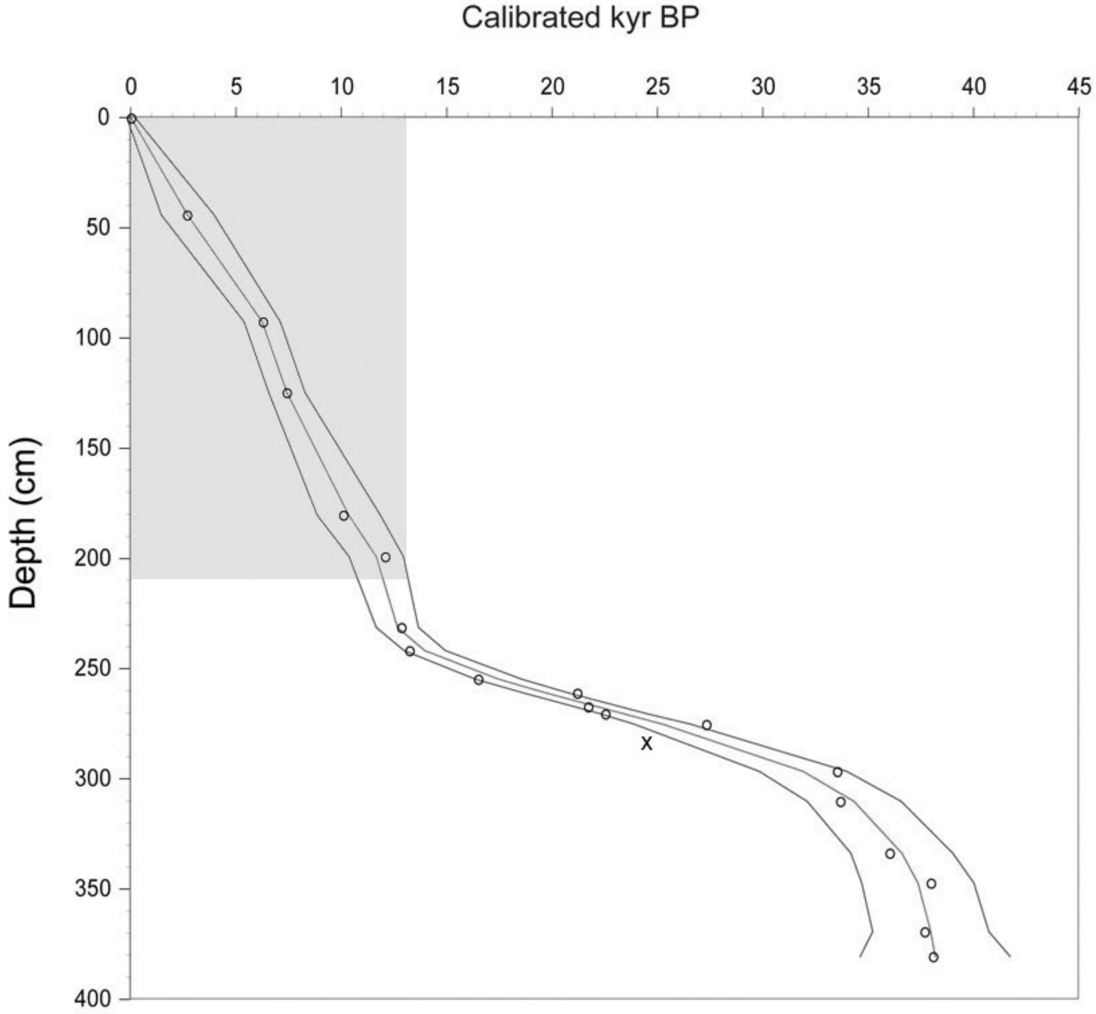

Fig. 4.3. The entire age-model for LLG based on 18 AMS ^{14}C dates and an assumed modern date for the uppermost 1 cm of sediment. The shaded area marks the section of core analyzed for this study. Black outer lines represent 2-sigma error, and ‘x’ denotes the one outlying date rejected from the age-model.

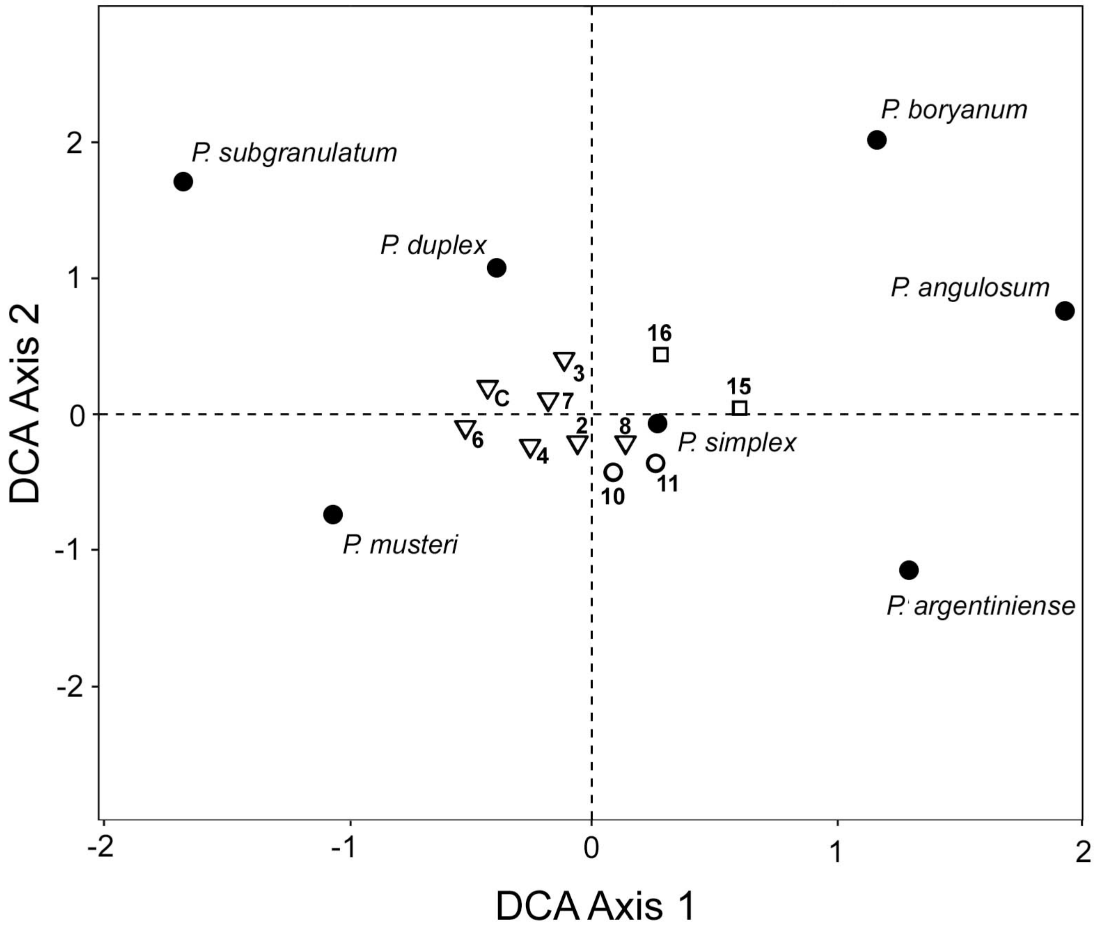

Fig. 4.4. Detrended Correspondence Analysis of relative percent abundance of *Pediastrum* taxa in LLG surface sediments. Symbols represent the location of the samples with the lake; inverted triangles = south basin, circles = central, squares = north basin (Fig. 4.2). Refer to Fig. 4.5 for the relative percent abundance of the taxa at each site.

information content, and three significant zonal boundaries were recognized using a broken-stick model (Bennett 1996). Percent abundance of fossil *Pediastrum* and key pollen types are presented in stratigraphic plots, constructed using C^2 (Juggins 2003).

4.5. Results

4.5.1. Modern *Pediastrum*

The percent abundance of *Pediastrum* taxa from each surface sample is plotted in Fig. 4.5. *P. simplex* (Fig. 4.6a) is the most abundant taxon in all samples

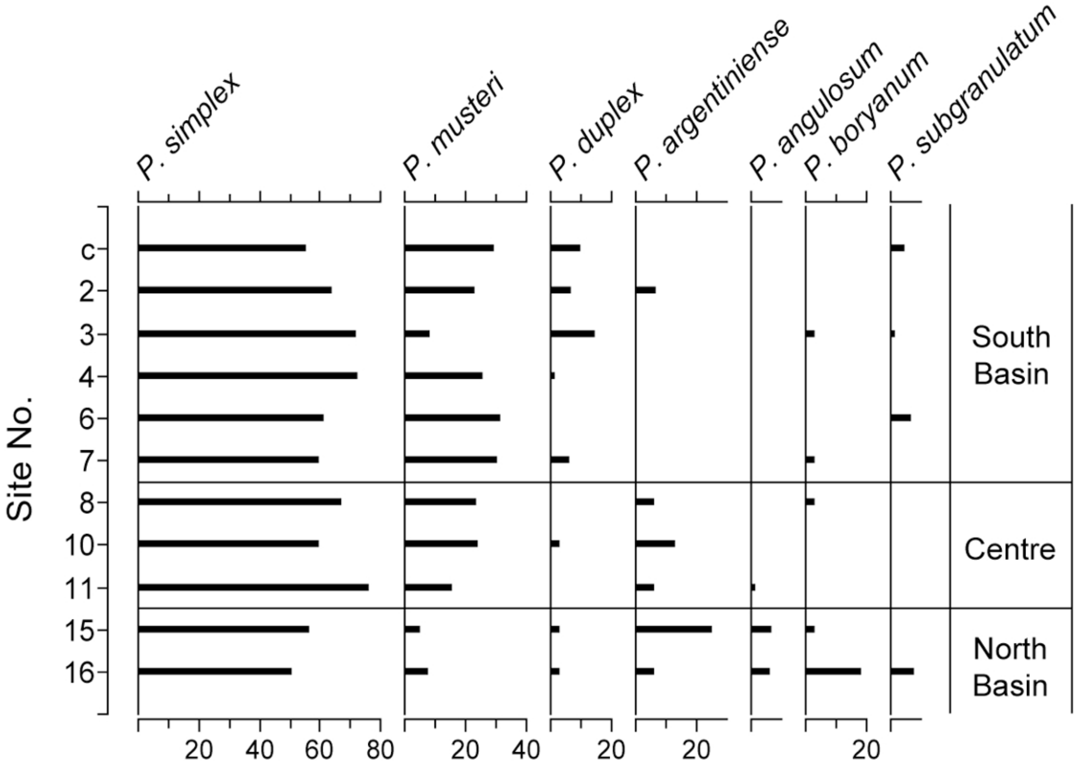

Fig. 4.5. Relative percent abundance of *Pediastrum* spp. in surface sediments at LLG. Samples are grouped by within-lake location.

(50 – 72%). Samples taken from the north basin and the centre of the lake (8, 10, 11, 15, and 16) are characterized by the presence *P. argentiniense* (Fig. 4.6b), a taxon also present in the south basin at site 2. With the exception of site 3, *P. musteri* (Fig. 4.6c) is most abundant in samples from the south basin and of lowest abundance at the three most northern sites (11, 15, and 16), which are also the only samples that contain *P. angulosum* (Fig. 4.6d). *P. duplex* (Fig. 4.6e) is present in low abundance at eight sites and occurs in highest abundance at site 3 (15%). *P. boryanum* (Fig. 6f) does not demonstrate a strong preference for any particular part of the lake and occurs in low abundance in samples 3, 7, 8, and 15, and it is the second most common taxon at site 16, reaching a value of 18%. *P. subgranulatum*, rarely occurring, does not demonstrate a habitat preference and occurs in low abundance in the core top and sites 3, 6 and 16.

The two taxa most commonly abundant (n ≥ 5) and that possess high species

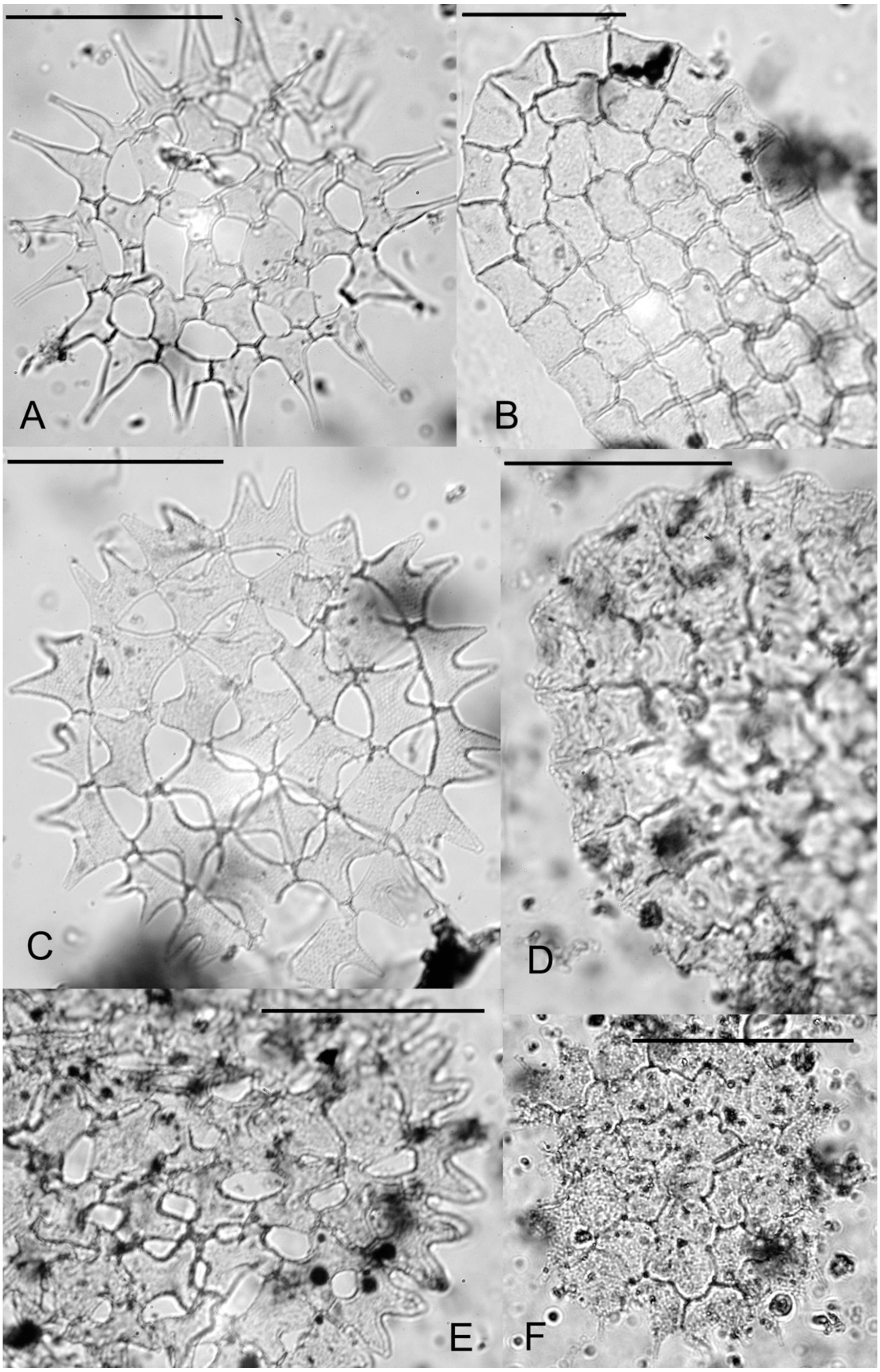

Fig. 4.6. Common *Pediastrum* species found in the surface and fossil sediments at LLG. (a) *P. simplex* (b) *P. argentiniense* (c) *P. musteri* (d) *P. angulosum* (e) *P. duplex* (f) *P. boryanum*. Scale bars represent 50 µm.

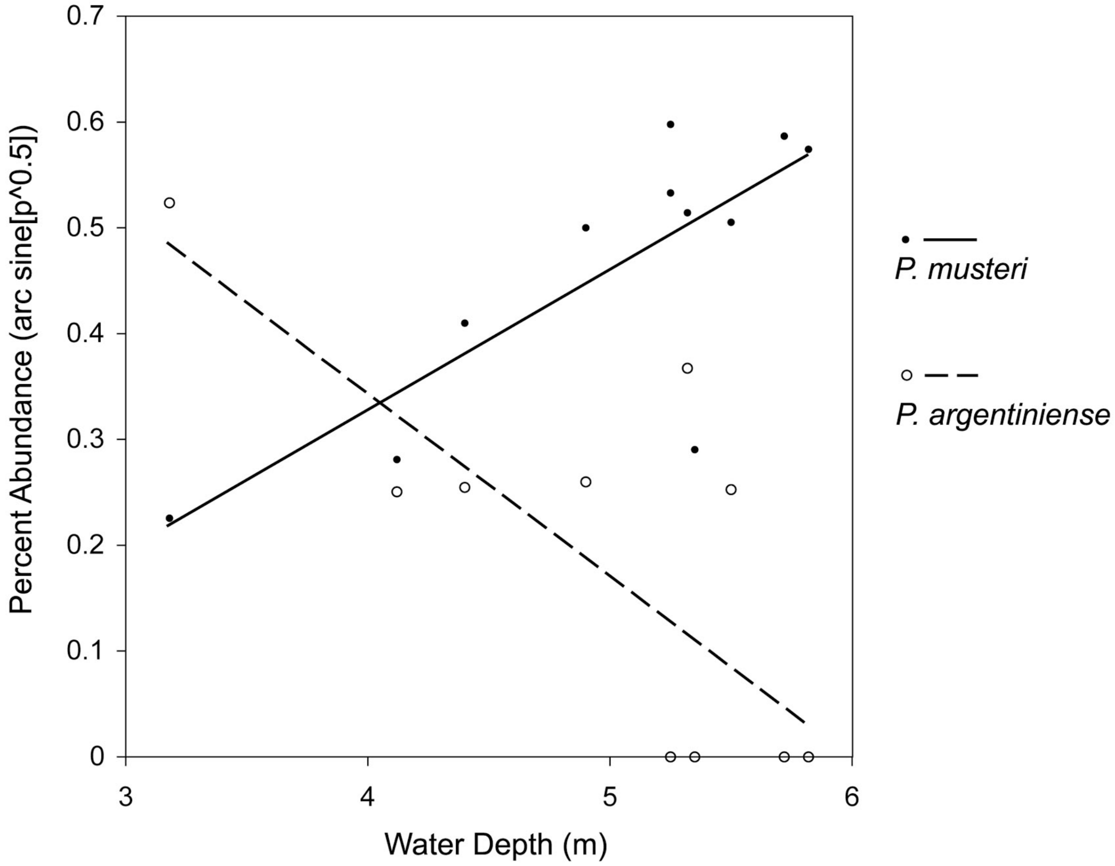

Fig. 4.7. Relative percent abundance of *P. musteri* and *P. argentiniense* in LLG surface samples regressed against lake depth (measured July 2006). *P. musteri*; $y = 9.5217x - 27.321$, $R^2 = 0.60$. *P. argentiniense*; $y = -7.5298x + 43.247$, $R^2 = 0.55$.

scores for DCA Axis 1 are *P. argentiniense* and *P. musteri* (Fig. 4.4). Both of these taxa demonstrate correlations with lake depth (Fig. 4.7). The abundance of *P. musteri* increases with water depth ($R^2 = 0.60$), whereas *P. argentiniense*, exhibits a negative correlation ($R^2 = 0.55$), suggesting the variance explained by DCA Axis 1 (33%) is largely influenced by water depth. *P. angulosum* and *P. boryanum*, though occurring in only three and four of the modern samples, respectively, also show high positive species scores for Axis 1.

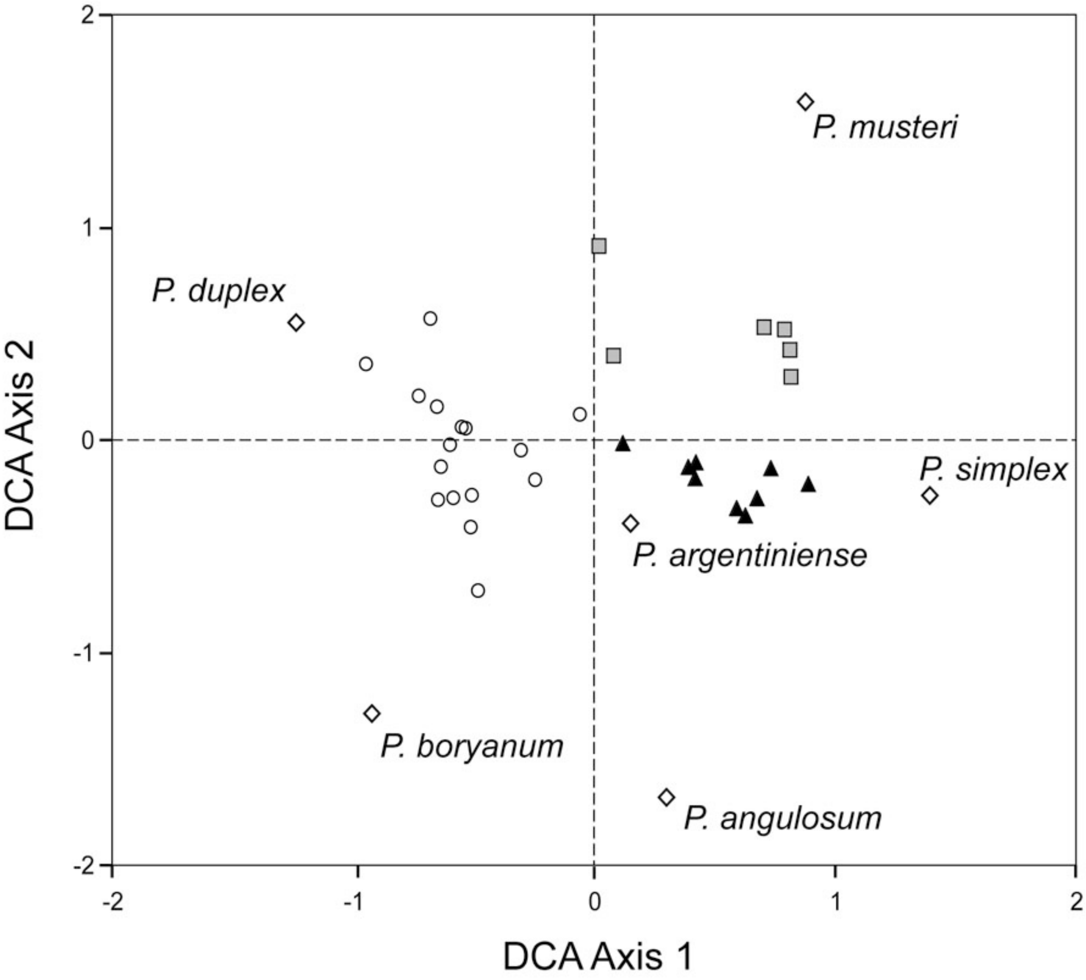

Fig. 4.8. Detrended Correspondence Analysis of relative percent abundance of fossil *Pediastrum* assemblages. Symbols refer to the stratigraphic position of the samples. Triangles = 12 to 9.8 ka BP; circles = 9.8 to 3.0 ka BP; squares = 3.0 ka BP to present.

4.5.2. Fossil *Pediastrum*

PED-I: 12.0 to 9.8 ka BP

The *Pediastrum* assemblages of this zone, often poorly preserved, are dominated by *P. simplex* and *P. argentiniense*, reaching maximum values of 90% and 43%, respectively. *P. musteri,* common in the deep, south basin, is also present, though in low abundances. *P. boryanum* and *P. angulosum* comprise a low proportion of the samples in this zone, as does *P. duplex*, with the exception of the sample at 11.7 ka BP, where it represents 35% of the assemblage.

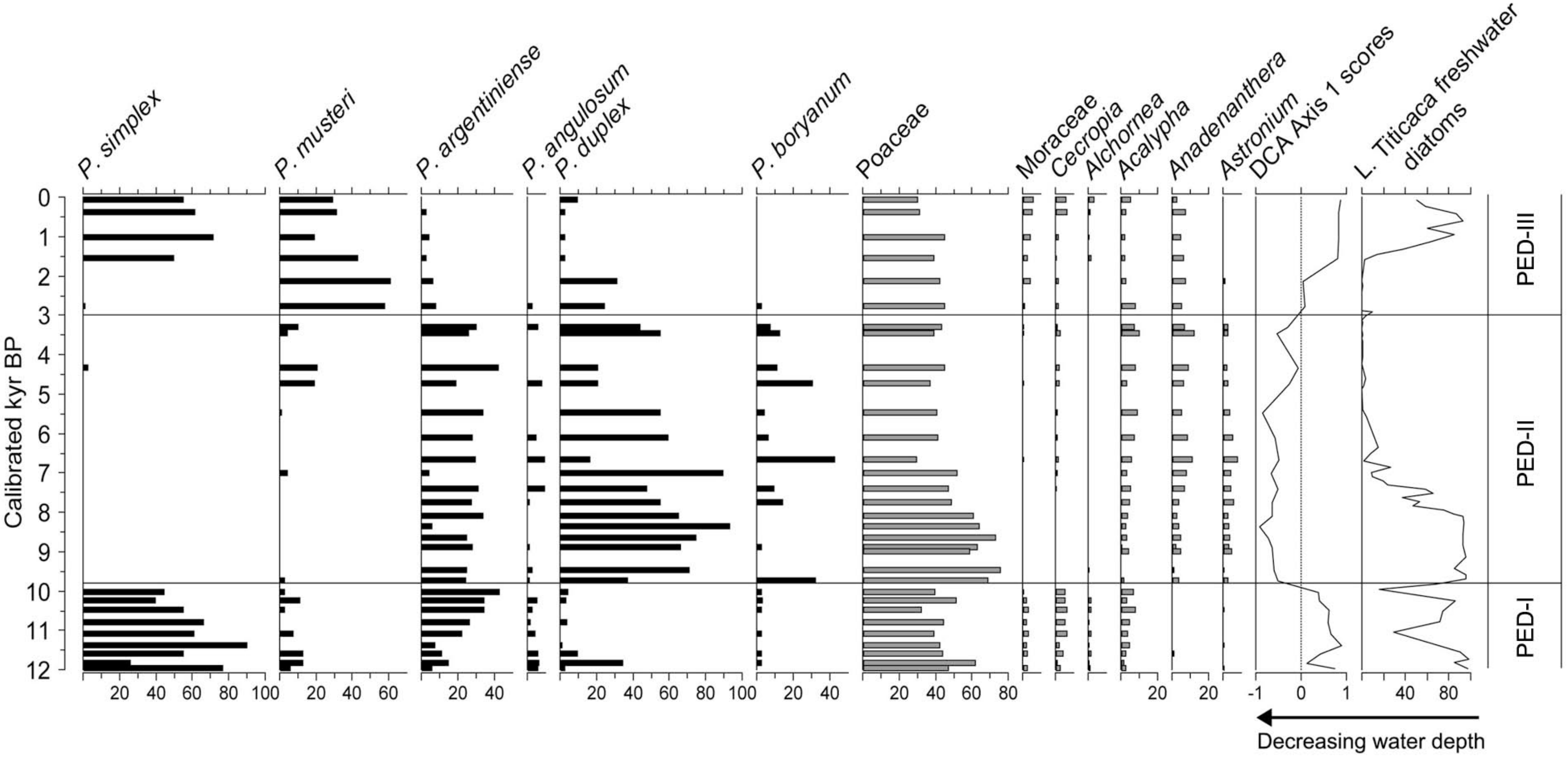

Fig. 4.9. Relative percent abundance of *Pediastrum spp*. calculated as a percentage of all identified *Pediastrum* (black bars) and dominant pollen types, calculated as a percentage of the sum of all terrestrial plant taxa (grey bars). Also shown are diatom data from Lake Titicaca. Samples are plotted against calibrated kyr BP.

PED-II: 9.8 to 3.0 ka BP

P. duplex is the dominant taxon in this zone. Also abundant are *P. argentiniense* and *P. angulosum*, taxa characteristic of the north basin in the modern assemblages. *P. musteri*, the taxon demonstrating preference for deeper water in the modern assemblages is rare. *P. simplex* also declines and it is absent in all but one sample. The abundance of *P. boryanum* varies greatly in this zone; it is absent in five samples and reaches a maximum 43% at 6.4 ka BP.

PED-III: 3.0 ka BP to present

The *Pediastrum* assemblages of PED-III are dominated by *P. musteri* and *P. simplex*. *P. musteri* abundances are highest at 1.9 ka BP (60%) and decrease to 30% at the top of the zone. Conversely, *P. simplex* is rare in the lower third of the zone, but comprises 50 – 70 % of the assemblages from 1.4 ka BP onward. In this zone, *P. argentiniense* and *P. duplex* decline in abundance, and *P. angulosum* nearly disappears from the record. Unlike the zonal boundary at 9.8 ka BP, the transition between mid- and late Holocene *Pediastrum* assemblages is gradual, as first shown by the rise of *P. musteri* at 4.4 ka BP, followed by the steady decline of *P. argentiniense* beginning at 2.9 ka. Finally, with the arrival of *P. simplex* at 1.4 ka BP, the fossil assemblages become most similar to the modern *Pediastrum* community at LLG.

4.6. Discussion

4.6.1. Interpretation of the *Pediastrum* signal

Despite a low sample size, the analysis of modern sediments at LLG highlights *P. musteri*, *P. argentiniense*, and *P. angulosum* as potential indicators for past lake level fluctuations. *P. musteri* is demonstrated to prefer the larger, deeper south basin at LLG, and although this taxon is little reported in palaeoecological studies, it has been shown to inhabit large, clear lakes in Greece (Komárek and Jankovská 2001). At LLG, *P. argentiniense* demonstrates a strong preference the shallower, macrophyte-influenced north basin, and although this species has not been previously reported from fossil sediments, our results are consistent with modern studies from tropical regions of the Americas that indicate this taxon is often associated with aquatic vegetation (Komárek and Jankovská 2001). Although *P. angulosum* is found in low abundance in the modern and fossil assemblages, this taxon may be a reliable indicator of very low water levels because it is restricted to the shallowest part of LLG. This finding is also corroborated by previous studies demonstrating that *P. angulosum* is found only in small water bodies and swamps, and mainly among aquatic plants (Komárek and Jankovská 2001).

P. simplex, *P. duplex* and *P. boryanum* are three species abundant in the fossil assemblages at LLG, but our limited modern study does not shed light on the environmental variable(s) controlling the distribution of these types. *P. simplex* is the most abundant taxon in the modern samples at LLG, reported to be found in relatively deep water (Komárek and Jankovská 2001), but the abundance of *P. simplex* does not vary with lake depth at LLG. It may be that the range of measured depths (3 – 6 m) is too narrow to demonstrate any response in *P. simplex* abundance, and this taxon is only absent from very shallow water.

P. duplex dominates the assemblages in PED-II, but again, the modern study at LLG did not elucidate the key environmental variable influencing the abundance and distribution of this taxon. *Pediastrum* taxa were not resolved to subspecies level due to the lack of reference material, and the fine detail required for subspecies identification is often lost in the fossil specimens. However, the cell walls of many of the *P. duplex* coenobia in this zone are coarsely sculptured, consistent with the descriptions of *P. duplex* var. *rugulosum*. Komárek and Jankovská (2001) report this subspecies often associated with aquatic macrophytes, the occurrence of which in PED-II would be consistent with the high abundance of macrophyte-associated taxa, *P. argentiniense* and *P. angulosum*. However, regardless of the subspecies that dominates PED-II, total *P. duplex* is of considerably higher abundance in the fossil record than the maximum 15% it reaches in the modern dataset, indicating the range of modern environments sampled did not include the optimal conditions for its growth.

P. boryanum was also not identified to a higher taxonomic level although there are nine described subspecies of *P. boryanum,* particularly because the relatively small coenobia of this taxon are highly susceptible to degradation, and the subspecies are often misidentified (Komárek and Jankovská 2001). However, the majority of the coenobia match the descriptions for *P. boryanum* var. *boryanum* and *P. boryanum* var. *brevicorne*. *P. boryanum* is reported to be cosmopolitan and a generalist, thus a poor indicator of past environmental conditions (Komárek and Jankovská 2001). However, in the DCA of modern assemblages, *P. boryanum* obtains a high positive score for Axis 1 (Fig. 4.4), suggesting it may be more abundant in shallow water, consistent with its co-occurrence with macrophyte-associated taxa *P. argentiniense* and *P. angulosum* in PED-II. However, this interpretation should be viewed with caution because the DCA axis 1 scores are likely influenced by site 16, where this taxon achieves 18% abundance.

4.6.2. Holocene lake level changes at LLG

Drawing on the results from the modern study, the abundance of *P. argentiniense* and *P. angulosum*, and the low relative proportions of *P. musteri* from 9.8 to 3.0 ka BP implies that LLG was most shallow and swampy in the mid-Holocene. The high proportion of macrophyte-associated taxa suggests that shallow lake levels allowed for aquatic vegetation to encroach into the south basin. The Rio Paraguay and associated lakes, including LLG, are hydrologically connected to the Pantanal floodplains (Hamilton 2002). Heightened river stage and rising lake levels result from the slow draining of monsoon precipitation from the 140,000 km^2 catchment of the Pantanal basin, thus the *Pediastrum*-inferred lake level decline at LLG is not just indicative of decreased precipitation, but also a regional pattern of climate change.

Though at present the interpretation of the *Pediastrum* dataset is tentative, the inferred lake level fluctuations are coincident with changes in indicator taxa in the pollen record (Fig. 4.8). The hills surrounding LLG were continuously covered by closed-canopy dry forest during the Holocene, but changes in the relative abundance of key pollen types are indicative of arid conditions in the early to mid-Holocene (Chapter 2). Moraceae, a key indicator of moisture-dependent vegetation communities (Mayle et al. 2000, Gosling et al. 2008), declines in this zone. Percent abundance of *Cecropia* and *Alchornea* pollen also decreases in the mid-Holocene, species of which are widely occurring, but are common along lake and river courses in the Pantanal (Prance and Schaller 1982, Willink et al. 2000, Damasceno-Junior 2005) and their decline is suggestive of a reduction in inundated habitat. Arid conditions are also inferred by increasing abundance of *Astronium fraxinifolium*, a species characteristic of drier savannah and SDTF (Jardim et al. 2003).

The *Pediastrum*-inferred lowering of lake levels in the mid-Holocene and the decline in moisture-dependent vegetation are corroborated by widespread evidence of a significant reduction in precipitation in the early to mid-Holocene in tropical South America (review by Mayle and Power 2008). The timing of this event varies latitudinally, where the onset of aridity occurs earliest at more northerly sites and progresses southward, but generally, this event is centred on 8.0 to 4.0 ka BP. Evidence includes peak dust concentrations and lowered snow accumulation in the Sajama ice cap (Thompson et al. 1998), increased erosion in the Bolivian Chaco (May et al. 2008), and diatom- and geochemically-inferred lake level lowering on the Andean plateau (Seltzer et al. 2000, Baker et al. 2001, Tapia et al. 2003). At Lake Titicaca, lake levels were as much as 100 m lower than present from 6.0 to 5.0 ka BP (Baker et al. 2001), their lowest stand over the past 25,000 yrs. Plant community change occurred at ecotonal regions, such as the replacement of forest with savannah in eastern Brazil (Absy et al. 1991, Sifeddine et al. 2001). Located 610 km northwest of LLG, quantitative climatic reconstructions from Laguna Bella Vista indicates that mean annual precipitation may have declined as much as 500 mm in the mid-Holocene (Burbridge et al. 2004, Punyasena et al. 2008).

Also reflected in the *Pediastrum*-inferred lake level reconstruction at LLG is the incremental nature of the late Holocene increase in precipitation, consistent with rising precipitation in the late Holocene demonstrated in records from the southern hemisphere tropics of South America (Mayle et al. 2000, Baker et al. 2001, Cruz et al. 2005). *P. musteri* begins to rise at 4.4 ka BP, coincident with an initial decrease in the macrophyte-associated taxon *P. argentiniense,* the abundance of which declines further to reach lowest levels at 3.0 ka BP, and remains low until present. With the appearance of *P. simplex* at 1.4 ka BP the fossil assemblages resemble the modern *Pediastrum* communities at LLG, reflective of deeply flooded conditions.

Similarly, at Lake Titicaca, the shift in benthic and salinity-tolerant to planktonic diatoms begins at 4.5 ka BP, and lake level did not reach modern levels until around 2.0 – 1.5 ka BP (Baker et al. 2001, Tapia et al. 2003). The southern rainforest boundary of Amazonia expanded southwardly in late Holocene, reaching 120 km and 30 km north of its current position, 2000 and 700 years BP, respectively (Mayle et al. 2000, Burbridge et al. 2004). Furthermore, the inferred lake level changes at LLG are consistent with strengthening of the South American southern hemisphere monsoon through the late Holocene to present, hypothesized to have been forced by increasing (austral) summer insolation due to the precession cycle (Baker et al. 2001, Cruz et al. 2005).

4.7. Conclusions

Despite a limited modern *Pediastrum* dataset and the narrow environmental range over which it was sampled, *P. musteri*, *P. argentiniense*, and *P. angulosum* are highlighted as possible indicator taxa for lake level change in lowland tropical lakes. The Holocene lake level changes inferred from the fossil *Pediastrum* assemblages at LLG correspond with the pattern of changing moisture availability previously demonstrated by pollen analysis at this site, and the Holocene climatic trends widely reported from the southern hemisphere tropics of South America.

Though a pilot study, this study demonstrates the unexplored potential of fossil *Pediastrum* as a proxy for lake level change in tropical lakes. In tropical South America, there are few reconstructions relating to past moisture availability, and owing to the scarcity of such reconstructions from the lowlands, vegetation reconstructions from these regions have relied heavily on Andean palaeoclimatic records. A key advantage of *Pediastrum* as a proxy is that can be analyzed alongside fossil pollen, therefore varying precipitation inferred through changing lake levels could help to disentangle the confounding effects of precipitation, temperature, and atmospheric CO_2 concentrations in the interpretation of tropical pollen diagrams.

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V. General Discussion

The journal-style chapters presented here focus on specific research questions, but in its totality, this thesis has substantially contributed to the overall understanding of palaeoecology and palaeoclimatology of tropical lowland South America. Examined in detail below, the contribution of this thesis can be categorized into three broad research themes: (i) palaeoclimatology; (ii) biogeography and ecosystem change; and (iii) proxy development. Finally, I discuss the further implications of this research and the full potential of Laguna La Gaiba as an archive of past environmental change.

5.1. Palaeoclimatology

5.1.1. Decoupled glacial precipitation regime of the lowland and Andean tropics

One of the debates central to tropical South American palaeoclimate is whether the lowlands experienced aridity during the last glacial period. Well-dated and robust archives in southern hemisphere Andes (Baker et al. 2001a,b, Fritz et al. 2004, Hillyer et al. 2008) demonstrate high (similar-to-modern) moisture availability during the last glacial maximum (LGM, centred on 21.0 ka BP), a trend attributed to the strengthening of the northeast trades due to the steepened thermal gradient in the northern hemisphere Atlantic, thereby increasing advected moisture from the Amazon basin into the Andes despite overall cooling (Baker et al. 2001b, Hillyer et al. 2008). By extension, it is therefore argued that Amazonia, the current source of Andean moisture, must have experienced high precipitation during the LGM. Evidence in favour of a 'wet LGM' precipitation levels in the lowlands includes; closed-canopy forest in central, equatorial Amazonia, argued to reflect a cool, moist climate (Colinvaux et al. 1996, Colinvaux et al. 2000), and travertine growth, indicative of flowing water, in the currently moisture-deficient Caatinga region of Brazil (Auler et al. 2004, Wang et al. 2004, 2007) (Fig. 5.1).

Furthermore, the steepened contrast between land and sea temperatures during periods of higher summer insolation due to the precession cycle are hypothesized to increase the strength of the South American summer monsoon (Baker et al. 2001a). That precessional-forcing is a dominant influence over the precipitation regime of tropical South America is backed by palaeoclimate modelling studies (Clement et al. 2004), demonstrating that regional hydrological change in the tropics is more sensitive to the precessional cycle than changes in boundary conditions over glacial-interglacial cycles (CO_2 concentrations, ice volume, temperature). Empirically, precessional-forcing of tropical climate has been demonstrated in palaeoclimate and vegetation reconstructions from Andean (Hooghiemstra and Melice 1993, Baker et al. 2001b, Fritz et al. 2004) and lowland regions (Auler et al. 2004, Bush et al. 2004, Wang et al. 2007).

In the southern hemisphere, a precessional 'high' during the LGM (centred at 21 cal. ka BP) is also hypothesized to have been the cause of increased precipitation over the Bolivian Altiplano (Baker et al. 2001a,b, Fritz et al. 2004, 2007) and in coastal Brazil (Figs. 5.1, 5.2). Therefore, it follows that the Pantanal basin and adjacent Brazilian highlands, also located in the southern hemisphere should have experienced similar-to-present precipitation levels during the LGM.

However, despite the climatological argument in favour of a wet LGM, the data presented here indicate the Pantanal experienced drier-than-present conditions during the last glacial period and across the glacial-Holocene transition (45.0 to 12.2 ka BP). Also, there is little variation among glacial assemblages at the LGM (precessional 'high') compared to those from a precessional 'low' between 35 – 30 cal. ka BP (Fig. 5.2), indicating that precessional-forcing is not a strong influence on the climate of this region. This study corroborates previous vegetation reconstructions from ecotonal regions that indicate glacial-aged savannah occupied regions now covered by rainforest (van der Hammen and Absy 1994, Mayle et al. 2000, Burbridge et al. 2004), as well as geomorphological evidence of past aeolian activity in the Pantanal (Assine and Soares 2004), also demonstrative of aridity in the

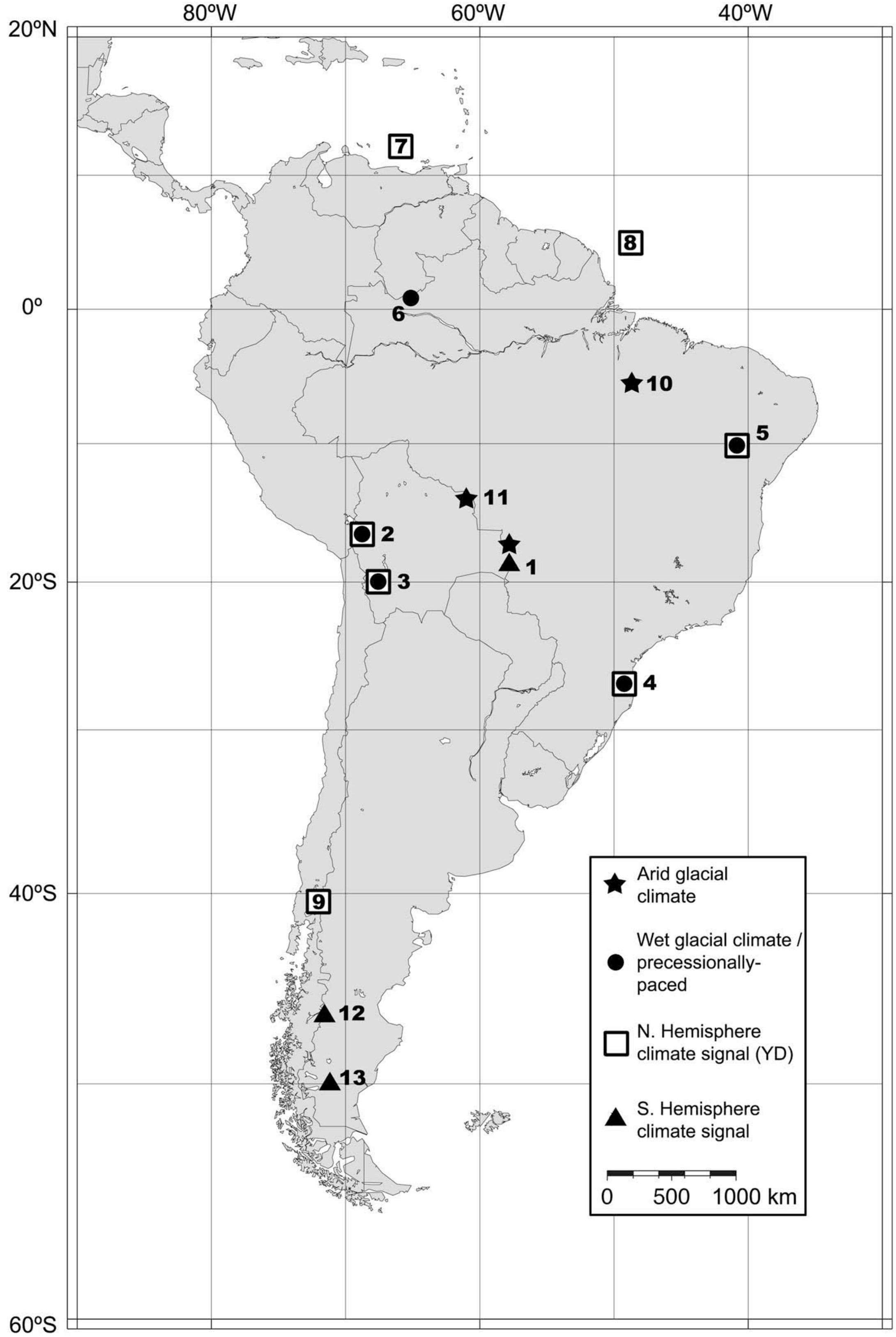

Fig. 5.1. See following page for caption.

Fig. 5.1. (previous page) Map of South America showing position of palaeoenvironmental archives discussed in the text. See below for site names and references. Symbols refer to precipitation regime during the last glacial period (stars = arid; circles = wet), and the hemisphere reflected in the pattern of deglaciation across the glacial-Holocene transition(northern hemisphere = square; southern hemisphere = triangle) (see inset).

1. **Laguna La Gaiba** (this study)

2. **Lake Titicaca** (Baker et al. 2001b, Fritz et al. 2007)

3. **Salar de Uyuni** (Baker et al. 2001a, Fritz et al. 2004)

4. **Botuverá Cave** (Wang et al. 2004, 2007, Cruz et al. 2005)

5. **Salvador travertines and speleothems** (Auler et al. 2004, Wang et al. 2004)

6. **Lake Pata** and the **Hill of six lakes** (Colinvaux et al. 1996, Bush et al. 2004)

7. **Cariaco Basin** ODP 1002 (Peterson et al. 2000, Hughen et al. 2004)

8. **Amazon Fan** ODP 942 (Maslin and Burns 2000)

9. **Chilean Lake District** (Moreno et al. 2001)

10. **Carajas** (Absy et al. 1991, van der Hammen and Absy 1994)

11. **Laguna Chaplin** (Mayle et al. 2000, Burbridge et al. 2004)

12. **North Patagonian ice field** (McCulloch et al. 2000, Sugden et al. 2005, Turner et al. 2005)

13. **South Patagonian ice field** (McCulloch et al. 2000, Sugden et al. 2005)

last glacial period.

However, compared to previous palaeoecological studies from lacustrine archives, the record from LLG is unique; changing hydrological conditions in the Pantanal are reflective of a broad, regional signal, representing >140,000 km^2 in the continental lowlands of the southern hemisphere tropics of South America (SHTSA). Therefore, this study presents strong evidence the precipitation regime of the continental interior of the southern hemisphere lowlands was decoupled from the climate of Andean regions during the last glacial period. Furthermore, the coherent pattern of 'dry' glacial vs 'wet' interglacial climates among sites located in the continental interior of lowland SHTSA indicates the climate of this region is dominantly influenced by boundary conditions imposed by glacial-interglacial cycles of the higher latitudes. However, whether this pattern extends into southern Amazonia is still largely unknown due to the paucity of palaeoenvironmental records.

Palaeoclimate modelling studies have simulated decoupled Andean and lowland precipitation regimes for the LGM (Hostetler and Mix 1999, Vizy and Cook 2007). A possible mechanism for higher glacial precipitation Andean regions is an eastern Pacific moisture source, rather than precipitation derived from convective activity over the Amazon basin (Hostetler and Mix 1999, Mayle et al. 2004). However, it has also been demonstrated that Andean precipitation is dominantly controlled by the mechanism of moisture delivery to the Andes, not the availability of moisture over the Amazon basin *per se*. Anomalous easterly flow simulated to occur at the LGM increases advection of moisture up the eastern slope of the Andes, resulting in high precipitation on the Altiplano, despite simulated aridity in the Amazon basin (Vizy and Cook 2007). Critically, these modelling data agree with pattern of glacial climate inferred from palaeoclimate reconstructions, that glacial precipitation regime of tropical South America was spatially complex (Bush and Silman 2004), however frustratingly few data exist to adequately capture this complexity.

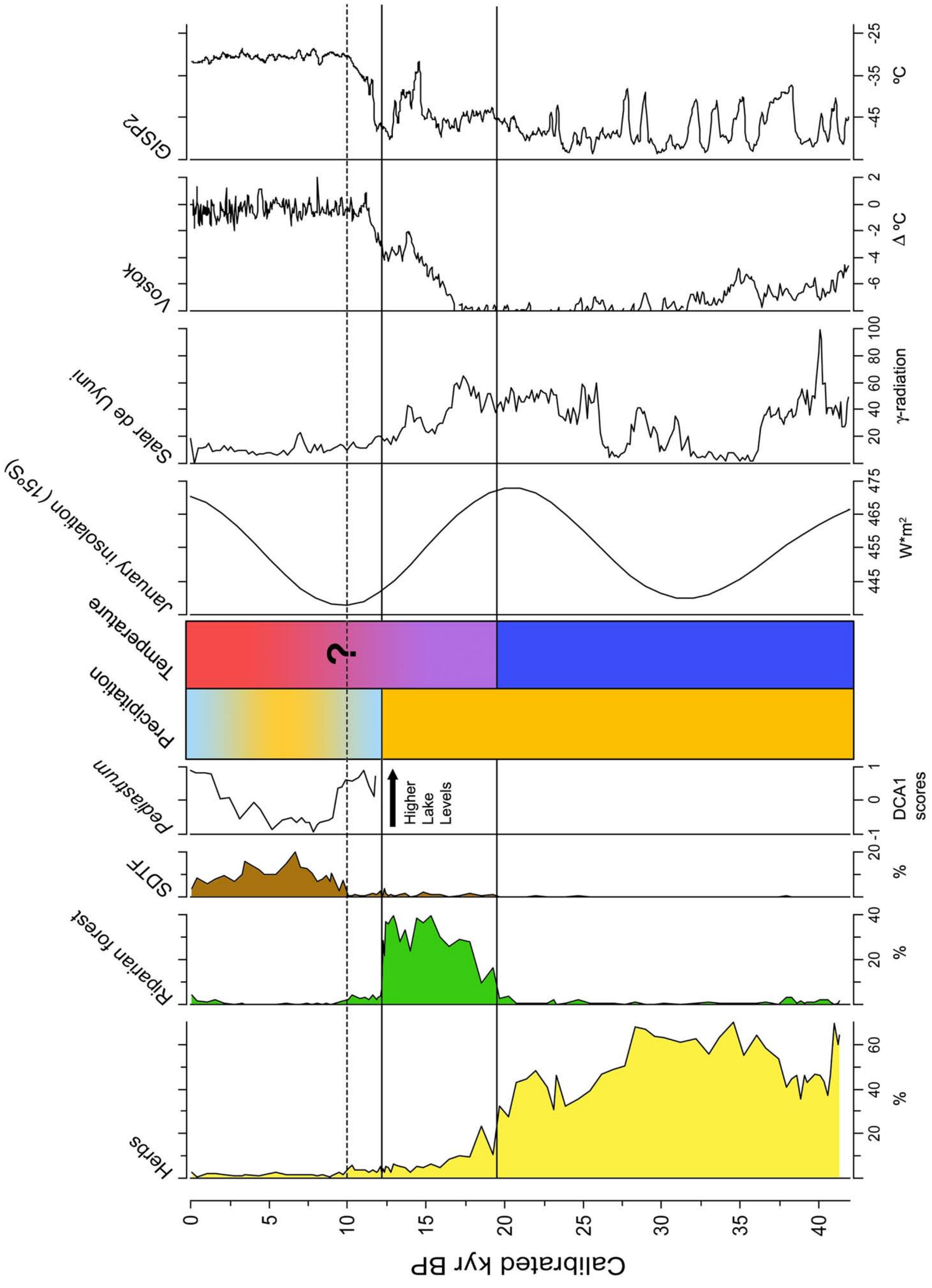

Fig. 5.2. Summary diagram plotted against cal. kyr BP. Percent abundance of three categories of vegetation (herbs without grasses, riparian forest, SDTF), relative Holocene lake levels inferred from *Pediastrum* DCA Axis 1 scores, and summarized temperature and precipitation inferred from changes in the pollen and *Pediastrum* data (coloured bars), presented on the left. Also shown are January (austral summer) insolation (Berger and Loutre 1991); Salar de Uyuni lake levels (Baker et al. 2001a); and temperature changes derived from the Vostok (Petit et al. 1999) and Greenland (GISP2) (Alley et al. 2000) ice cores.

5.1.2. Southern vs. Northern hemisphere climate forcing

Two climatic events mark the transition from glacial to interglacial climate in the Pantanal region. Temperatures rise at 19.5 ka BP, marking an early end to full glacial conditions in the southerly latitudes of the lowland tropics. This well-dated event provides unprecedented evidence of warming in lowland regions contemporaneous with early warming demonstrated in Andean temperature reconstructions (Seltzer et al. 2002, Hillyer et al. 2008). Warming in the South American tropics precedes deglaciation in the mid- to high-latitudes of the southern hemisphere by as much as 2.5 kyr, as initial stages of glacial retreat in the Patagonian ice fields and Magellan Strait occur at approximately 17.0 ka BP (McCulloch et al. 2000, Turner et al. 2005, Sugden et al. 2005).

Abrupt vegetation change at 12.2 ka BP marks the second climatic event of the glacial-Holocene transition, as LLG experiences higher flooding, reflective of increased precipitation in the Pantanal basin. Occurring in the middle of the YD chronozone, the timing of this event coincides with the final step of deglaciation in the mid- to high-latitudes of the southern hemisphere (McCulloch et al. 2000, Sugden et al. 2005), and the end of the Antarctic Cold Reversal (ACR, occurring 14.5 to 12.5 ka BP). This pattern of climate change at the Pleistocene-Holocene boundary is contrary to tropical Andean and coastal regions, where sub-millennial scale climate fluctuations characteristic of glacial-Holocene transition in the North Atlantic, such a precipitation anomaly during the YD chronozone, are found to occur (Baker et al. 2001a,b).

Although the timing of initial warming at LLG precedes that of the higher southern latitudes, the ‘two-stepped’ nature of deglaciation in the continental interior of SHTSA inferred from LLG mirrors the pattern of deglaciation in Patagonia (McCulloch et al. 2000, Sugden et al. 2005), the Magellan Straits (McCulloch et al. 2000), and warming in the Southern Ocean (Lamy et al. 2004). That this step-wise pattern of deglaciation occurs in the continental interior of SHTSA is suggestive of Antarctic climate forcing.

This finding is surprising given that high-resolution vegetation reconstructions from three lakes in the Chilean lake district (Moreno et al. 2001), argued to reflect YD-like climate fluctuations, have led some researchers to hypothesize that the influence of northern hemisphere climate forcing was as far-reaching as 40ºS in South America, lending support to proponents of synchronous climate change in the southern and northern hemispheres (Denton et al. 1999). However, this study demonstrates that not only are the southern tropical latitudes of continental South America out of phase with North Atlantic forcing, but the influence of southern hemisphere high latitude climate likely reached the southern tropics, much further north than previously recorded (i.e., Sugden et al. 2005). Critically, the reconstruction from LLG demonstrates not only asynchroneity of southern *versus* northern hemisphere climate change in tropical regions, but also between high elevation and lowland regions at similar latitudes, suggesting a spatial complexity to interhemispheric climate change hitherto unobserved.

5.1.3. The Holocene

Unlike the precipitation regime of the last glacial period and glacial-Holocene transition, Holocene climate change in Andean and lowland regions are broadly synchronous, exhibiting a common trend of aridity in the early to mid-Holocene. Although the timing of Holocene precipitation changes vary spatially in tropical South America (Mayle and Power 2008), they adhere to the overall trend of relatively high moisture availability in the early Holocene, followed by aridity in the early- to mid-Holocene, and a subsequent rise in precipitation from the late Holocene to present. Precipitation and lake level changes inferred at LLG corroborate this broad pattern of change, though the onset of aridity occurs earlier than most sites, beginning at 10.0 ka BP, and lasting until 3.0 ka BP.

The abundance of macrophyte-associated *Pediastrum* taxa in the early to mid-Holocene assemblages is higher than in any of the modern assemblages sampled from the surface-water interface at LLG, implying lake levels were possibly lower than in the range of depths measured for the modern study at LLG (3 – 6 m).

However, extrapolation of lake levels beyond the range of the modern 'calibration set' should be viewed with caution, especially given the low number of modern surface samples. Nonetheless, aquatic macrophytic vegetation likely dominated the south basin, suggestive of low lake levels.

Pediastrum-inferred lake levels, as well as the ratio of drought-tolerant to moisture-dependent pollen indicators, show a rise in precipitation from the mid-Holocene until present. LLG did not reach deeply flooded conditions until around 1.4 ka BP, a trend also demonstrated in the diatom-inferred reconstruction at Lake Titicaca (Baker et al. 2001b). This pattern of increasing wetness in the late Holocene has been attributed to the strengthening of the SASM, due to precessionally-forced variations in summer (austral) insolation (Baker et al. 2001b, Cruz et al. 2005, Mayle and Power 2008). The similar trend of late Holocene climate change at LLG suggests that although climate in the continental lowlands of SHTSA is paced by global glacial-interglacial cycles, precessionally-forced insolation has a secondary influence on the climate of this region.

5.2. Biogeography and Ecosystem change

5.2.1. The influence of temperature and precipitation on tropical vegetation

Debate over the glacial precipitation regime of lowland tropical South America has been greatly influenced by assumptions concerning the key climatic drivers of tropical ecosystem change, that is, the relative roles of temperature and precipitation in shaping ecosystem change. Proponents for a 'wet' LGM in the Amazon basin argue that cooler temperatures, combined with near-modern levels of precipitation, would have formed the unique glacial-aged flora of Amazonia, incorporating elements of Andean forests (Colinvaux et al. 2000, Bush et al. 2004). On the other hand, proponents the rainforest refugia (Haffer 1969) and 'Pleistocene dry forest arc' (Prado and Gibbs 1993, Pennington et al. 2000) hypotheses have largely focused on the role of precipitation in shaping ecosystem change over glacial-interglacial cycles.

The record at LLG demonstrates that although it was arid during the last glacial period, the climatic parameter most likely limiting the growth of tropical forest in the Pantanal was temperature, particularly since atmospheric CO_2 concentrations were at glacial levels when tropical trees colonized the landscape (19.5 ka BP), thereby precluding rising CO_2 concentrations as a trigger for the expansion of forest (Cowling and Sykes 1999). That temperature is a key driver of vegetation change in the Pantanal is not surprising given the southerly position of this region. The Pantanal currently experiences a narrow range of annual temperatures (20 – 27ºC), but occasional winter polar advections can drop the temperature to 1 – 4ºC (Alho 2005). Combined with depressed glacial temperatures (average lowering of 5 – 6ºC in tropical South America (Stute et al. 1995)), and strengthened incursions of polar fronts, sub-zero winter temperatures would have prevented the establishment of frost-intolerant tropical forest.

Despite relatively warm, dry conditions from 19.5 to 12.2 ka BP, forest that is floristically similar to the modern Chiquitano SDTF remained absent until 10.0 ka BP, when *Anadenanthera* colonized the landscape. Although the discussion of what changing environmental parameter allowed for the development of floristically-modern SDTF is largely speculative, the pollen of the cold-adapted Andean genus *Podocarpus*, present in several lowland records prior to the early Holocene, suggests there may have been a final increase in temperature at 10.0 ka BP across the lowland tropics of South America. Warmer temperatures, combined with lower precipitation in the early Holocene, likely afforded optimal conditions for the expansion of Chiquitano SDTF (Colinvaux et al. 1996, Ledru et al. 2001, Burbridge et al. 2004).

Whereas rising temperatures allowed for the establishment of trees after the LGM, and likely encouraged the expansion of taxa characteristic of the modern Chiquitano flora, the vegetation changes associated with varying precipitation are more subtle. Abrupt and rapid flooding at 12.2 ka BP, indicative of rising precipitation in the Pantanal, caused widespread elimination of riparian forest in low-lying areas. However drastic the riparian community change, it is forced by habitat-loss due to flooding, not the inception of a climate unsuitable for these taxa. Rising precipitation has no effect on the early dry forest occupying bedrock slopes above the level of inundation.

Although lake level reconstructions from Lake Titicaca (Baker et al. 2001b) and quantitative pollen-inferred estimates of precipitation from Laguna Bella Vista (located 610 km northwest of LLG) (Burbridge et al. 2004, Punyasena et al. 2008) demonstrate that aridity in the mid-Holocene was severe, the reduction in precipitation did not induce ecosystem change at LLG. Instead, the relative abundance of key dry forest taxa varied in response to changing moisture availability, such as an increase in drought-tolerant *Astronium* and a decline in Moraceae abundance. Pollen richness, a proxy for biodiversity, was also influenced by mid-Holocene aridity, but closed-canopy SDTF was maintained throughout the Holocene.

Overall, the interpretation of glacial-interglacial ecosystem change at LLG has produced several key findings. (i) Climate was arid during the glacial period, but SDTF was absent because of low temperatures; (ii) precipitation rose at the Pleistocene-Holocene boundary, but this climatic transition affected only the riparian community through habitat-loss, having little impact on the composition of the *terra firme* forest; (iii) the mid-Holocene reduction in precipitation was likely substantial, but closed-canopy SDTF was maintained in the eastern Chiquitanía.

A critical result of this study is that in the southerly tropical latitudes, temperature has a greater influence than precipitation on ecosystem structure and composition, and both forested and unforested ecosystems occurred under conditions of lower precipitation. In particular, detractors of glacial aridity in Amazonia should be cautious in their interpretation of pollen diagrams (i.e., Colinvaux et al. 1996, Colinvaux et al. 2001, Bush et al. 2004), because the presence of closed-canopy forest is not indicative of the absence of aridity. The results from this study are corroborated by Punyasena et al. (2007), who demonstrate that temperature is the climatic parameter that most influences family-level abundance and richness in

Neotropical plant communities. In particular, richness and number of individuals in the Fabaceae, a dominant family in the Chiquitano SDTF, are shown to positively correlate with temperature (Punyasena et al. 2007).

5.2.2. The Chiquitanía-Pantanal region: A dynamic vegetation corridor

The Chiquitanía-Pantanal region occupies a climatically-sensitive ecotone at the intersection of humid, evergreen rainforest, Brazilian cerrado (savannahs), and dry Chaco scrub. Endemism is low among Pantanal plant communities, reflecting the inundation-tolerant, mesic, and xeric elements of the Pantanal vegetation complex, comprised of taxa from the surrounding biogeographic regions (Prance and Schaller 1982, Alho 2005). Inundation-tolerant riparian communities characteristic of Amazonian floodplains occupy river levées, the eastern edge of the Chiquitano SDTF blankets the steep-sided slopes of the Amolar hills, and seasonally-inundated savannahs, formations floristically similar to Brazilian cerrado, occupy the higher elevation plains in the eastern Pantanal.

Unsurprisingly, given the ecotonal position of the Pantanal, variations in the thermal and precipitation regimes, possibly combined with changing atmospheric CO_2 concentrations, resulted in the formation of distinctive plant communities over the past 45,000 years. Although each of the three main pollen zones is dominated by a broad vegetation class (herbs, riparian forest, SDTF) (Fig. 5.2), they are comprised of pollen types representative of taxa in the modern Chiquitano SDTF and Pantanal floras. After 19.5 ka BP, all the pollen types encountered in the modern assemblages (with the exception of *Anadenanthera*, arriving at 10.0 ka BP) are present in the fossil assemblages, though their relative abundance varies depending on zone. This suggests that all components of the Pantanal complex were present after 19.5 ka BP, although the dominant vegetation component at any given time was dependent on the prevailing environmental conditions. That the various plant communities of the Pantanal have rapidly retreated or expanded in response to changing climate and/or hydrological conditions demonstrates the Pantanal complex is highly dynamic and adaptable to change.

5.3. Proxy Development

The *Pediastrum* signal has too often been glossed over or ignored in palaeoecological studies, but here I demonstrate this genus of green alga could provide a useful tool for the reconstruction of past lake level change in the lowland tropics. A key advantage of *Pediastrum* analysis is that it can be applied in conjunction with pollen analysis, thus no additional sediment (a precious commodity in tropical palaeoecology) or laboratory preparation is required. Most importantly, however, the relationship between lake depth and *Pediastrum* assemblages allows the pollen analyst to disentangle an important climatic variable from the host of environmental parameters that shape tropical ecosystems, thereby shoring up the interpretation of pollen diagrams.

At present, the relative abundance of the *Pediastrum* species identified as potential indicator taxa cannot be used for quantitative reconstructions of lake level change because of the low sample size (11) and narrow geographical range of the modern *Pediastrum* study. However, given the robustness of the results based on this small sample size, this study merits additional research to take it beyond the pilot stage. Further analysis of the modern ecology of *Pediastrum* taxa in the Pantanal could potentially allow for quantitative estimates of the mid-Holocene lowstand in Laguna La Gaiba, and given the hydrological links between lake level in LLG and mean annual precipitation in the Pantanal basin and the adjacent western Brazilian highlands, past variations in lake level could be scaled-up to infer past precipitation over a large part of the continental interior of SHTSA.

These remarks may seem premature given that the modern study is comprised of 11 samples, but it is imperative that tropical palaeoecologists begin to develop new tools if we are to address any of the overwhelmingly broad themes in Neotropical palaeoecology and palaeoclimatology still largely unexplored, such as quantitative estimates of climate change for the validation of climate models; (in) stability of tropical ecosystems and their ability to adapt to changing environments;

the effects of climate change on community composition and biodiversity; and the ability and speed of plant migration in the event of environmental change.

5.4. Broader Implications and Future Work

The full potential of the palaeoenvironmental archive from Laguna La Gaiba is far from realized. Although the sedimentary record obtained for this research extended to ~ 45.0 ka BP, coring operations were halted after 6 m of sediments were extracted, not because the lake basement was reached, but the sediments were too stiff to core further with the available equipment. However, with appropriate coring equipment, several glacial-interglacial cycles might be reached.

The basin of the Pantanal wetlands is a graben created approximately ~ 2.5 million yrs BP by the final compression of the Andes. The course of the Rio Paraguay follows a N-S oriented fault on the western margin of the Pantanal (Assine and Soares 2004), pinned between steep-sided bedrock hills on the west, and a shallow, but uphill slope to the east. Therefore, it is unlikely the main channel of the river would have ever deviated greatly from its present course (Alho 2005) and the situation of LLG along the course of the Rio Paraguay makes it probable that a lake has long occupied the area. In addition, drilling operations in the 1960s indicate the half-kilometre of unconsolidated sediments that fill the Pantanal basin extends into the Pliocene-Pleistocene (Assine and Soares 2004), therefore it is not unfounded that an extended sedimentary record from LLG would contain several uninterrupted glacial-interglacial cycles.

Such a palaeoenvironmental archive, situated in the continental interior of South America between the extended and detailed archives of the Salar de Uyuni (170 ka BP) and Lake Titicaca (370 ka BP) (Fritz et al. 2004, 2007) in the high Andes, Botuverá Cave in coastal, subtropical Brazil (90 ka BP) (Wang et al. 2007), and the Cariaco Basin (90 ka BP) in the northern hemisphere tropics (Peterson et al. 2000), would be invaluable to further understanding of tropical palaeoclimate on large geographic and temporal scales, shedding light on topics such as; the pacing of orbital-scale tropical climate change in the continental interior SHTSA (precession *versus* eccentricity); (a)synchroneity of interhemispheric climate change; and spatial complexity of lowland *versus* high Andean, and terrestrial *versus* coastal climate systems during glacial and interglacial periods.

However, a full complement of palaeoenvironmental analyses has yet to be applied to the existing 45,000-yr record. Diatoms are currently being analyzed, and the expected lake-level reconstructions could bolster the results of the pilot *Pediastrum* study, as well as test the hypothesis, inferred from changes in the riparian vegetation, that LLG was seasonally-isolated from the Rio Paraguay prior to 12.2 ka BP. Macroscopic charcoal, also soon to be analyzed, will complement the precipitation signal inferred here from pollen analysis, and provide a clearer picture of the changing role of fire in the Pantanal SDTF and savannah ecosystems.

Furthermore, the Holocene reconstructions of precipitation has broader implications for the global carbon budget. The tripartite nature of the Holocene methane curve has been the focus of some interest (Ruddiman and Thomson 2001, Ruddiman et al. 2008). Methane concentrations rise steeply in the early Holocene, consistent with post-glacial initiation of peatland growth in the northern hemisphere (MacDonald et al. 2006), encouraged by latent heating of northern hemisphere land masses due to a precessionally-forced insolation maximum (Berger and Loutre 1991). Atmospheric methane concentrations decline in the mid-Holocene, again consistent with changes in northern hemisphere insolation, and possibly a reduction in peatlands due to post-glacial vegetation development. However, methane concentrations subsequently rise in the mid-Holocene, and maintain a steadily increasing trend, a pattern inconsistent with precessional-forcing, as well as the pattern of methane concentration change during several previous interglacials.

Ruddiman and Thomson (2001) argue that because of these inconsistencies, the rise in methane after 5000 yrs BP must be the result of human activity. The impact of early human agriculture on atmospheric gas concentrations, particularly

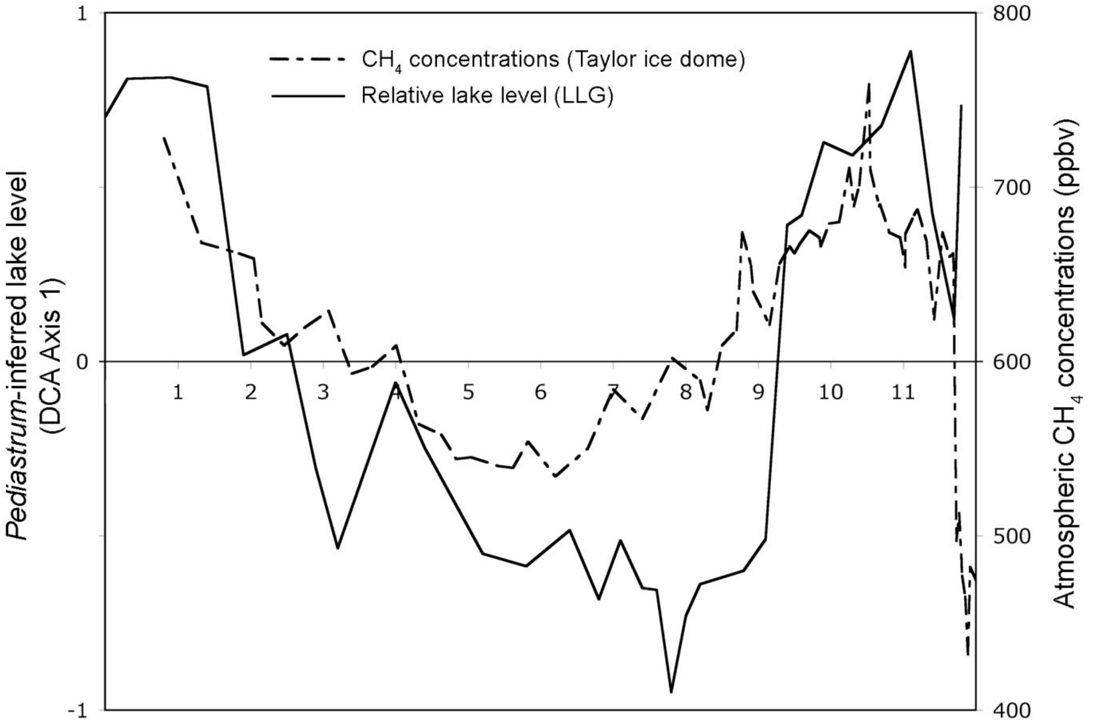

Fig. 5.3. Relative lake level change inferred from DCA Axis 1 scores of fossil *Pediastrum* assemblages at LLG and atmospheric methane concentrations obtained from the Taylor Dome C (Brook et al. 2000) throughout the Holocene, plotted against calibrated kyr BP.

rice-paddy cultivation in Asia, is argued to have been considerably greater than previously hypothesized (Ruddiman et al. 2008). Ruddiman (2003) goes on to suggest this period of human impact, defined by rising CO_2 and methane concentrations at 8000 and 5000 years BP, respectively, be termed the 'Anthropocene', to encompass the several millennia of intensive environmental alteration due to human activity.

However, the data presented in this thesis demonstrates that Holocene climate change in the Pantanal follows the coherent pattern of aridity demonstrated in palaeoclimatic reconstructions from sites across the Neotropics; rising precipitation in the early Holocene is followed by mid-Holocene aridity, and precipitation subsequently increases in the late Holocene to present. That the pattern of Holocene precipitation changes at LLG closely mirror the global atmospheric methane curve (Fig. 5.3) implies the contribution of southern hemisphere tropical wetlands to global methane concentrations might be underestimated. Detailed quantitative reconstructions of changing lake levels at LLG, scaled up to infer the extent of Pantanal inundation patterns over the Holocene, could offer clearer picture of the relative contribution tropical wetlands to Holocene methane concentrations, and whether the 'Anthropocene' boundary should be positioned at 8000 yrs BP as proposed by Ruddiman (2003).

Although the role of humans in shaping past environments at LLG is outside the scope of this thesis, petroglyphs on the bedrock shores of LLG (Mayle *pers. observation*) demonstrate that people have long inhabited the region, although little is known of the culture and society that created the artwork. Questions concerning the scale of pre-Columbian occupation in the region, and the impact of climate change and European settlement on human societies, are key concerns of South American archaeologists and palaeoecologists interested in determining the legacy of human impact in 'pristine' tropical environments. Variations in macroscopic charcoal record inconsistent with changing climate inferred from other proxies, as well as pollen analysis focusing on economically important plant taxa, such as *Zea mays* (maize), Cucurbitaceae (the gourd family), and *Anacardium* (cashews) (Denevan 2003), could further understanding of the role of humans in shaping past environmental change at LLG.

Put simply, there is incredible scope for further research on the sediment record at LLG. It has been a privilege to generate some of the first data from this site, described as a possible 'Cariaco basin of the southern hemisphere' (Hughen *pers. comm.*) in its importance to further understanding of tropical climate and ecosystem dynamics over glacial-interglacial timescales.

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VI. Conclusions

The original aims of the three journal-style research chapters are detailed below, followed by the key findings of each chapter. General conclusions of the entire thesis, and how this research contributes to the overall picture of South American tropical palaeoclimatology and palaeoecology are briefly presented after the conclusions of the focused research chapters.

Chapter 2 focused on the long-term changes in SDTF and Pantanal vegetation composition and diversity, and I aimed to determine the probable climatic drivers of these changes. A key goal of this research was to ascertain whether the Chiquitano SDTF was extant during the last glacial period in accordance with the ‘Pleistocene dry forest arc’ hypothesis. Key findings include:

- The Pantanal-Chiquitanía region experienced aridity during the last glacial period, but SDTF did not occupy the catchment, as predicted by the ‘Pleistocene dry forest arc’ hypothesis. Instead, colder temperatures limited the growth of tropical trees, and open, herbaceous vegetation dominated the landscape.
- The modern Chiquitano SDTF developed at 10.0 ka BP, demonstrated by the expansion of *Anadenanthera* and *Astronium*.
- The relative abundance of key SDTF taxa in the Chiquitano SDTF varied in response to the changing Holocene precipitation regime.
- Chiquitano plant diversity (pollen richness) also positively co-varied with Holocene precipitation changes, and rising pollen richness in the late Holocene implies the relatively high α-diversity of Chiquitano SDTF is of recent origin.

Chapter 3 focused in detail on the climate and vegetation changes across glacial-Holocene transition. In particular, I attempted to determine whether there is any evidence of a precipitation anomaly during the YD chronozone. Key findings include:

- Rising temperatures at 19.5 ka BP allow for the establishment of tropical riparian forest on the seasonally-inundated lake bed around LLG.
- The elimination of riparian forest around LLG at 12.2 ka BP occurs because of permanent flooding in the lake basin, reflecting rising precipitation in the Pantanal region and adjacent Brazilian highlands.
- There is no evidence of a precipitation anomaly associated with the Younger Dryas chronozone, but flooding of the basin at 12.2 ka BP occurs in the middle of the YD chronozone.

Chapter 4 reported on the results of a pilot study exploring the potential of *Pediastrum*, a genus of green algae, as a proxy for reconstructing lake levels in tropical regions. Results from the preliminary study indicate:

- *P. musteri*, *P. argentiniense*, and *P. angulosum* are possible indicator species a lake level change in Pantanal lakes.
- *Pediastrum*-inferred lake level changes at LLG are corroborated by precipitation changes demonstrated through pollen analysis (Chapter 2), and the widespread and coherent pattern of Holocene precipitation changes in the southern hemisphere tropics of South America (SHTSA).
- Further analysis of modern *Pediastrum* species' ecology in lowland tropical lakes may allow for quantitative estimates of past lake level changes.

The general conclusions of this thesis that furthered understanding of glacial-interglacial climate and ecosystem dynamics in tropical South America are as follows:

- In the continental interior of SHTSA, temperature change over glacial-interglacial cycles shapes ecosystem composition and structure, whereas changing precipitation influences the relative abundance of composite taxa in SDTF.
- The Pantanal-Chiquitania region high demonstrated a high degree of ecosystem dynamism from the last glacial period to present, reflective of its ecotonal position at the intersection of moisture-dependent evergreen forest, SDTF, Brazilian cerrados (savannah) and xeric Chaco scrub.
- The presence of closed-canopy forest in glacial assemblages is not necessarily indicative of high moisture availability, therefore tropical palaeoecologists should exercise caution in the inference of palaeoclimate from pollen data (i.e., pollen records from central Amazonia).
- The pattern and timing of climatic change across the glacial-Holocene transition reflects the stepped deglaciation of the mid- and high-latitudes of the southern hemisphere, implying an Antarctic climatic influence on the continental interior of the southern hemisphere tropics of South America (SHTSA).
- Orbital-scale climate change in the continental interior of the SHTSA is dominantly influenced by global glacial-interglacial cycles, although rising precipitation in the late Holocene is consistent with a precessionally-forced strengthening of the South American summer monsoon.

A. Appendix

A.1. Core correlation

Overlapping parallel cores were extracted from LLG in consecutive 1 m sections. Core 1a, measuring 5.6 m, is longer and the more complete of the two, having shorter gaps in the sequence, therefore pollen analysis was applied to this core. Core 1, measuring 4.8 m, was split along the long axis, and 1 cm 'half-moon' samples were sieved for datable material. The remaining 'archive half' of Core 1 was scanned using the Itrax® XRF core scanner.

The stratigraphic position of the material obtained for radiocarbon dating and the geochemical data from the XRF scan (Core 1) had to be calibrated to 'Core 1a' depths to compare the geochemical data to the results of pollen analysis, as well as to plot the pollen data on a chronological scale. This was achieved through 'wiggle-matching' peaks and troughs of magnetic susceptibility curves obtained through whole-core logging using a loop sensor. Magnetic susceptibility data points near section breaks were removed to remove the 'end effects' (Nowaczyk 2001) before the two curves were matched. The two cores were also matched at two key pollen zonal boundaries.

Additionally, the unconsolidated surface core, consisting of 110 cm of sediments extracted with a Perspex tube® and piston, and sampled in the field, was correlated to Core 1a through wiggle-matching loss-on-ignition at 550ºC curves (Dean 1974). Tables A.1 and A.2 list the depths of Core 1 and LGS (surface core) and the equivalent 'Core 1a' stratigraphic position. The magnetic susceptibility (Core 1 and Core 1a) and LOI (LGS and Core 1a) curves are plotted against 'Core 1a' depths in Fig. A.1.

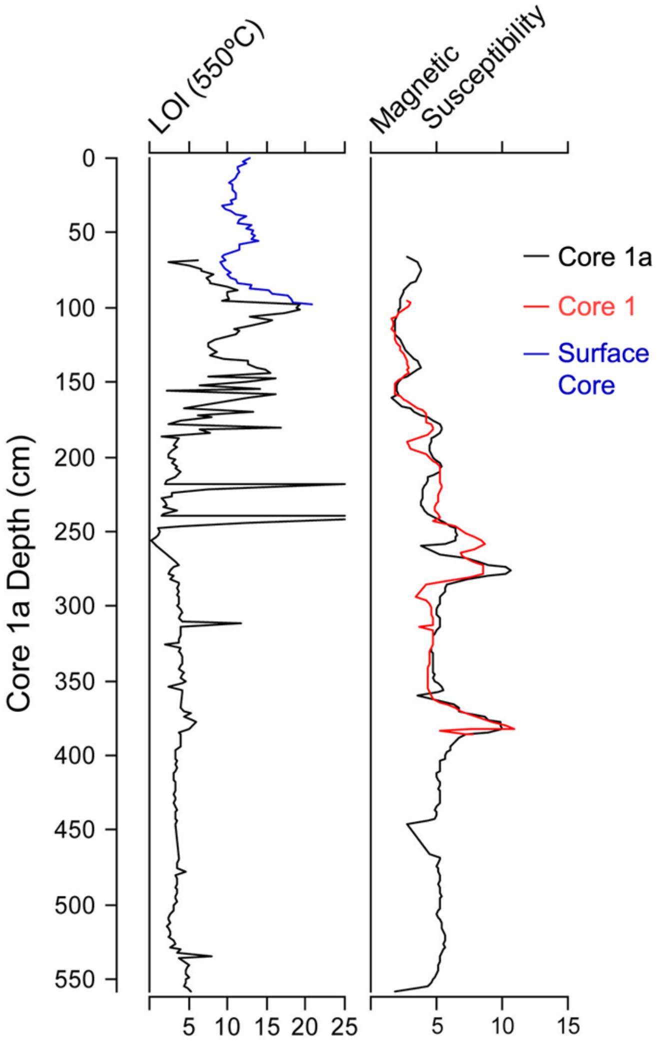

Fig. A.1. Core 1a and surface core (LGS) loss-on-ignition (550ºC), and Core 1 and Core 1a magnetic susceptibility measurements. LGS and Core 1 depths are plotted on the Core 1a depth scale.

A.2. Pollen types indicative of inundation-tolerant forest

Symmeria and *Piranhea* are two pollen types critical to the characterization of post-LGM pollen assemblages (19.5 to 12.2 ka BP) as being reflective of inundation-tolerant riparian forest. Unlike the herbaceous and SDTF pollen types frequently occurring in the glacial- and Holocene-aged assemblages, such as *Anadenanthera*, *Astronium*, *Alternanthera*, and Asteraceae (photos in Gosling et al. 2009), the key riparian pollen types, *Symmeria* and *Piranhea* are little described in palynological literature, and reference material from the herbarium at the Royal Botanic Gardens, Edinburgh, was needed to confirm their identification. A brief description of the ecology of the reference species, as well as photos and descriptions of the fossil and modern pollen are presented below.

A.2.1. *Symmeria paniculata*

The single species of *Symmeria* (*S. paniculata*) in South America is a shrub restricted to seasonally-flooded habitats (Waldhoff et al. 2002), and has been found to be a palynological indicator of inundation-tolerant forest (Burn 2008). The pollen of this species is distinctive, morphological similar to the pollen of other genera of Polygonaceae, such as *Rumex* and *Ruprechtia*, but the exine is noticeably less sculptured than *Ruprechtia*, and the colpi of *Symmeria* are more pronounced than those of *Rumex*.

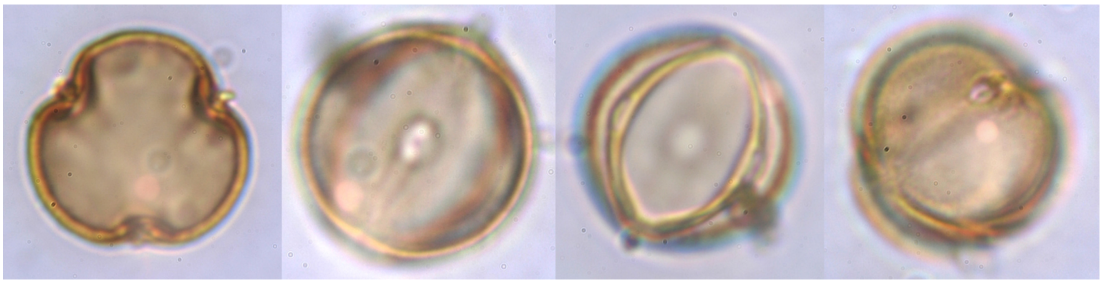

Fig. A.2. Photos of *Symmeria paniculata* pollen prepared from a herbarium specimen, obtained from the Royal Botanic Gardens, Edinburgh

Fig. A.3. Photos of fossil *Symmeria paniculata* pollen from sediments extracted from LLG.

Symmeria paniculata pollen is tricolporate, lobate in polar view, and spheroidal in equatorial view. Colpi are 7/8th the length of the grain. Pores are annulated, lolongate, and measuring approximately 4 µm in length. The exine is finely scabrate. Dimensions are 20 µm x 20 µm x 20 µm (Figs. A.2, A.3).

A.2.2. *Piranhea sp.*

There are only four species of *Piranhea* (Picrodendraceae, formerly Euphorbiaceae) in the Neotropics, two of which are found in the study region (*P. trifoliata* and *P. securinega*). A species typical of Amazonian floodplains, *Piranhea trifoliata* is known to occupy *terre firme* habitats, but it is commonly associated with

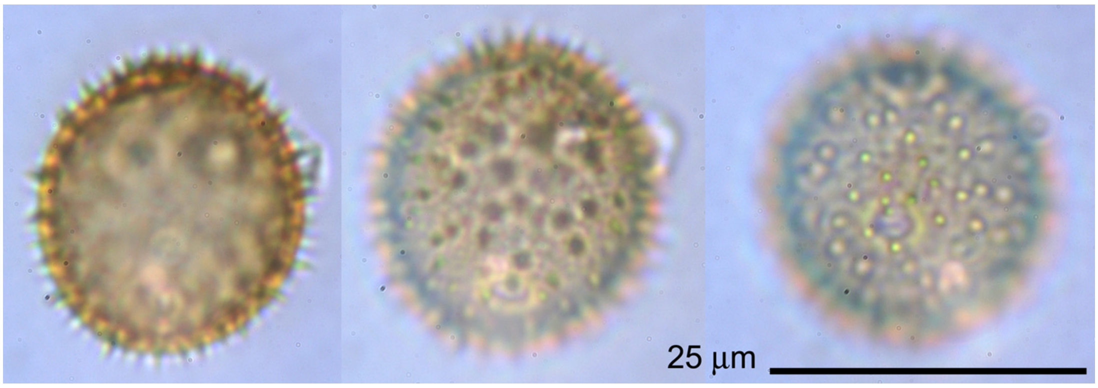

Fig. A.4. Photos of *Piranhea trifoliata* pollen prepared from a herbarium specimen, obtained from the Royal Botanic Gardens, Edinburgh

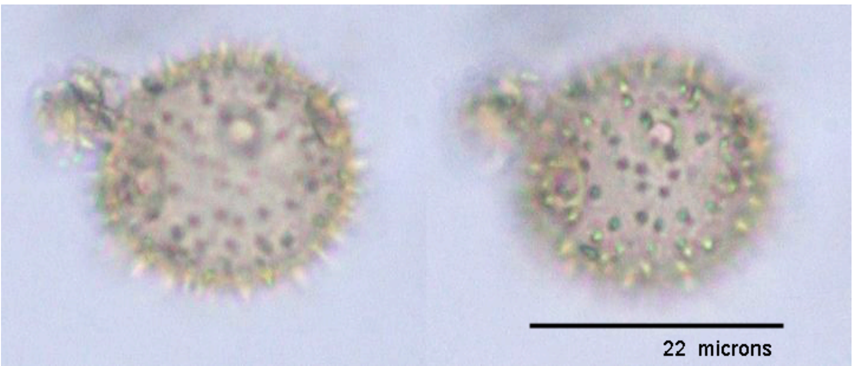

Fig. A.5. Photos of fossil *Piranhea sp.* pollen from sediments extracted from LLG.

Symmeria paniculata in seasonally-inundated forest where it frequently occupies river levées 1 to 2 m above the lowest strata of vegetation (Junk 1989, Worbes et al. 1992). In the post-LGM assemblages, the abundance of *Piranhea sp.* pollen is likely representative of *Piranhea trifoliata* because it co-occurs, and subsequently declines, with *Symmeria paniculata*.

The pollen morphology of *Piranhea trifoliata* is very distinctive; a sub-oblate grain, the exine of *P. trifoliata* is echinate (echinae height of 1 – 2 μm), and the 6 annulated pores are distributed about the equator (and *Piranhea* is sometimes 5- and 7-porate). Dimensions are 20 μm x 20 μm (polar view), and 25 μm (equator) (Figs. A.4, A.5).

A.3. Microscopic charcoal analysis

A.3.1. Rationale for charcoal analysis

Microscopic charcoal analysis was performed on samples spanning the Pleistocene-Holocene transition and the Holocene with the intention of improving the interpretation of abrupt changes in the pollen diagram. I hypothesized that under conditions of lower-than-present precipitation, the seasonally-inundated grasslands of the Pantanal would be more susceptible to burning, thereby resulting in higher concentrations of charcoal particles preserved in the sediments of LLG. Additionally, the abundance of charred grass cuticle fragments, as well as ‘woody’ charcoal, might provide a stronger estimation of past fire dynamics in the Pantanal savannahs.

Microscopic charcoal fragments are generally thought to reflect a regional signal (Whitlock and Larsen 2001), therefore this analysis could provide a broad pattern of precipitation change (e.g., Pantanal-wide) from the Pleistocene-Holocene boundary to present. In particular, the microscopic charcoal data were intended to compliment the high-resolution geochemical and pollen data in Chapter 3 to determine whether the climate of the continental interior SHTSA experienced a precipitation anomaly associated with the YD chronozone.

A.3.2. Methodology

The number of pollen slide charcoal fragments measuring > 25 µm along the long axis were counted together with *Lycopodium* exotic markers to determine total particles per cm^3 (see Chapters 2 and 3 for detailed methodology of pollen preparations), and fragments were counted until a total of 50 *Lycopodium* grains was reached. Charcoal particles were grouped into two broad categories; 'charred cuticles', those fragments that displayed features characteristic of grass cuticles remains (see Wooller et al. 2000 for an overview of grass cuticle morphology), and 'other' or 'woody' charcoal, those fragments that did not exhibit any distinctive

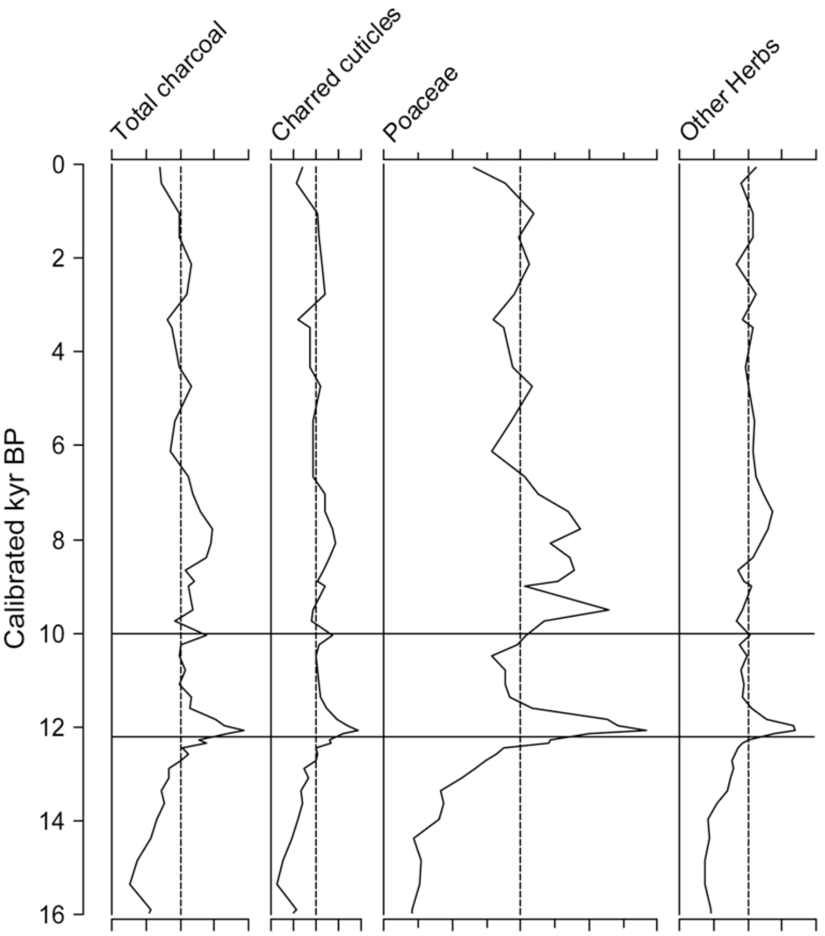

Fig. A.6. Transformed (z-score) total charcoal and charred grass cuticle (>25 µm) influx (particles·cm^{-2}·yr^{-1}), and Poaceae and other herbs influx (grains·cm^{-2}·yr^{-1}) plotted against calibrated kyrs BP.

structure and were entirely opaque. Fifty horizons spanning 16.5 to present, including high resolution analysis across the YD chronozone, were examined for microscopic charcoal.

Woody charcoal and charred cuticle count data were converted in influx values (particles·cm^{-2}·yr^{-1}), and influx values were z-score transformed, a statistical method that normalizes the data and expresses the values as a deviation from a baseline standard (in this case, charcoal influx from 1,000 yrs BP to present) (Power et al. 2008).

A.3.3. Results and Interpretation

The interpretation of the pollen data highlighted several periods of aridity when higher-than-modern microscopic charcoal influx values would be expected. However, the z-score transformed data exhibit the opposite trend. Prior to the onset of higher flooding in the Pantanal basin at 12.2 ka BP, and during the mid-Holocene, the clear signal of aridity from the pollen data is inconsistent with the lower-than-modern influx of charcoal into the lake basin (Fig. A.7). Also, the charcoal peaks that occur shortly after the inundation of the Pantanal basin at 12.2 ka BP is unexpected given that this boundary marks the beginning of a wetter interglacial in the continental interior of SHTSA (Chapter 3).

The positive correlation between charcoal influx and the pollen-inferred precipitation signal could be linked to biomass; where moister conditions encourage the growth of fuel in fire-tolerant ecosystems. However, prior to 12.2 ka BP, the Pantanal basin likely supported a greater coverage of trees and shrubs capable of withstanding the extremes of flooding and drought (Chapter 2), and likely susceptible to fire in drier periods. However, charcoal influx values are noticeably low.

A more parsimonious explanation is increased transport of allochthonous charcoal to LLG through the Rio Paraguay during periods of higher flooding due to increased precipitation in the Pantanal basin. Rising concentrations of Poaceae pollen contemporaneous with higher lake levels at LLG (Chapter 3) are reflective of

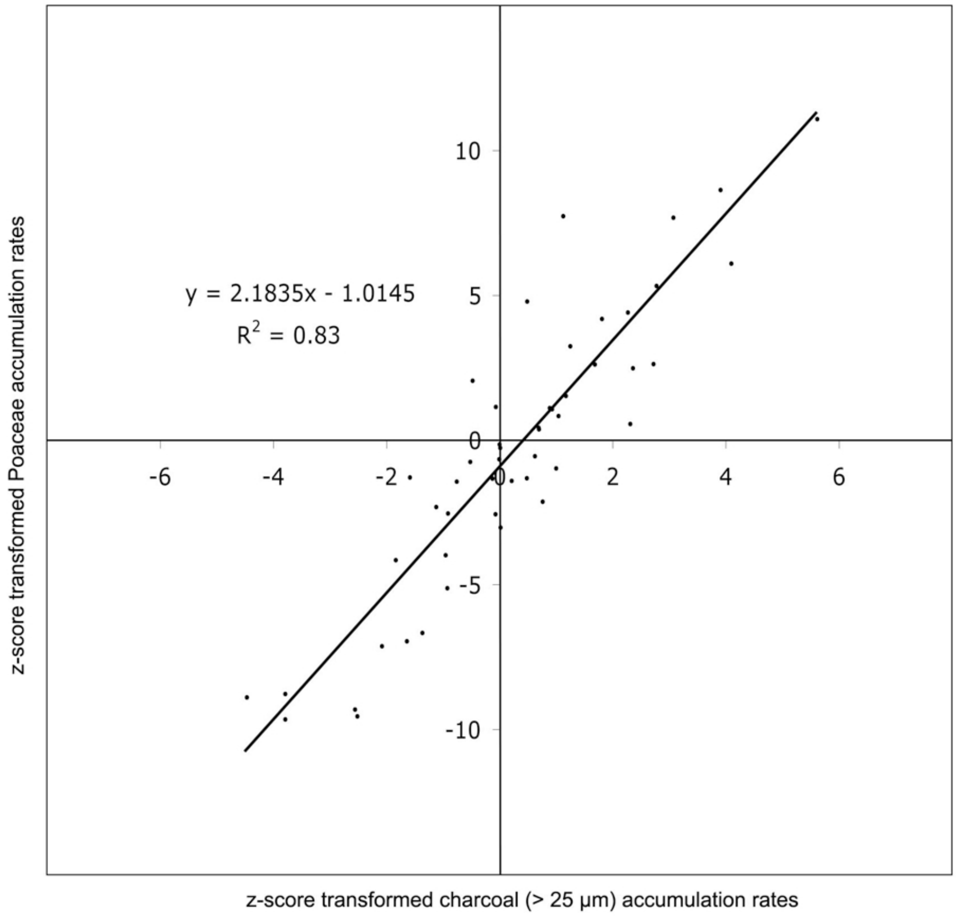

Fig. A.7. Regression of z-score transformed Poaceae and charcoal influx data.

inwashed pollen from the grass-dominated communities of the Pantanal, and the strong positive correlation between z-scored transformed grass pollen influx and charcoal values (Figs. A.7, A.8) suggests the same mechanism is responsible for the higher charcoal influx after 12.2 ka BP.

Although variations in the microscopic charcoal data is likely reflective of hydrologically-forced changes in the connection between LLG and the Rio Paraguay, heavier, macroscopic charcoal may be less easily transported in floodwater from the Pantanal savannahs, and could offer an interesting comparative study between the two methods of charcoal analysis. The macroscopic charcoal data are currently being generated by another postgraduate student as part of ongoing research on the record from LLG.

Table A.1. Uncorrected depths of Core 1 (C1) correlated to Core 1a (C1a). Depths highlighted in red and green refer to magnetic susceptibility and pollen ‘tie points’, respectively.

C1	C1a
91	95.2
92	96.2
93	97.3
94	98.3
95	99.4
96	100.4
97	101.4
98	102.5
99	103.5
100	104.6
101	105.6
102	106.7
103	107.7
104	108.8
105	109.8
106	110.9
107	111.9
108	113
109	**114**
110	115.2
111	116.4
112	117.5
113	118.7
114	119.9
115	121.1
116	122.3
117	123.5
118	124.6
119	125.8
120	127
121	128.2
122	129.4
123	130.5
124	131.7
125	132.9
126	134.1
127	135.3
128	136.5
129	137.6
130	138.8
131	**140**
132	140.9
133	141.8
134	142.6
135	143.5
136	144.4
137	145.3
138	146.1
139	147
140	147.9
141	148.8
142	149.6
143	150.5
144	151.4
145	152.3
146	153.1
147	**154**
148	154.9
149	155.9
150	156.8
151	157.7
152	158.7
153	159.6
154	160.5
155	161.5
156	162.4
157	163.3
158	164.3
159	165.2
160	166.1
161	167.1
162	168
163	168.9
164	169.9
165	170.8
166	171.7
167	172.7
168	173.6
169	174.5
170	175.5
171	176.4
172	177.3
173	178.3
174	179.2
175	180.1
176	181.1
177	**182**
178	182.9
179	183.9
180	184.8
181	185.7
182	186.7
183	187.6
184	188.5
185	189.4
186	190.4
187	191.3
188	192.2
189	193.2
190	194.1
191	195
192	196
193	196.9
194	197.8
195	198.7
196	199.7
197	200.6
198	201.5
199	202.5
200	203.4
201	204.3
202	205.3
203	206.2
204	207.1
205	208
206	209
207	209.9
208	210.8
209	211.8
210	212.7
211	213.6
212	214.6
213	215.5
214	216.4
215	217.3
216	218.3
217	219.2
218	220.1
219	221.1
220	**222**
221	223.1
222	224.2
223	225.3
224	226.3
225	227.4
226	228.5
227	229.6
228	230.7
229	231.8
230	232.9
231	233.9
232	235
233	236.1
234	237.2
235	238.3
236	239.4
237	240.5
238	241.5
239	242.6
240	243.7
241	244.8
242	245.9
243	247
244	248.1
245	249.1
246	250.2
247	251.3
248	252.4
249	253.5
250	254.6
251	255.7
252	256.7
253	257.8
254	258.9
255	**260**
256	260.8
257	261.6
258	262.4
259	263.2
260	264
261	264.8
262	265.6
263	266.4
264	267.2
265	268
266	268.8
267	269.6
268	270.4
269	271.2
270	272

C1	C1a
271	272.8
272	273.6
273	274.4
274	275.2
275	**276**
276	277.1
277	278.3
278	279.4
279	280.5
280	281.6
281	282.8
282	283.9
283	285
284	286.1
285	287.3
286	288.4
287	289.5
288	290.7
289	291.8
290	292.9
291	294
292	295.2
293	296.3
294	297.4
295	298.6
296	299.7
297	300.8
298	301.9
299	303.1
300	304.2
301	305.3
302	306.4
303	307.6
304	308.7
305	309.8
306	311
307	312.1
308	313.2
309	314.3
310	315.5
311	316.6
312	317.7
313	318.9
314	320
315	321.1
316	322.2
317	323.4
318	324.5
319	325.6
320	326.7
321	327.9
322	329
323	330.1
324	331.3
325	332.4
326	333.5
327	334.6
328	335.8
329	336.9
330	338
331	339.1
332	340.3
333	341.4
334	342.5
335	343.7
336	344.8
337	345.9
338	347
339	348.2
340	349.3
341	350.4
342	351.6
343	352.7
344	353.8
345	354.9
346	356.1
347	357.2
348	358.3
349	359.4
350	360.6
351	361.7
352	362.8
353	364
354	365.1
355	366.2
356	367.3
357	368.5
358	369.6
359	370.7
360	371.9
361	373
362	374.1
363	375.2
364	376.4
365	377.5
366	378.6
367	379.7
368	380.9
369	**382**
370	382.2
371	382.3
372	382.5
373	382.6
374	382.8
375	382.9
376	383.1
377	383.2
378	383.4
379	383.5
380	383.7
381	383.8
382	384
383	384.2
384	384.3
385	384.5
386	384.6
387	384.8
388	384.9
389	385.1
390	385.2
391	385.4
392	385.5
393	385.7
394	385.8
395	**386**
396	388
397	390
398	392
399	394
400	396
401	398
402	400
403	402
404	404
405	406
406	408
407	410
408	412
409	**414**

Table. A.2. Uncorrected surface core depths (LGS) correlated to Core 1a (C1a). Depths highlighted in blue refer to LOI 'tie points'.

LGS	C1a
1	0.9
2	1.8
3	2.7
4	3.6
5	4.5
6	5.4
7	6.3
8	7.2
9	8.1
10	9
11	9.9
12	10.8
13	11.7
14	12.6
15	13.5
16	14.4
17	15.3
18	16.2
19	17.1
20	17.9
21	18.8
22	19.7
23	20.6
24	21.5
25	22.4
26	23.3
27	24.2
28	25.1
29	26
30	26.9
31	27.8
32	28.7
33	29.6
34	30.5
35	31.4
36	32.3
37	33.2
38	34.1
39	35
40	35.9
41	36.8
42	37.7
43	38.6
44	39.5
45	40.4
46	41.3
47	42.2
48	43.1
49	44
50	44.9
51	45.8
52	46.7
53	47.6
54	48.5
55	49.4
56	50.3
57	51.2
58	52.1
59	52.9
60	53.8
61	54.7
62	55.6
63	56.5
64	57.4
65	58.3
66	59.2
67	60.1
68	61
69	61.9
70	62.8
71	63.7
72	64.6
73	65.5
74	66.4
75	67.3
76	68.2
77	69.1
78	**70**
79	71.7
80	72.6
81	73.5
82	74.4
83	75.3
84	76.2
85	77.1
86	78
87	78.9
88	79.9
89	80.8
90	81.7
91	82.6
92	83.5
93	84.4
94	85.3
95	86.2
96	87.1
97	88
98	88.9
99	89.8
100	90.7
101	91.6
102	92.6
103	93.5
104	94.4
105	95.3
106	96.2
107	97.1
108	**98**

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