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**A diatom-based Late Quaternary
precipitation record for lowland tropical
South America**

Katharine Anne Fitzpatrick

Declaration of Originality

All the work included in his thesis is original and my own, unless otherwise stated.

The research in this thesis has not been submitted for any other degree or professional qualification.

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Preface

This thesis is formatted in journal style and is typical of research submitted to peer-reviewed journals. Some of the data collected for the two research chapters has been collected by collaborating authors. A list of collaborating authors is listed at the beginning of each chapter and their contribution to the research is detailed below. Chapter II includes data collected in the field in 2006 by Bronwen Whitney and Frank Mayle. A survey of lake depth at LLG was carried out by Frank Mayle in 2008. Training in identification of diatom species was provided by Sarah Metcalfe and David Mann. Sarah Metcalfe, from Nottingham University, has been crucial to diatom data interpretation and discussion.

The research in Chapter III relies on a sediment core extracted from LLG by Frank Mayle. Pollen data was collected and identified by Bronwen Whitney. Bronwen Whitney played an integral role in my understanding of climate systems in South America and the ecological response to them.

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Abstract

The late Quaternary palaeoclimatic history of the lowland Southern Hemisphere Tropics of South America (SHTSA) has been little studied and analysis of key climatic events, such as the Last Glacial Maximum (centred ~ 21,000 years ago (21 cal. ka BP)) and the glacial-Holocene transition is limited. Studies from the SH tropical Andes and the Atlantic seaboard demonstrate a strengthening of the South American summer monsoon during the LGM, in tune with the ~ 20 kyr precession orbital cycle. However, palynological studies from SHTSA suggest a drier LGM. There are difficulties in interpreting different palaeoenvironmental proxy records and the extent to which they reflect changes in temperature, precipitation, and/or atmospheric CO₂ concentrations. In particular, the palaeoenvironmental significance of palynological data is often unclear. Also, high frequency, millennial-scale events have not been captured in records from the lowland SHTSA due to a lack of high resolution temporal records. Diatoms have been used widely in other parts of the world to reconstruct lake level change and therefore provide an independent proxy for precipitation, and an understanding of the modern diatom ecology is essential for accurate palaeoreconstruction. The main rationale of this thesis is to address the uncertainty of the glacial-Holocene climate in South America. To this end, this thesis aims to: (a) investigate the distribution, ecology, and flora of diatom taxa at Laguna La Gaiba (17°45'S, 57°40'W) (LLG) in the heart of lowland tropical South America, where very few modern diatom studies exist; (b) determine whether modern diatom assemblages at LLG will provide a useful analogue for palaeoenvironmental reconstructions, in particular, lake depth reconstruction; (c) provide a detailed late Quaternary lake level reconstruction for the lowland interior of SHTSA, based upon fossil diatom analysis of a sedimentary core in LLG.

Descriptive, quantitative and multivariate analyses were applied to modern diatom assemblages and environmental variables to ascertain the modern diatom

environment of LLG. Diatom, pollen, and geochemical analyses, chronologically constrained by 18 AMS ^{14}C dates, were performed on a sediment core extracted from LLG. Key findings indicate: (1) *Aulacoseira ambigua*, *A. ambigua* var. *robusta*, *A. distans* and *A. granulata* var. *angustissima* were the most abundant species. Shallow-water species, such as *Staurosira* and *Eunotia* spp., dominated the shallows and littoral zone, whilst deep-water species, such as *Aulacoseira* sp., dominated in open water; (2) The highest percent variance in the diatom data was explained by depth and pH; (3) Analysis of fossil diatom assemblages from the LLG core demonstrated that the Last Glacial Maximum (LGM) and late glacial period (prior to 12.5 kyr BP) was drier than present. This corroborates and significantly strengthens pollen-based palaeo-hydrological reconstructions from the same core; (4) An abrupt shift from 12.5 kyr BP from shallow water to deep water diatoms signals major flooding of LLG associated with the transition from relatively drier glacial conditions to wetter Holocene conditions and also highlights an anomalously wet period centred over 12.2 kyr BP that falls within the Younger Dryas chronozone; (5) Deep-water diatoms remain high throughout the Holocene, which means that the mid-Holocene aridity inferred from the pollen data (expansion of seasonally-dry tropical forest) is not captured by the diatom data.

These results not only present the modern diatom ecology of a little studied area in lowland Bolivia, but also highlight the potential of diatoms as a proxy for past lake level fluctuations, improving the understanding of late Quaternary palaeoclimate of tropical South America. Used as part of a multiproxy reconstruction, this record has provided a more complete picture of the variation between regions of late Quaternary climate change in South America, as evidence of a dry LGM climate contrasts with the robust, well-dated climate archives of the central Andes and E Brazil. This suggests the climate in the continental interior of SHTSA was not driven by the precessionally-forced monsoon cycle but is in step with changes in glacial-interglacial cycle boundary conditions.

I. General Introduction

1.1 Thesis rationale

A major aim of tropical ecosystem research is to investigate environmental conditions and transitions during the Late Quaternary in order to understand the how present-day tropical environments respond to climate change. These investigations can be then used to further understand global climate change and interhemispheric climatic teleconnections. Traditionally, palaeoecological and palaeoclimatological studies have focused on Northern Hemisphere study sites, but due to the emerging importance of interhemispheric climate connections, the numbers of studies focussing on South America are increasing. However, many studies in South America particularly in the little-studied lowland regions, do not extend back in time further than the Holocene and so do not capture the climatically important Last Glacial Maximum (LGM) or the glacial-Holocene transition. This means interpretations of a few records have been extrapolated over the entire lowland region which has led to controversy, particularly in regards to precipitation inferences. The central aim of this thesis is to improve understanding of late Quaternary precipitation changes in tropical South America using high temporal resolution analysis of a sedimentary core and examination of modern environmental variables from a lake in lowland Bolivia.

1.2 Glacial climate in South America

The lack of identified mechanisms driving late-Quaternary climate (Denton et al., 1999) remains a fundamental problem of global climate dynamics. Climatic fluctuations of the Quaternary period have followed a series of distinctive patterns, and early explanations for long-term climatic change have tended to focus on the factors that have given rise to both the periodicity and frequency of climatic fluctuations (Hays et al., 1976; Imbrie and Imbrie, 1980; Bradley, 1985). Fluctuations in climate during the Quaternary have been attributed to a number of cycles

A diatom-based Late Quaternary precipitation record for lowland tropical South America influenced by orbital variations. Lowe and Walker (1997) state that the hypothesis that has attracted the greatest attention is undoubtedly the “Astronomical Theory”. The Astronomical Theory of climate (Milankovitch, 1920) has become a useful hypothesis, holding that variations in insolation caused by changes in the Earth’s orbital eccentricity and precession, and changes in spin-axis obliquity caused the great ice ages of the Pleistocene (Rial and Anaclerio, 2000). While the 100,000 year eccentricity signal modulates the length of a glacial cycle, the precession cycle (21,000 year) combines with other frequencies to influence climatic fluctuations within a glacial cycle. (Figure I.1).

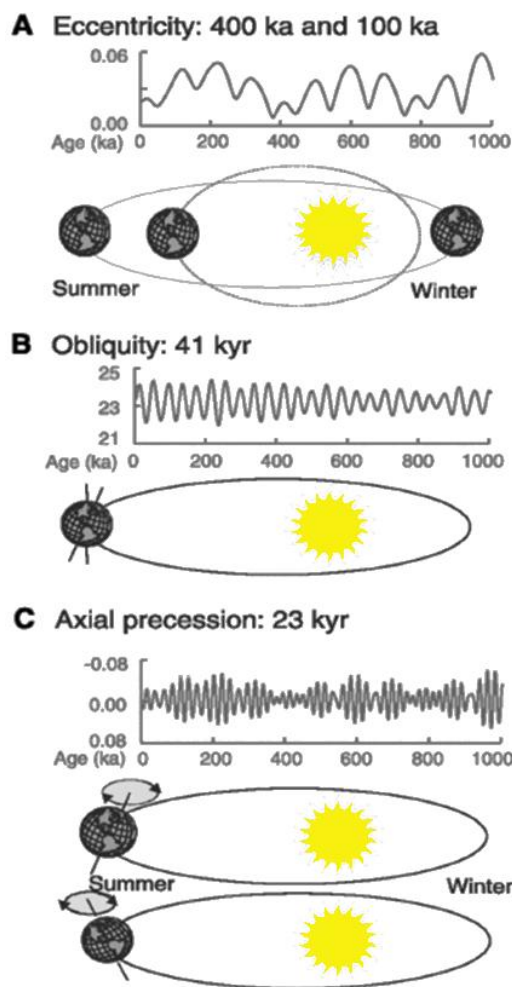


Figure I.1: Earth orbital elements. A: eccentricity of the Earth, B: axial tilt (obliquity) and C: precession (‘wobbling’) of the Earth’s axis (Zachos et al. 2001).

Conditions over the LGM were different to present conditions in tropical South America. Global ice cover was at its greatest extent since 130 000 years BP, temperatures were up to $\sim 5^{\circ}\text{C}$ cooler, CO_2 levels were half what they are today and precipitation regimes were presumably different than present (Markgraf, 1999) and so it is an exciting period of time to investigate ecosystem response to climate change. Research in tropical South America is particularly interesting because while it is generally agreed that temperatures were cooler than today (International CLIMAP project, 1981), precipitation levels in lowland tropical South America are still a matter for debate. A clear pattern emerges from the northern and southern latitudes which were respectively drier and wetter but the pattern in the southern hemisphere lowlands remains unclear. Moist conditions at the LGM in South America can be explained by precessional forcing mechanisms involving the southward shift of the Inter-tropical Convergence Zone (ITCZ) and the reinforcement of the South American Summer Monsoon (SASM), bringing more precipitation over tropical South America (Baker et al., 2001a; Cruz et al., 2005).

The migration of the ITCZ can be explained by orbital forcing according to the Milankovitch Theory (Mayle et al., 2000, Baker et al., 2001a; Cruz et al., 2005) in terms of the controls over summer insolation (Cross et al., 2000). The theory predicts that in opposite hemispheres, trends in tropical precipitation seasonality should have behaved in anti-phase with one another over 19-23 kyr precessional cycles. If instead, they behaved in a broadly synchronous manner, this would suggest non-orbital factors were the overriding precipitation controls. By making inter-hemispheric comparisons and understanding the glacial-interglacial precipitation history of the southern hemisphere tropics of South America (SHTSA), it will be possible to shed light on the dominant drivers responsible for orbital-scale, and possibly millennial-scale, precipitation changes in the tropics.

The climate at the LGM has been recorded at a number of sites in South America. The palaeoclimate record varies across the continent. In northern South America,

A diatom-based Late Quaternary precipitation record for lowland tropical South America Bradbury et al. (2001) and Bush et al. (1990) find evidence for a cooler and more arid LGM from palynological records. Through vegetation analysis of sediment cores from the Amazon basin, Colinvaux et al. (1996) and Colinvaux et al. (2000) argue for a wet LGM due to the prevalence of tropical rainforest at the time. Ledru et al. (1998) challenge Colinvaux et al. (1996) to argue for a dry LGM indicated by hiatuses in the pollen record suggesting a dry period. This is corroborated by Burbridge et al. (2004) who also argues for a dry LGM. Travertine and speleothem deposits from north eastern Brazil in the Amazon basin suggest a wet LGM (Artz et al. 1998 and Wang et al. 2004). There is a clear pattern of prevailing dry conditions over the northern latitudes of the continent at the time of the LGM and there is strong evidence for wetter conditions over a large range of latitudes of the southern half of South America which argues for the equatorward displacement of the westerlies. In the subtropical latitudes it is still difficult to clarify a pattern due to the paucity of palaeoclimatic reconstructions. The pattern in the tropical Andes is clear where wetter conditions prevailed during the LGM, except in Northern Chile, where the palaeodata is controversial due to the dating strategy (Farrera et al., 1999). Currently, the moister conditions in the Andes and Brazil are explained by a precessional forcing increasing continental heating causing a southern shift of the ITCZ and reinforcement of the SASM, leading to more humidity in the tropical Andes reaching southern Brazil (Baker et al., 2001a,b; Wang et al., 2006).

1.3 High frequency climate change in tropical South America

It is debated how much high frequency climate fluctuations in the North Atlantic influenced global climate during the glacial-Holocene transition, particularly in the case of the southern hemisphere (Blunier et al., 1998; Markgraf and Seltzer, 2001, Sugden et al., 2005; Ackert et al., 2008). Sub-Milankovitch climate changes are best known from marine and ice-core records from the North Atlantic region but high frequency climatic perturbations such as Heinrich (H) events and the Younger Dryas

A diatom-based Late Quaternary precipitation record for lowland tropical South America (YD) have been shown to occur at a global scale (Voelker et al. 2002) although whether these North Atlantic events were transmitted to the lower lowland latitudes of the continental interior of South America is still unknown.

1.3.1 Heinrich Events

Heinrich events are defined by pulses of ice-rafted debris (IRD) in North Atlantic sediments and appear to be connected with the climaxes of cooling cycles in the Northern Hemisphere (Heinrich, 1998; Broecker et al., 1992; Bond et al., 1992,) which are spaced 5,000 – 17,000 years apart. The transport of IRD can be explained by the enhanced discharge of icebergs and their subsequent melting. Considerable sea surface cooling during these events has been associated with a collapse of the North Atlantic thermohaline circulation (Alvarez-Solas et al., 2010). Recent studies have suggested that the collapse of the Atlantic Meridional Overturning Circulation (AMOC) preceded Heinrich events and therefore indicates H events are a response to, rather than a cause of AMOC collapse as previously thought (Hall et al., 2006; Clark et al., 2007). Six H events have been identified during the period of 70 ka – 12 ka BP. Bond et al. (1992) identified 2 events in the late glacial, H1 at 17.1 ka BP and H0 at 12.9 ka BP, which signals the start of the Younger Dryas (Hessler et al., 2010). Although it appears that H events registered globally, the response to the events varies geographically and the mechanisms behind it are still poorly understood.

Although Heinrich events have been mainly recorded the North Atlantic region, evidence for climatic perturbations which appear to be related to H events have also been recorded in some records from South America. Records from the central Andes recognize H events as 'wet' episodes. High lake levels in Titicaca and the Salar de Uyuni (Baker et al., 2001b; Placzek et al., 2006) and γ -radiation peaks in Salar de Uyuni (Baker et al., 2001b) between 16.6 ka BP and 14.1 ka BP are attributed to Heinrich event 1 (H1). Wet episodes corresponding with H1 are also visible in stable isotope records off the north east coast of Brazil (Arz et al., 1998), speleothem growth phases in coastal Brazil (Salvador) (Wang et al., 2004) and a drop in $\delta^{18}\text{O}$ in

A diatom-based Late Quaternary precipitation record for lowland tropical South America speleothem records in Botuvera Cave, south east Brazil (Wang et al., 2007). The increase in precipitation in these regions is attributed to an anomalous southward shift in the ITCZ caused by cool sea surface temperatures (SSTs) in the North Atlantic, steepening the pole-to-equator thermal gradient and strengthening northeasterly trade winds.

1.3.2 The Younger Dryas

The Younger Dryas (YD) (GS-1 stadial, 12.9-11.6 cal. kyr BP, also called H0), is the most studied of millennial-scale high frequency climate events and is thought to have influenced 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). It is thought that during the YD cooling event, aridity was brought on in the Northern Hemisphere tropics of South America by the mean position of the ITCZ being forced southward. This was caused by reduced overturning circulation in the North Atlantic which resulted in a steepened pole-equator thermal gradient in the northern Hemisphere and precipitation south of the equator also increased (Dahl et al., 2005). This is supported by well-dated palaeoclimatic reconstructions from tropical South America that demonstrated general increased (south of 10° S) and decreased (north of 10° N) precipitation during the YD chronozone. At Lake Titicaca and Salar de Uyuni in the Andes, lake levels were high (Baker et al., 2001a, b; Placzek et al., 2006) and in the currently moisture deficient region of north-eastern Brazil, there is evidence of travertine growth indicating running water (Auler et al., 2004). These records provide robust evidence for higher precipitation during the YD in areas south of the equator and are of high chronological control and temporal resolution however they are largely based in the Andean and coastal regions. In the continental interior of South America, most lacustrine records have low sedimentation rates and relatively young basal ages and so it is unknown whether a precipitation anomaly occurred during the YD chronozone in this region. (Figure I.2)

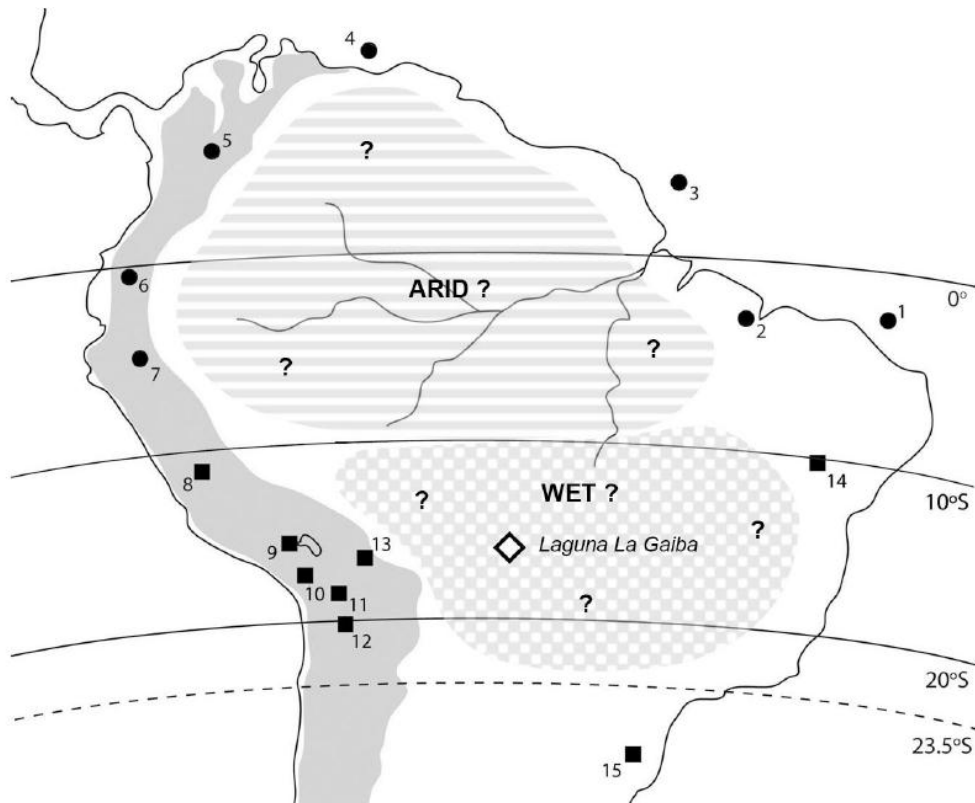


Figure I.2: South American precipitation at the YD, showing sites from the coastal and Andean regions (Whitney, 2009). Only records that are high-resolution, well-dated that cover the YD are shown. Open diamond represents LLG study site which is well placed to test whether the interior of tropical South America experienced a YD-type anomaly. Closed circles = arid, close squares = wet (See Table I.1 for site data)

No.	Site	Country	Proxy	References
1	GeoB 3104-1	Brazil	Geochemistry, Isotopes.	Arz et al. 1998, Behling et al. 2000
2	Lake 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	Lake Baja	Peru	Pollen, Charcoal	Hansen 1995

No.	Site	Country	Proxy	References
8	Lake Junin	Peru	Pollen, Isotopes	Seltzer et al. 2000
9	Lake 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 I.1: Sites featured in Figure I.2

1.4 The Holocene climate in tropical South America

Precipitation changes in the northern and southern tropics of South America are generally thought to be in phase with summer insolation (in the respective hemispheres) and so are in anti-phase with each other. Records from the southern tropics demonstrate that abundant summer monsoon precipitation is coherent with summer insolation. For example, when summer insolation was at a minimum at 10kyr BP, widespread drying across the southern tropics was noted during early and middle Holocene. At this time, insolation was 7% lower at 20° S than its maximum during the LGM at 20kyr BP (Berger and Loutre, 1991). Again, there are relatively few Holocene-age, high resolution palaeoclimatic records in tropical South America. This further emphasises the gap in high resolution palaeoclimatic records from the continental interior of SHTSA. It has been suggested that the mid-

Holocene dry period was regionally widespread over SHTSA by records from sites in the northern Andes (Berrio et al., 2002), central Andes (Abott et al., 1997; Seltzer et al., 1998; Baker et al., 2001a; Rowe et al., 2002; Paduano et al., 2003) and western Amazonia (Mayle et al., 2000; Defreitas et al., 2001; Bush, 2005). However, the timing and duration of mid-Holocene aridity is not synchronous among the records.

There are a few records of particular interest; i) Laguna Pallcacocha in the southern Ecuador Andes (Rodbell et al., 1999; Moy et al., 2002) is primarily a record of El Niño Southern Oscillation (ENSO) variability but climatic changes may be related to North Atlantic cold events (Bond et al., 2001); ii) the Cariaco basin off the North Coast of Venezuela indicating dry periods during North Atlantic cold events throughout the last Glacial and Holocene in northern tropical South America; iii) the Quelccaya ice core from the Cordillera Oriental of southern Peru (Thompson et al., 1995) is an isotopic record that indicates that precipitation has varied inversely with tropical North Atlantic SST on decadal timescales; vi) records from Lake Titicaca indicate Mid-Holocene aridity. Maximum aridity and lowest lake level occurred in the early and middle Holocene (8000 to 5000 cal yr BP) during a time of low summer insolation (Baker et al., 2001a). However, compared to the northern hemisphere, there are relatively few studies of climate dynamics in South America. Most of the studies in South America have focused on the response of abiotic climate proxies, such as glaciers and oxygen isotopes, and biotic proxies, such as pollen, to interpret climate change in the Late Quaternary (Markgraf and Kenny, 1997; Bennett et al., 2000; Moreno, 2000; Moreno, 2004; Moreno et al., 2001; Heusser, 2002). Ammann et al. (2000) and Birks et al. (2000) emphasised the value of using independent indicators in multi-proxy studies to provide a detailed and unambiguous impression of ecosystem response to climate change. A high resolution, continuous record of precipitation over the Holocene is needed in the SHTSA to understand whether drying during the mid-Holocene was widespread in South America and if the lowland tropics are climatically synchronous with the High Andes and coastal Brazil.

1.5 Palaeoclimate reconstruction from lowland Bolivia.

To address the palaeoclimate reconstruction gap in continental South America, Whitney et al. (2011) analysed a 6m sediment core from Laguna La Gaiba, a lake in lowland Bolivia. The high resolution, well-dated, 45kyr record inferred regional temperature and precipitation change from a palynological record. Results revealed three main climatic shifts, a colder and drier landscape than present between ~45.0kyr and 19.5kyr BP, warming with a persistently drier climate from 19.5kyr to 12.8kyr BP, a wetter Holocene marked by flooding at 12.2kyr BP with a drier period between 10.0kyr and 3.0kyr BP. In terms of the vegetation change at the site, the study suggests that the present day semi-deciduous dry forests that dominate the upland areas surrounding the lake are only Holocene in age (Mayle, 2004). The Pleistocene inorganic clays are dominated by herbaceous pollen taxa and are entirely devoid of arboreal pollen taxa. The high levels of herbaceous pollen taxa indicate an open, sparsely vegetated landscape dominated by sand dunes under a drier-than-present climate as suggested by Assine and Soares (2004). For the full paper Whitney et al. (2011), see Appendix B. Summer insolation is driven by the precession cycle and numerous research studies have shown that the climate in South America follows the precession cycle. However, as the palynological record from Laguna La Gaiba suggests a more arid than modern LGM, this warrants an explanation as it counters the suggestion of a precessional-cycle-driven climate. However, from this record alone it is difficult to truly define a precipitation record as it is difficult to disentangle the proxy indicators such as CO₂, precipitation and temperature from a pollen record. What is needed is comparison with independent climate proxies that will highlight a particular climate pattern. A high resolution diatom record for this site could be used to infer lake level change, and therefore precipitation and also capture in detail high frequency, abrupt climatic shifts in the late-glacial-Holocene.

1.6 Diatoms

Diatoms are microscopic, unicellular organisms and belong to the Division Chrysophyta, Class Bacillariophyceae and are photosynthesising algae. They are found almost anywhere in the world where there is water or moisture. Diatoms are usually between 2-200 microns in diameter or length and are estimated to contribute about 25-35% of the world's productivity (Kelly et al., 2005). Depending on taxonomic identification and one species concept, diatoms are represented by 50-200 species. Diatom cell walls (frustules) have two valves, an older and a younger half each with a series of linking bands (girdle bands). Diatom valves vary in shape and symmetry. The arrangement of slits, pores and other features of the silica wall differ, which allows for identification and classification. Diatoms are usually divided into two major groups. Centric diatoms are circular valves with radial symmetry and pinnate diatoms with bilateral symmetry. On some species of pinnate diatom, there is a slit-like groove or channel down the siliceous cell frustule called a raphe. The raphe secretes mucilaginous material which allows limited movement along a substrate (Kelly, 2006).

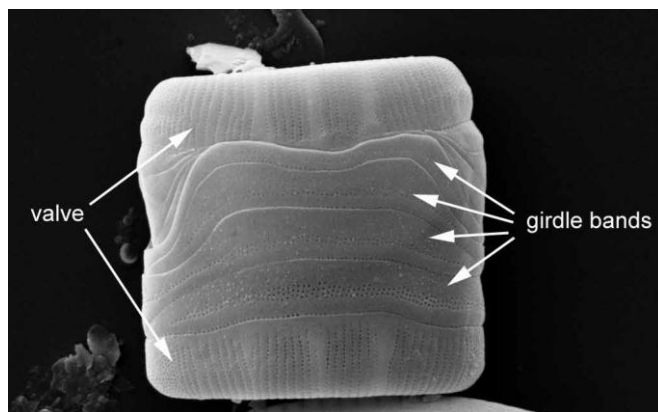


Figure I.3 SEM image of a diatom frustule (Craticula.ncl.ac.uk)

Changes in the physical, chemical and biological characteristics of the aquatic environment are reflected in the nature of the sediment that is deposited at the bottom of a lake. Diatoms are composed of large number of species with different tolerances to physical and chemical variables (Battarbee et al., 1999) and are extremely sensitive to conditions prevailing in different aquatic environments (Gasse et al., 1983). Diatoms possess several characteristics that make them excellent palaeo-indicators. Their short cell cycle and narrow and well defined ecological requirements means they respond rapidly, and are highly sensitive to fluctuations in a changing environment. Their siliceous cell wall (silica resists degradation) is readily preserved in the sedimentary record and can be identified to at least species level (Moser et al., 1996). Palaeoecology relies on the assumption that the ecological requirements of species were the same in the past as they are in the present. Correct interpretation of the palaeolimnological record therefore requires accurate taxonomic identification and a thorough understanding of the ecological preferences of individual species.

Diatoms are generally well preserved in sediments due to their siliceous cell walls however during their descent through the water column and during digenesis, dissolution of the diatom frustule may occur which would alter the preserved assemblages as lightly silicified forms would preferentially dissolve (Burgess et al., 2005). Diatom analysis provides additional information to pollen-based reconstructions and can give a clearer picture of the hydrological evolution of the area. Diatoms are sensitive to a number of physical limnological characteristics and water depth is a significant factor governing diatom distributions, as this has an effect on the nature and amount of benthic habitats available. As photosynthetic organisms, diatoms are restricted to the photic zone of aquatic environments. There are differences, however, in the light requirements of the species (Velez et al., 2005). Therefore as water levels fluctuate, corresponding changes occur in available habitat, light, chemical conditions, stratification and mixing regimes. In general, as lake levels fall, benthic and epiphytic habitats expand, nutrient and chemical and

A diatom-based Late Quaternary precipitation record for lowland tropical South America salt concentrations increase and corresponding changes in pH occur. High water levels generally result in the opposite effect (Wolin and Duthie, 1999). Life-form or habitat group changes based on depth distributions (i.e. benthic vs. planktonic) produce the most reliable evidence of water level change.

A range of biological, geological or climatological processes can influence water level changes in a freshwater lake. Changes in hydrological conditions are one of the most important factors that control water level change. The balance between moisture gains and losses determine the lake level change. Inputs into a lake system include groundwater inflow, streams/river inflow, basin runoff and lake surface precipitation. Losses happen through groundwater outflow, stream/river outflow and evaporation from the lake surface (Mason et al., 1994). Changes in vegetation in the surrounding area also need to be taken into account as it can affect drainage and groundwater flow.

One of the most important factors influencing the composition of diatom assemblages is lake water chemistry (Battarbee, 1992). An assemblage will tend to be dominated by species with environmental optima closely reflecting the lake environment. Environmental conditions of a lake might shift in response to water level change which would in turn affect the diatom signal. Early researchers realised the sensitivity of diatoms to pH (Fritsch, 1931; Hustedt, 1937-1939). Although many diatom species have a wide range of tolerance to pH, optimal development occurs within a narrow range of hydrogen ion concentrations. Changes in pH can also be connected with lake level change. In Lake Ontario (Delorme et al., 1986), decreases in moisture (i.e. lake level) correspond with increases in humification and lower diatom-inferred pH whereas increasing water levels caused increases in alkaliphilous (higher pH) diatom taxa. An opposite effect was found by Bradbury (1986) in Tasmania, where acidophilous (low pH) taxa increases when water entered the lake from high precipitation or snowmelt, flushing the lake basin with low pH.

It is therefore necessary to be aware of the natural environment of a study lake and its associated hydrological processes.

In more recent years, nitrogen and phosphorous have been identified as components that typically limit the growth of diatoms under natural conditions. Studies on lake enrichment have shown that phosphorous loading amplifies diatom biomass and diatom assemblages are strongly influenced by nitrogen to phosphorous ratios (Schindler and Fee, 1974). Diatoms response to nutrients is usually used as an indicator of human impact, erosional changes or water quality within a lake basin. However, nutrients can also be a signal of climate change if separated from anthropogenic signals. Increases in nutrient conditions can occur at low water level (Rippey et al., 1997). An increase in diatom inferred total phosphorous reflected this nutrient signal in a lake in Northern Ireland. *Cyclotella stelligera* percentages increased during a low water period as a response to nutrient inputs (Schelske et al., 1997) in Lower Herring Lake. This was also accompanied by a similar increase in benthic forms.

The site of this study, Laguna La Gaiba (LLG) is a shallow lake, and diatom signals are likely to be dominated by their response to water level change where the influence of the littoral zone is strong. In LLG, if there is spatial chemical heterogeneity, then depth may be a strong controlling variable on sedimentary diatom distribution (Yang and Duthie, 1995).

1.6.1 Diatoms as a palaeo-tool in South America

At a regional or global scale, lakes are sensitive to climatic fluctuation (Battarbee, 2000). The concept that an abundance of benthic diatoms indicates shallow water and planktonic diatoms indicate deeper water has been used to reconstruct lake level across the tropics. For example, in Glacial-age sediments in Lake Titicaca, the fraction of benthic diatoms is low and the fraction of freshwater planktonic diatoms

A diatom-based Late Quaternary precipitation record for lowland tropical South America is high. A dry period between about 15,000 and 13,000 cal yr BP, coinciding with the Bølling-Allerød warm period of the high-latitude North American region, is marked in Lake Titicaca by the small increase in benthic diatoms. Increased wetness was marked in Lake Titicaca by a minimum of benthic diatom abundance and a maximum of freshwater planktonic diatoms (Baker et al., 2001a). Other diatom-based lake-level reconstructions have been made in Mexico (Metcalf et al., 1991; Metcalf et al., 2000), Columbia (Velez et al., 2001; Velez et al., 2005), Malawi (Gasse, 2000), Madagascar (Gasse and Campo, 2001), and Indonesia (van der Kaars et al., 2001), to name a few. However in this latter study, diatom response to lake level change was not driven by precipitation changes but as a result of basin in-filling. Consequently, the difficulty with using growth-habit ratio for palaeolimnological reconstruction is that the same signals may be caused by other factors therefore, it is essential to know the bathymetry, hydrology, and other environmental variables of the study lake.

As with any biological proxy, there are some problems with using diatoms as a palaeo-tool. Diatom taxonomy and nomenclature are very complex, often leading to confusion which sometimes makes use of published ecological information problematic. There are differences of opinion concerning taxonomic limits, even of common taxa, and naming conventions are presently in a state of flux. The dissolution or breakdown of diatom valves in sediments means more fragile diatom taxa maybe under-represented as preservation is poor which is why it is important to gain an understanding of diatom assemblages in the present-day water environment from the lake as well as examining surface sediment samples. In terms of using modern diatom assemblages to help reconstruct fossil records, diatom species that are not found in modern samples may lead to problems with accurate interpretation of data. However, ecological data from other similar regions may help with this 'no-analogue' situation. Many diatom-based reconstructions from South America use this method of using 'foreign' autoecological data to assist with making interpretations about fossil assemblages in a limnological record. However,

A diatom-based Late Quaternary precipitation record for lowland tropical South America ideally, examination of the modern environment of the study site where a sediment core was taken from for palaeo-reconstruction would provide more accurate analysis of the fossil record. Essentially, study of the modern environment should elucidate whether different water levels have an effect on present-day diatom assemblages and therefore if they are valuable as lake-level change proxy.

1.6.2 Modern diatoms studies in South America

The information about the diatom flora of South America, particularly in the tropical lowlands is incomplete. The most recent and general analyses of these flora were held by Metzeltin and Lange-Bertalot (1998, 2007) in tropical areas and by Rumrich et al. (2000) in the Andes. Metzeltin and Lange-Bertalot (1998) suggested that in warm or cold regions of South America, there are many cosmopolitan species or species of temperate climatic zones, while in tropical regions the flora is completely different and many endemic taxa were found. Rumrich et al. (2000) confirmed these ideas although found many endemic taxa at high altitudes in the Andes. As these studies are based on a limited number of samples in relation to the geographic size of the studied area, it is important to obtain more detailed modern floristic studies from particular regions to test these suggestions. There are very few modern diatom studies in the tropical lowlands and there is a distinct lack of detailed information on local modern diatom distribution and its relation to environmental data in Bolivia. What few studies there are, are restricted to the Bolivian Andes or cloud forests in the Eastern Cordillera of the Andes (Morales et al., 2009). There have not been any modern diatom studies in Bolivia that test diatoms as a proxy for palaeoreconstruction.

To test whether diatoms can be used as a palaeoreconstruction proxy in a particular context, the ecological relevance of the modern dataset has to be evaluated. It is crucial to test the statistical relationship between diatom assemblages and the lake environment. A canonical correspondence analysis (ter Braak, 1986) is a constrained ordination technique which simultaneously combines the ordination of sites, species

A diatom-based Late Quaternary precipitation record for lowland tropical South America and environmental variables. The advantage of CCA over other ordination methods is that it allows the examination of the relationship between biological assemblages of species and known variations in the environment (Justwan and Koc, 2007). Other studies have used CCA as a means of assessing the relationship between a proxy (specifically diatoms) and environmental parameters. Juggins (1992) and Cumming and Smol (1993) investigated the relationship between diatom assemblages and salinity. A CCA was used to study the relationship between diatoms and pH (Christie and Smol, 1993). Yang et al. (2003) used CCA to find a relationship between diatom assemblage and water depth in lakes in the Tibetan plateau and the USA respectively.

1.7 The study site

1.7.1 The present-day climate of South America

The modern distribution over South America ranges from tropical to extratropical climates and is defined by several different regions and factors such as shape of the continent and topography (encompassing the Andes and the Amazon rainforest). The climatic variability of the continent is impacted by its relationship with sea surface temperature (SST) anomalies associated with El Niño/Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), Antarctic Annular Modes and North Atlantic Oscillation (NAO). Today, the tropical latitudes of South America are dominated by a precipitation system, the South American Summer Monsoon (SASM) which has two main components; one associated with convection over Amazonia, a near equatorial Inter Tropical Convergence Zone (ITCZ), and a subtropical one, South Atlantic Convergence Zone (SACZ) which is associated with features over southeast South America. The Chaco Low drives the connection for these systems to provide moisture over subtropical latitudes (Figure I.4).

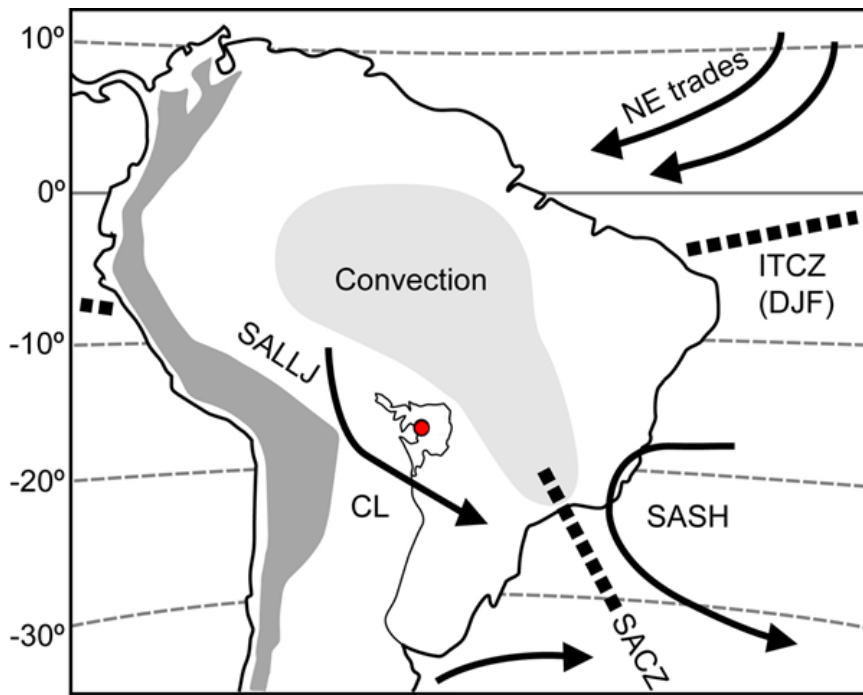


Figure I.4: Schematic map of climate features in tropical and subtropical South America (adapted from Whitney et al., 2011). This map expresses climatic features during December-January-February (DJF) when the Intertropical convergence zone (ITCZ) is at a southerly position and the South American summer monsoon (SASM) is at its peak. The South American low-level Jet (SALLJ) brings convective moisture from the Amazon basin to the Pantanal basin via the eastern foothills of the Andes and correlates with an intensified Chaco Low (CL). The SALLJ converges with the South Atlantic subtropical high (SASH) to form the South Atlantic convergence zone (SACZ) which brings moisture to SE Brazil. The red circle denotes the location of LLG.

The climate of South America today is strongly coupled to the latitudinal positions of the ITCZ, a low pressure belt of warm, moist air near the equator (Ruddiman, 2001). The position of the ITCZ follows a seasonal pattern due to the strong linkage between variations in atmospheric and oceanic conditions. The ITCZ abruptly shifts from the northernmost position during boreal summer to its southernmost position during austral summer. During austral summer in South America when the ITCZ is at its southernmost position, moisture is transported by trade winds from the equatorial Atlantic towards the Amazon basin causing the South American Monsoon (Gan et al. 2004). During the winter season, the ITCZ moves to its northernmost position at 10°N (Figure I.5).

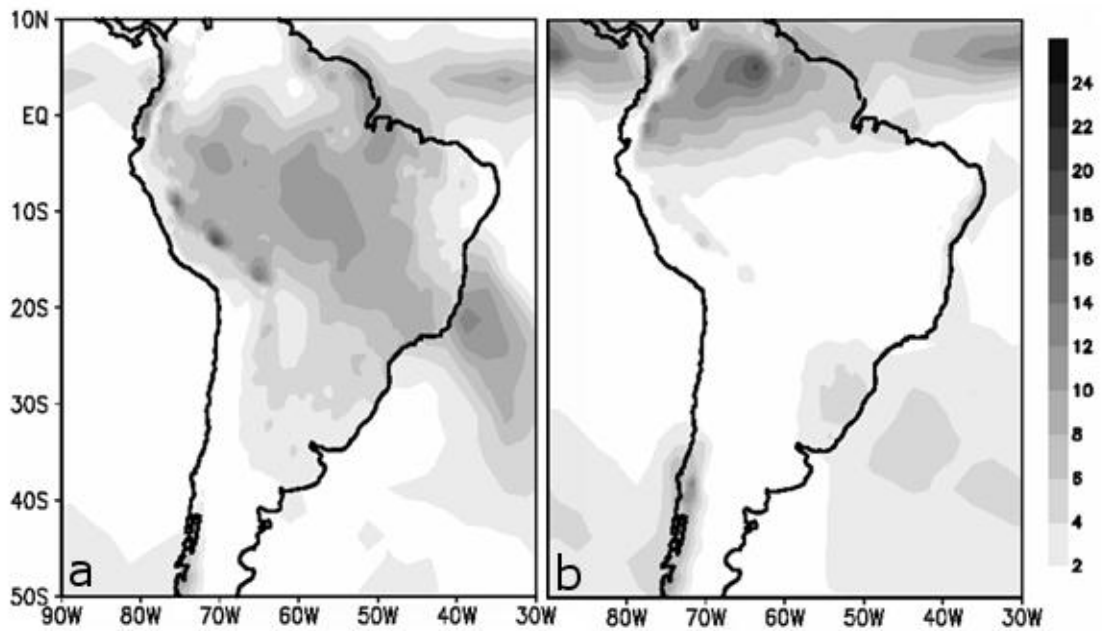


Figure I.5: Modelled results of present day precipitation over South America in a) January and b) July (adapted from Garreaud, 2009).

The Pantanal wetland covers approx. 135,000km² of the Upper Paraguay drainage basin. (Figure I.6). It is the world's largest freshwater wetland and the hydrologic basin of the Upper Paraguay River. Mean annual precipitation in the Pantanal is 1000-1700mm and is highly seasonal. Widespread flooding occurs in the austral summer from December to February and the mosaic of ecosystems comprising the Pantanal is defined by this flooding. The Pantanal is an active sedimentary basin filled up with a thick sequence of Quaternary sediments. Many of the geomorphological features are relicts of a complex history of palaeoclimatic and palaeogeographic changes that have been occurring since the Late Pleistocene (Assine and Soares, 2004). Topography and seasonal climate of the Pantanal give a striking combination of mesic and xeric vegetation growing side by side. The Pantanal wetland borders the eastern edge of Chiquitano Seasonally Dry Tropical Forest and the vegetation make-up depends on topography and flooding regimes (Dubs 1992, Alho 2005).

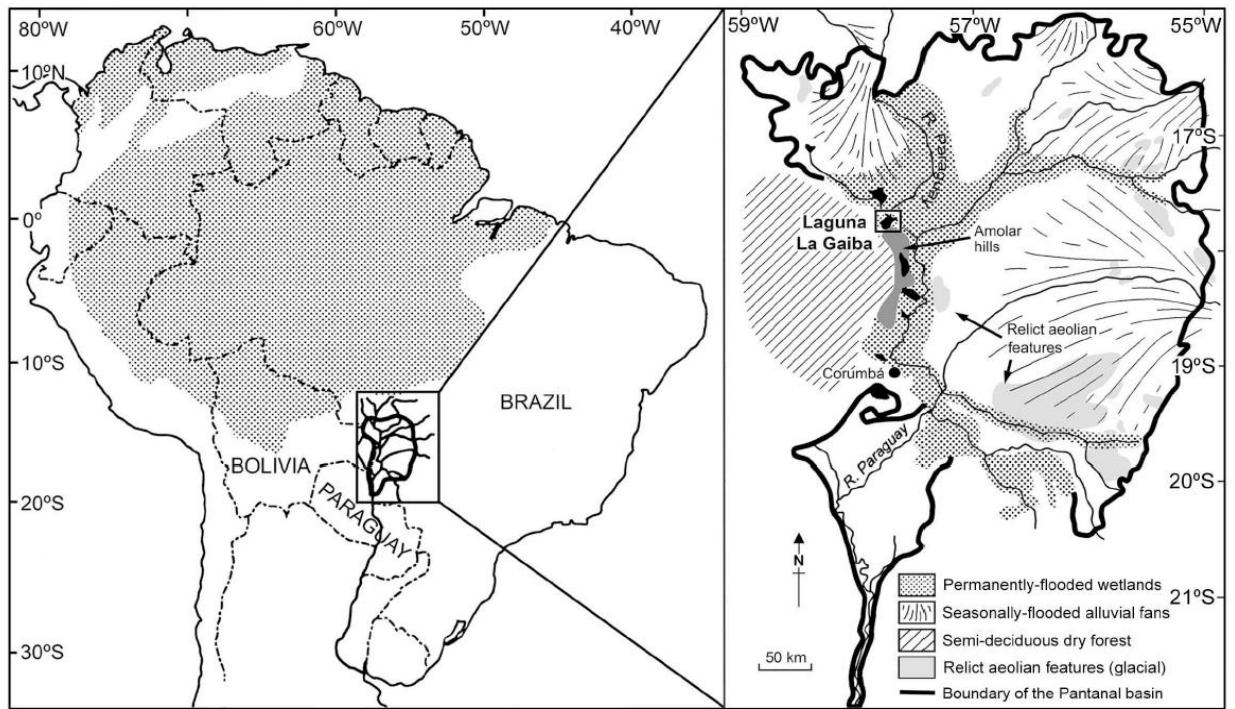


Figure I.6: *Left panel:* Location of the Pantanal wetland in relation to the Amazon rainforest (shaded). *Right panel:* Location of study site Laguna La Gaiba in relation to surrounding forest (Courtesy of Whitney, 2009).

Laguna La Gaiba (LLG) ($17^{\circ}45'S$, $57^{\circ}40'W$), is situated on the western edge of the Pantanal wetlands and is one of the largest lakes in the Pantanal ($50\text{-}95\text{km}^2$). The Pantanal is dotted with thousand of lakes and LLG is situated on the River Paraguay floodplain. The lake is relatively shallow (6 m in its deepest part), well-mixed and consists of a shallower northern portion ($\sim 3\text{m}$) and a much larger, southern portion ($\sim 6\text{m}$) intersected by the River Paraguay, that drains the seasonally-inundated savannahs of the Pantanal, thus the lake is connected to the Pantanal wetlands. Lake levels at LLG peak in the austral summer when 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.



Figure I.7 Photos of Laguna La Gaiba

(A). Evergreen vegetation fringes the lake margin with increasing deciduousness up the steep sided hills.

(B). Sediment rich beaches lay between the lake margin and shallow soils of the bedrock hills (western shore).

(C). Steep-sided Serra do Amolar hills form the steep-sided boundaries of the lake margins (eastern shore).

1.7.2 Hydrology of the Pantanal wetland and its associated lakes.

The hydrology of the River Paraguay, and its tributaries and associated lakes is controlled by (austral) summer precipitation in the Pantanal region (Hamilton, 2002). The River Paraguay runs from north to south along the western edge of the Pantanal wetland. The River Paraguay receives its water from precipitation that falls over the savannahs of the eastern Pantanal basin and western Brazilian highlands, flowing westwards across the low gradient of the floodplains to the river. Water levels in the River Paraguay fluctuate seasonally by 2-5m which is more than water level fluctuation in most other parts of the Pantanal (Hamilton, 2002). Water levels peak several months after the summer months in the River Paraguay and its associated lakes, including LLG. The lag between the monsoon and a peak in lake levels varies with location but, at a measured site closest to LLG in Corumbá, located 135km south of LLG, the lag time is approximately 3 months (Hamilton, 2002, Damasceno-Junior et al., 2005). When water levels are high in the River Paraguay the flow of the tributaries is reversed and flooding occurs on the adjacent floodplain. Therefore, in the region adjacent to the River Paraguay, flooding is indirectly related to annual precipitation, and the extent of inundation in floodplains of the River Paraguay and associated lakes is determined by the height of the river stage (Alho, 2005).

Annual flooding of the River Paraguay shows the most regular, predictable flood pattern in the Pantanal region and the flood pulse is unimodal. The total inundated area at a given time fluctuated between 10,000 and 110,000km² during 1979-1987 (Hamilton, 2002), indirectly influencing the extent of flooding in low-lying areas around the River Paraguay. Although annual flooding is regular, interannual variability in the flooding regime is high. Low precipitation between 1960 and 1973 resulted in a maximum river stage of 3m lower than the succeeding decades in the Pantanal. This halved the maximum inundated area in the Paraguay region of the Pantanal (40,000km²) compared to the following decade (>80,000km²) (Hamilton, 1996; Hamilton, 2002) therefore changes in the flooding regime linked to

A diatom-based Late Quaternary precipitation record for lowland tropical South America precipitation are likely to be recorded in the diatom record as lake levels respond to the amount of precipitation.

Diatoms are a proxy for regional changes in effective moisture (P:E) rather than a direct proxy for the amount of precipitation in a region. As effective moisture rates have not been calculated for LLG, we need to be aware of the hydrology of the Pantanal system and LLG as the assumption is that as precipitation increases, lake levels at LLG will rise and there will be an increase in planktonic habitat. However, groundwater interactions must be taken into account. Evapotranspiration in the Pantanal ranges from 1100-1300 mm per year (Hamilton et al., 1997) which exceeds precipitation during 6 months of the year at least.

Hamilton et al., (2006) investigated flood extent in relation to the seasonality of Pantanal Rivers. However, there is still little information on how flooding proceeds and how a river and groundwater interact, particularly there is no such study of the River Paraguay and how it affects LLG flooding systems. However, a study by Girard et al. (2003) describes water flow between the Cuiabá River in the Pantanal and adjacent floodplain, and surface water and groundwater relations. This may shed some light on the hydrological systems in place at LLG. This study showed that annual flooding of the Cuiabá River was the main mechanism of groundwater replenishment. Recharging the groundwater maintains floodplain channel flow during the low river stage (Girard et al., 2003). Similarly, the LLG groundwater system could be linked to the seasonal flood-pulse which is directly linked to regional precipitation. Indeed, McGlue et al. (2011) notes that “direct rainfall and groundwater inputs are less important to morphometrics and bathymetry than the River Paraguay flood-pulse” in LLG.

In freshwater lakes, changes in ratios of planktonic to non planktonic diatoms can be used to infer lake level change. Diatoms can respond to a variety of environmental conditions that may change as lake levels fluctuate such as changes

A diatom-based Late Quaternary precipitation record for lowland tropical South America in available habitat, chemical conditions, mixing regimes and nutrient concentrations. Therefore, diatoms that are known to respond to particular changing conditions can then be used as a proxy to infer lake level change as well as being a direct indicator for water depth. For example, *Aulacoseira ambigua* is common in open water and the planktonic environment of a lake inferring high lake levels and a deep lake. Another diatom might indicate turbulent conditions, which indirectly infer lowered lake levels. However, as LLG is an open system, equifinality needs to be taken into account; the same diatom assemblage signals may be caused by factors other than water levels change. In an open system such as LLG, a given end state (such a particular diatom assemblage) can be reached by many potential causes.

A tributary channel connects LLG to the River Paraguay and exchange between LLG and the River Paraguay is strongest after the flood wave, occurring several months after peak austral summer precipitation (McGlue et al., 2011). A study by McGlue et al. (2011) shows that in LLG, a broad, sandy fan emanates from the basin sill occupying the northern sub-basin. Average clastic particle size is also higher in the north basin. This suggests that deposition of sediment and a higher energy environment from flooding is concentrated in the north basin. Diatoms from the river environment may be transported into the lake and the percentage of river diatoms found in LLG may be greatest when precipitation is high, flooding is strong and the water levels are high. McGlue et al. (2011) noted that after austral summer monsoon, the flood pulse arrives in LLG and the surface area, fetch distances and bathymetric gradient reaches its maxima as wind speeds begin to reach peak velocity. However, it is unclear what the fluvial-lacustrine diatom environment is like at LLG.

1.8 Thesis aims

Overall, this thesis aims to characterise the modern diatom environment and late Quaternary precipitation in a lowland site in Bolivia. Using diatoms as a proxy for lake level change and combining this record with other proxy indicators will be an invaluable resource and provide crucial insights into the late Quaternary history of South America.

The focused aims of this thesis are presented over 2 chapters and formatted for submission as journal papers.

- Chapter II: The principal aim is to investigate the controlling variables on diatom assemblages in order to explore the potential of diatoms as a tool for palaeo-reconstruction in lowland Bolivia.
- Chapter III: A detailed discussion of late Quaternary precipitation change at LLG with a focus on a diatom record and in particular examining high frequency, millennial-scale events.

The papers will be submitted to *Journal of Paleolimnology* (Chapter II) and *Quaternary Research* (Chapter III).

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II. Diatom ecology in the Pantanal wetlands of tropical South America

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2.1 Abstract

Diatom assemblages preserved in sedimentary successions of the Pantanal basin in the continental interior of South America can provide useful indicators of past environmental changes. Ecological data, however, are scarce. In order to obtain modern data for diatom-based palaeoenvironmental reconstructions, sediment, water and vegetation samples from Laguna La Gaiba (LLG), a lake on the western edge of the Pantanal wetland, were analysed. LLG is a broad, shallow lake intersected by the River Paraguay. Lake depth is maximum of 6m at its deepest point in the southern portion of the lake. A total of 64 diatom species were identified from 41 different samples. Canonical correspondence analysis was used to identify the physical and chemical environmental parameters that best explained the distribution of taxa. *Aulacoseira ambigua* var. *robusta*, *A. distans*, *A. granulata*, *A. granulata* var. *angustissima* and *Cyclostephano* sp. were the most widely distributed species. The highest percentage variance in diatom data from the lake water samples was explained by pH and depth. The diatom assemblages from the surface sediment samples showed a significant relationship with depth. The results obtained in the present work provide useful analogues for late Quaternary lake level reconstruction of Laguna La Gaiba in the Pantanal basin and highlights the potential for the application of this technique in other lowland lakes in the continental interior of South America.

2.2 Introduction

Diatoms are well established as indicators for monitoring modern changes in water condition and also for identifying past environmental changes through analysis of the assemblages preserved in sediments (Moser et al., 1996; Smol and Cumming, 2000). They reproduce rapidly, respond quickly to environmental change and they can be well preserved in lake sediments due to their siliceous cell walls (Cohen, 2003). Diatoms have been used as proxy indicators to reconstruct late Quaternary climate variability worldwide and the application of diatoms for palaeoenvironmental research has increased over the past 30 years (Davies et al., 2002). Diatoms are well established as a palaeoenvironmental proxy in temperate regions and parts of the Neotropics (e.g. Battarbee and Charles, 1986; Fritz et al., 2004; Velez et al., 2005a,b, 2006; Wilson et al., 2008; Metcalfe et al., 2009) but relatively little is known about diatoms as a palaeo-tool in lowland tropical South America.

A number of palaeoclimatological reconstructions have been carried out in tropical regions worldwide and several of these studies include reconstructions of water level by diatom analysis (Bradbury, 1989; Metcalfe & Hales, 1994; Gasse et al., 1997; Bradbury, 1999; Baker et al., 2001a; Velez et al., 2006; Fritz et al., 1999, 2007; Metcalfe et al., 1995, 2007). Interpretation of these studies is qualitative and generally relies on autecological data from areas other than the study site combined with (usually more limited) autecological data from the study area. In order to interpret paleolimnological records accurately, information is needed on the ecological requirements of diatoms and the availability of this information from all over the world has increased (e.g. Gasse et al., 1983; Servant-Vildary and Roux, 1990; Jones et al., 1993; Metzeltin and Lange-Bertalot, 1998, 2007; Rumrich and Lange-Bertalot, 2000).

Diatoms have been used widely for reconstructing water balance change by inferring lake level change as fluctuations in lake levels affect the habitats available for diatom colonization. However, caution needs to be exercised when reconstructing water level changes from open drainage lakes as reconstructions from these systems can be problematic. Closed basin lakes are better recorders of local and regional hydrology as the basin experiences changes in water volume (depth) and water chemistry (e.g. pH and salinity) that are mainly caused by variations in the precipitation-evaporation balance (Wolin and Duthie 1999). However open basin lakes are more likely to be affected by the hydrological inputs and outputs of the system and therefore do not reflect such a clear record. Freshwater diatom assemblages respond indirectly to changes in the aquatic ecosystem which result from changes in water level, but in open-systems in particular, these same environmental changes can be caused by other environmental perturbations such as changes in water chemistry including nutrient availability, salinity concentrations and pH. Therefore, gaining modern diatom assemblage information, combined with environmental variables, is vital for understanding the modern aquatic environment so inferences about fossil diatom reconstructions can be made (Juggins, 1992; De Sève, 1999; Jiang et al., 2001).

In freshwater systems, lake level signals are usually recorded as increases of deep water or planktonic forms when lake levels rise and increases in species inhabiting shallow environments (such as benthic or aerophilous forms) when lake levels fall (Wolin and Duthie, 1999). This is not always the case, however; in lake Titicaca (Tapia et al., 2003) during lake high stands the lake floods into the surrounding basin and therefore vastly increases the area of shallow and littoral environments and so an increase in precipitation and therefore lake level rise is indicated by higher abundance of epiphytic, aerophilous and benthic diatoms. For that reason, it is essential to know the bathymetry of the study lake so proper inferences about diatom ratios can be made.

While there are an abundance of studies of present-day diatoms globally, information about the diatom flora of South America is incomplete and the diatoms of the tropical lowland interior are poorly studied. The most recent and general analyses of South American diatom flora were carried out by Metzeltin & Lange-Bertalot (1998, 2007) in tropical areas, by Rumrich et al. (2000) in the Andes from Venezuela to Tierra del Fuego, by Velez et al. (2005a) in northern South America and Metzeltin et al. (2005) from temperate zones. There are some modern diatom studies in South America from lake surface sediments such as Miretzky et al. (2002) in Chascomús Lake (Argentina), Sylvestre et al. (2001) in Araruama lagoon (Brazil), Nascimento et al. (2010) in Caçó lake (NE Brazil) and Hassan et al. (2009) in southern Pampas (Argentina). However, the understanding of diatom taxa related to environmental variables is lacking compared to other regions such as North America and Europe (Lotter et al., 1997; Rosén et al., 2000; Reavie and Smol, 2001; Bigler and Hall, 2003). As interpretations of the fossil diatom records from the southern hemisphere tropics of South America (SHTSA) are largely restricted to the Andean Altiplano and the modern ecological data used in these studies is often based on autecological data from elsewhere (Morales et al., 2008), studies that directly consider diatom ecology from the lowland SHTSA are needed to be able to reconstruct diatom-based records from this region. As yet, the diatom flora from the Bolivian lowlands is poorly studied (Morales et al., 2009).

Although Laguna La Gaiba (LLG) in the Bolivian lowlands is not a closed-basin system, it is in an ideal location for palaeoprecipitation reconstruction for the SHTSA. LLG is centrally situated within South America between the sites of major palaeoclimate archives (Figure II.1); limnological records in the Bolivian Altiplano, (Baker et al., 2001a, 2001b; Fritz et al., 2007, 2010) and speleothem records from NE and SE Brazil (Auler 2004; Wang et al. 2007) and therefore well placed for filling in the palaeoclimate record gap in continental South America (Whitney et al., 2011). Lake levels at LLG peak when summer monsoon rainfall drains from the low-lying terrain in the Pantanal region and adjacent Brazilian highlands, causing the river

A diatom-based Late Quaternary precipitation record for lowland tropical South America 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 (Whitney et al., 2011).

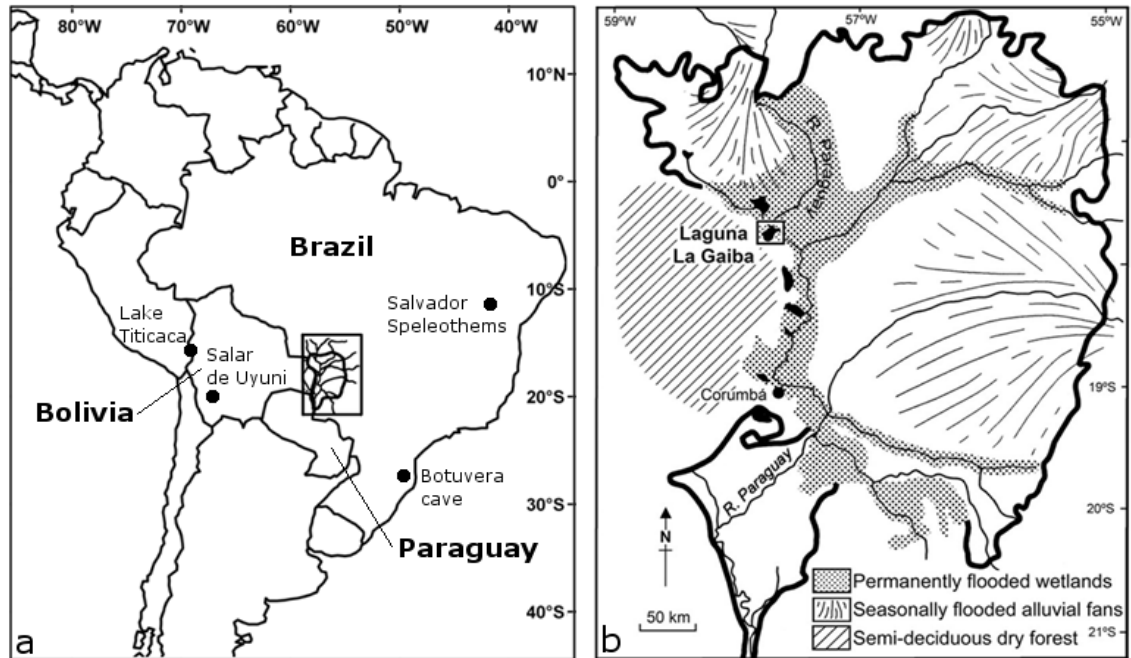


Figure II.1: (a) Location of the Pantanal basin relative to South American countries and sites of palaeoclimatic archives from Bolivian Andes and eastern Brazil, (b) The study site, Laguna La Gaiba, is situated along the Rio Paraguay and lies between the permanently flooded wetlands and gallery forests 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 (adapted from Whitney, 2009).

2.2.1 Environmental setting

Laguna La Gaiba ($17^{\circ}45'S$, $57^{\circ}35'W$, LLG), is a large shallow lake on the western edge of the Pantanal basin LLG and has an average area of 95km^2 . The River Paraguay runs through LLG and they are both hydrologically linked to the Pantanal basin (Figure II.1). The seasonally flooded Pantanal is the world's largest tropical wetland ($\sim 135,000\text{km}^2$) and together with the Brazilian highlands constitutes the headwaters of the River Paraguay. The wetland is located in a tectonic depression in the lowland, continental interior of the SHTSA. To the north of the Pantanal is the Brazilian shield and to the west is the Andean foreland (Clapperton, 1993; Alho,

A diatom-based Late Quaternary precipitation record for lowland tropical South America (2005). Most of the rainfall in the Pantanal region falls in the austral summer causing extensive flooding and the Pantanal is able to retain large amounts of rainfall. Mean annual rainfall in the Pantanal is 1000-1700mm and the climate is characterized by a 6 month dry season (Hamilton, 2002). Water levels peak several months after the summer months in the River Paraguay and its associated lakes, including LLG. Although LLG is an open-drainage system, it is climatically sensitive and responds to climate variations over a regional area. LLG is intersected by the River Paraguay however, the southern part of the basin is bounded by hills and the bathymetry is broad and flat, demonstrating < 1 m change across much of the south basin (Figure II.2). As much of the lake is bounded by hills and due to the shape of the (southern) lake basin, a rise in lake level should increase the abundance of planktonic diatoms rather than littoral diatoms as was the case in Lake Titicaca (Tapia et al. 2003). The northern part is hydrologically connected to the Pantanal wetland which means that changes in the water volume and water chemistry are reflective of a very large area.

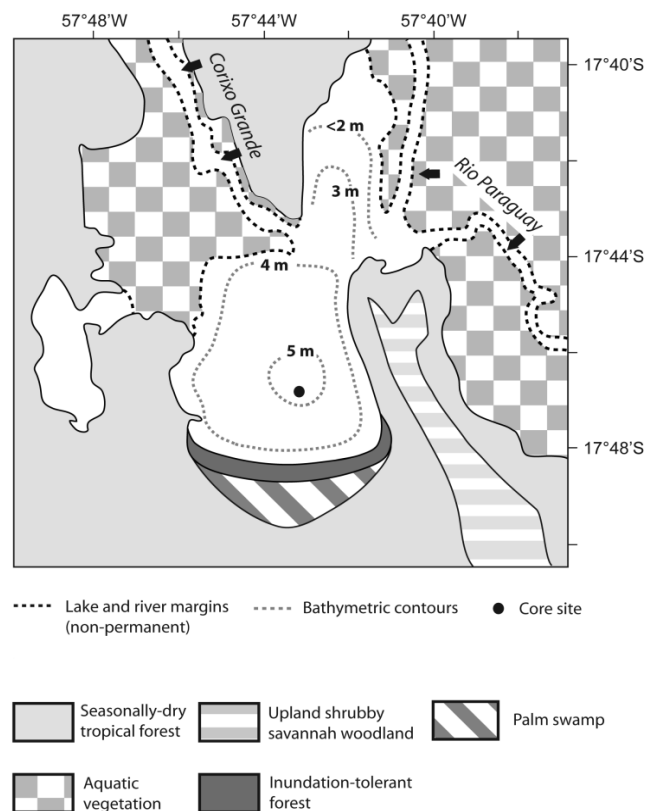


Figure II.2: Schematic map of modern LLG catchment bathymetry. Bathymetry contours were based on depth data taken in 2008 (Figure II.4). LLG is comprised of two distinct portions; the shallower, smaller, northern portion and the deeper, larger southern portion.

In turn, there is evidence that water level changes and river flow in the Pantanal and connecting river systems reflect climatically forced precipitation changes.

Collischonn et al. (2001) found that flow from the river Paraguay and changing water levels at a gauging station on the River Paraguay were linked to rainfall measurements across the Pantanal. Figure II.3 shows inundation measurements in the Pantanal derived from inter-annual and decadal variability in the river stage (Hamilton et al., 2002). Heightened river stage and rising lake levels result from the slow draining of monsoon precipitation from the 140,000 km² catchment of the Pantanal basin. Therefore, as LLG is connected to the River Paraguay, there is a direct relationship between river flooding and LLG lake-level, and so changes in water level at LLG are reflective of precipitation over a wide area.

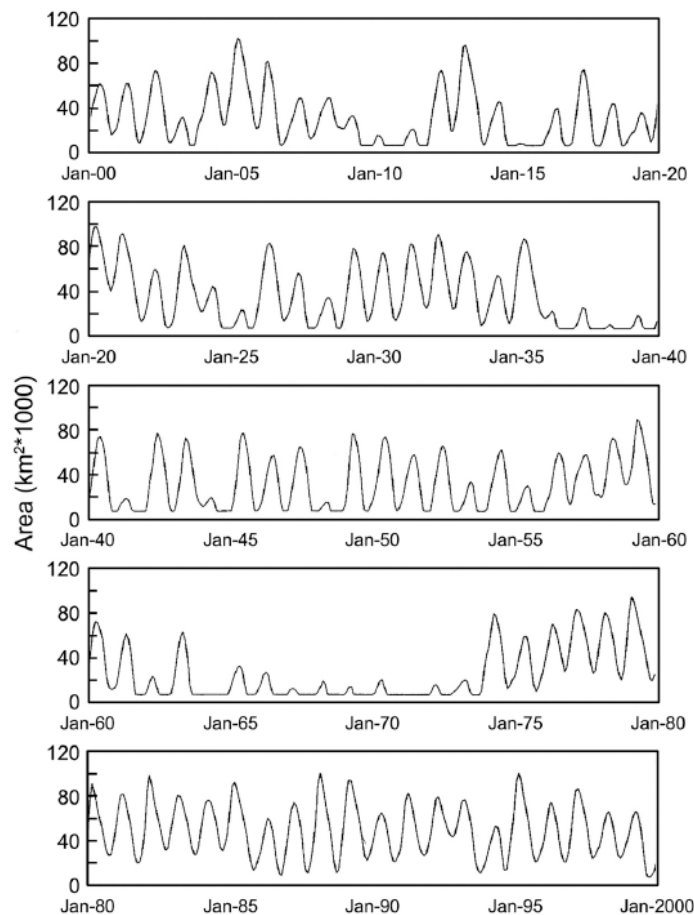
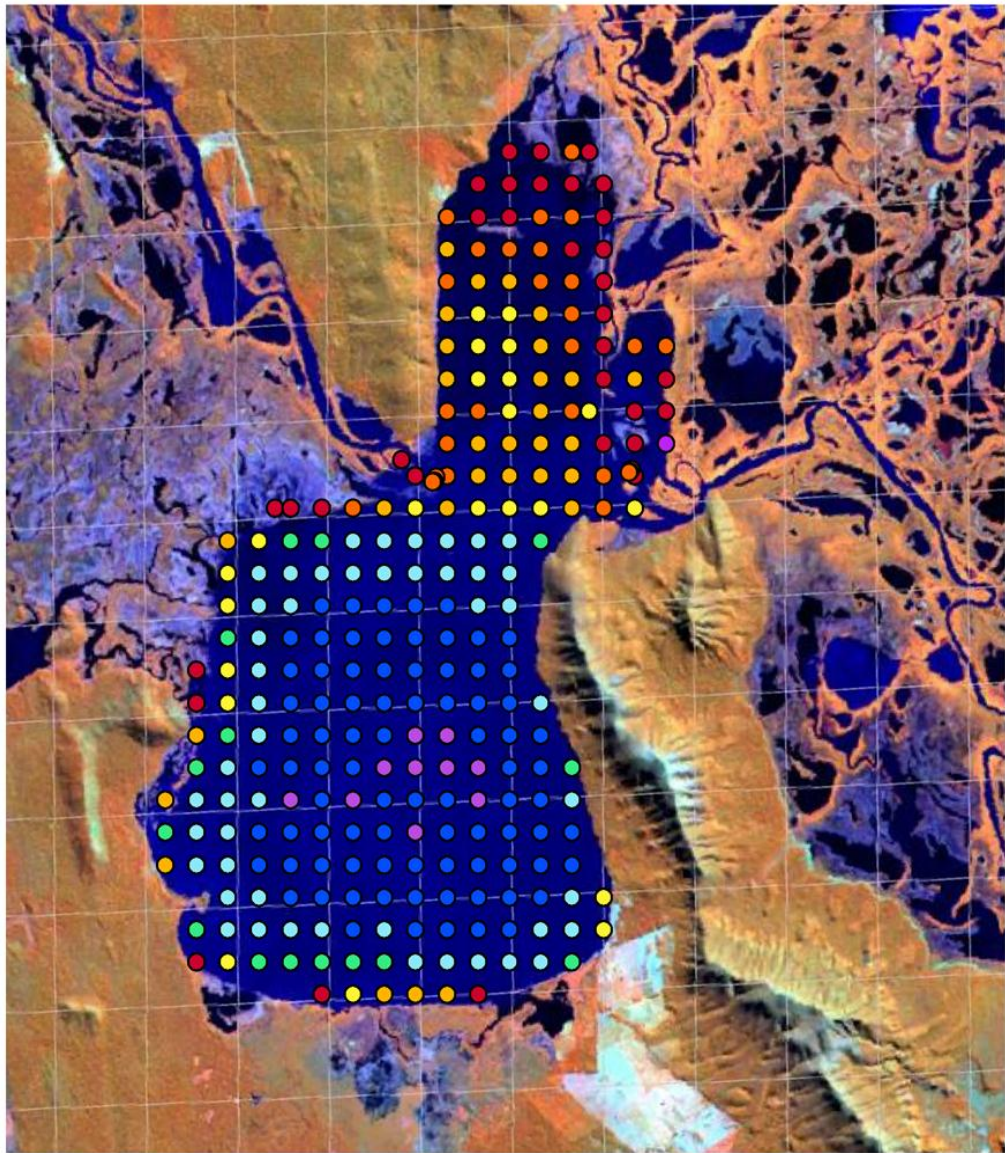


Figure II.3: Rivers stage measurements show the area of the Pantanal inundated over the last century as calculated by Hamilton et al. (1996). Remote sensing data (from between 1979-1987) was used to produce a predictive relationship between the river stage and the inundated area. Figure adapted from Hamilton (2002).

A diatom-based Late Quaternary precipitation record for lowland tropical South America

Maximum water depth in LLG varies from 4-6m. There are 2 distinct portions to the lake intersected by the River Paraguay (Figure II.2). The northern part is shallower (~3m) and merges with the Pantanal wetlands on the east and the western margin is bounded by hills. The southern part of the lake is deeper (~4-6m) and is bounded on almost all sides by steep hills. Sediment rich beaches fringe the southern margin of the lake. Aquatic grasses and water hyacinths (*Eichhornia* spp.) are present in the northwestern margin of the south portion of the lake and the eastern margin of the north portion of the lake. Figure II.2 shows a schematic of the bathymetry of LLG. This schematic map is based on depth data taken in August 2008 from 270 points across the lake (Figure II.4).



- 1.6 - 2.0
- 2.0 - 2.5
- 2.5 - 3.0
- 3.0 - 3.5
- 3.5 - 4.0
- 4.0 - 4.5
- 4.5 - 5.0
- 5.0 - 5.5

Figure II.4: Landsat image of LLG and the surrounding terrain. Coloured circles correspond to water depth (m) measured at 270 points across LLG (August 2008).

Lake depth was also taken by hand using a plumb line from the lake during the dry season in 2006 and 2008. Overall water depth at LLG in the 2006 dry season was likely 0.84 m higher than in 2008 dry season (see methods section for calculations). This highlights the intra-annual variation in water depth. Annual inundation measurements from the Pantanal (Figure II.3) and water depth measurements from the River Paraguay (Figure II.5) show that the level of inundation of the Pantanal is linked to river depths in its connecting rivers. Low precipitation between 1960 and 1973 resulted in a maximum river stage of 3m lower than the succeeding decades in the Pantanal. This halved the maximum inundated area in the Paraguay region of the Pantanal (40,000km²) compared to the following decade (>80,000km²) (Hamilton, 1996; Hamilton, 2002). These figures not only illustrate the seasonality of the Pantanal basin and its connecting rivers and lakes but also the fluctuation of lake depth over a 100 year period (Hamilton et al., 1996; Junk et al., 2006). There are very few studies of diatoms in the Pantanal.

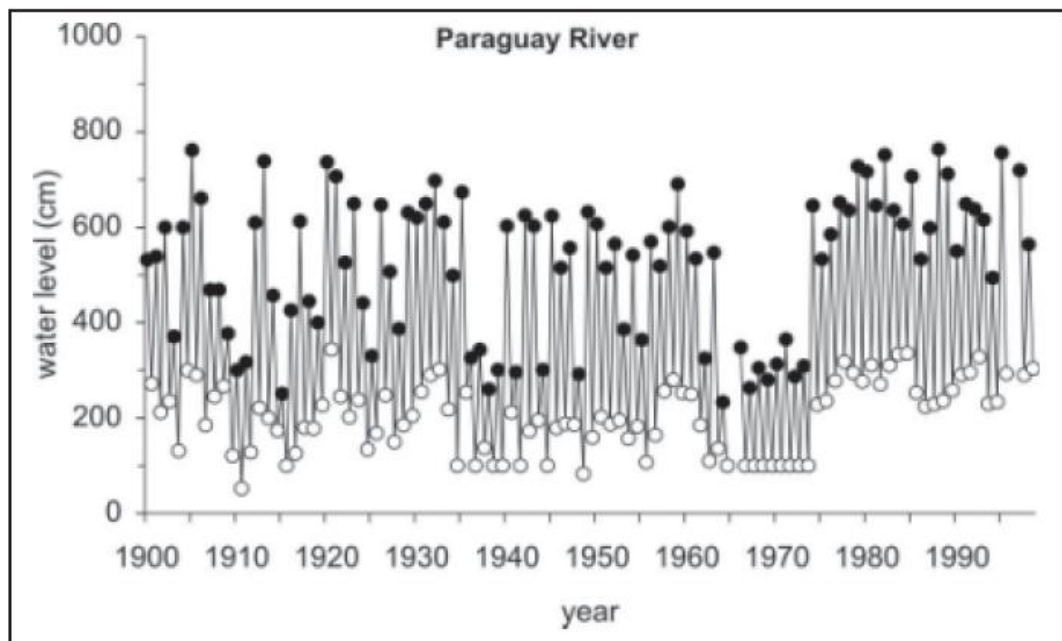


Figure II.5: Annual water level fluctuations of the Paraguay River at Ladário from 1900 to 2000 (data according to DNAEE – Departamento Nacional de Águas e Energia Elétrica). ● = maxima; ○ = minima. Figure adapted from Junk et al. (2006).

Due to the lack of modern diatom studies in the lowlands of continental South America, it is not clear what the diatom blooming patterns are on a seasonal basis. Melack (1979) found that most tropical lakes exhibit pronounced seasonal fluctuations and the phytoplankton blooms usually correspond with variations in rainfall and river discharges. This is likely associated with nutrients released into the water from the seasonal floods (Loverde-Oliveira and Huszar, 2007). A study from Sá Mariana Lake in the eastern Pantanal noted that diatoms might be among the dominant phytoplankton species in the lakes that form the Pantanal complex. Many of the Pantanal lake systems have a high degree of connectivity and are submitted to annual fluctuations in water level, like LLG. These variations promote transformations in the limnological properties and in the structure of the aquatic communities, which respond with adaptations to the flood pulse (Loverde-Oliveira and Huszar, 2007). The seasonality of the phytoplankton of Sá Mariana lake was strongly related to the flood pulse, with high biomass in the low water phase and peaks occurring in high waters. As there is an influx and outflux of materials into the lakes of the Pantanal, nitrogen can be thought as limiting to phytoplankton growth in the lake, which has been argued by other authors writing about tropical regions (Lewis, 1996).

To gain a water level signal from the study area (as a proxy for palaeoprecipitation) we first need to know if the present day diatom assemblages are controlled by water depth. Water depth is one of several limnological parameters that diatoms respond to, others being pH, salinity, conductivity, nutrient availability, turbidity and temperature (Wolin and Duthie, 1999). The purpose of this study is to determine the key environmental controls upon diatom assemblages in LLG. If water depth is found to be a key control, then diatoms at LLG have the potential to provide a powerful proxy for lake level change and consequently precipitation change in the poorly studied heart of tropical South America.

2.3 Methods

2.3.1 Field methods

During the dry season in August of 2006 and 2008, diatom samples were taken from different aquatic ecosystems in LLG including open lake water, shallow littoral environment, river inflow and outflow, vegetation and rock scrapings. It should be noted that although the samples were taken in the dry season, lake levels at LLG were still relatively high as it takes several months for the Pantanal basin to drain after the annual summer floods (Hamilton, 2002). Environmental variables including pH, temperature and water chemistry were analysed to investigate the diatom species composition in these habitats and the environmental parameters that control the assemblages. Many studies have linked changes in diatom assemblages to changes in water chemistry such as pH, nitrogen and phosphorous (Carrick et al., 1998; Pan et al., 1999; Winter and Duthie, 2000). Diatoms are very sensitive indicators of water depth and chemistry fluctuations which are driven by local hydrological factors (Gasse et al., 1997; Telford et al., 1999) and by changes in the precipitation-evaporation (P-E) balance in the catchment area (Fritz et al., 1999). pH and water chemistry were measured to provide information on the chemical facies which may change, depending on the mineral precipitation processes, especially that of carbonate minerals (Chalie and Gasse, 2002). The nutrients, phosphate and nitrate were measured to determine the nutrient concentration of the lake and also spatial variation in nutrients as an indicator of nutrient input from the River Paraguay. Alkalinity was tested as the concentration of alkalinity in a lake may determine the lake environments ability to “buffer” against changes in pH and may also be an indicator of the influence of in-wash into the lake. Chloride was measured to indicate the salinity of LLG.

Where possible, water depth was taken at the sample site. This was not possible for the rock samples and vegetation samples that were taken on the lake shore. Figure II.6 shows the location of all of the sites samples in 2006 and 2008. Although the

A diatom-based Late Quaternary precipitation record for lowland tropical South America sampling regime is less than exhaustive, the importance of these data lies in their rarity, as relatively few diatom ecological samples from lowland tropical lakes have been acquired.

In 2006, nineteen surface sediment samples, and eight 500 mL water samples were collected from three different lake environments of LLG (shallow, macrophyte-dominated lake margins; deep, open water; river inflow/outflow). Due to time constraints, it was not possible to obtain surface sediment samples in the field season of 2008. The uppermost 1 cm of sediment was collected using a Perspex® tube and piston. Samples were extruded in the field and stored in airtight plastic jars. Water depth was measured with a plumb line. For the water samples, basic water chemistry and lake parameters were measured at each site (Table II.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. Lugol's iodine solution (50g potassium iodide, 25g iodine in 500ml distilled water) was added to the vegetation samples to kill the zooplankton and preserve the algae.

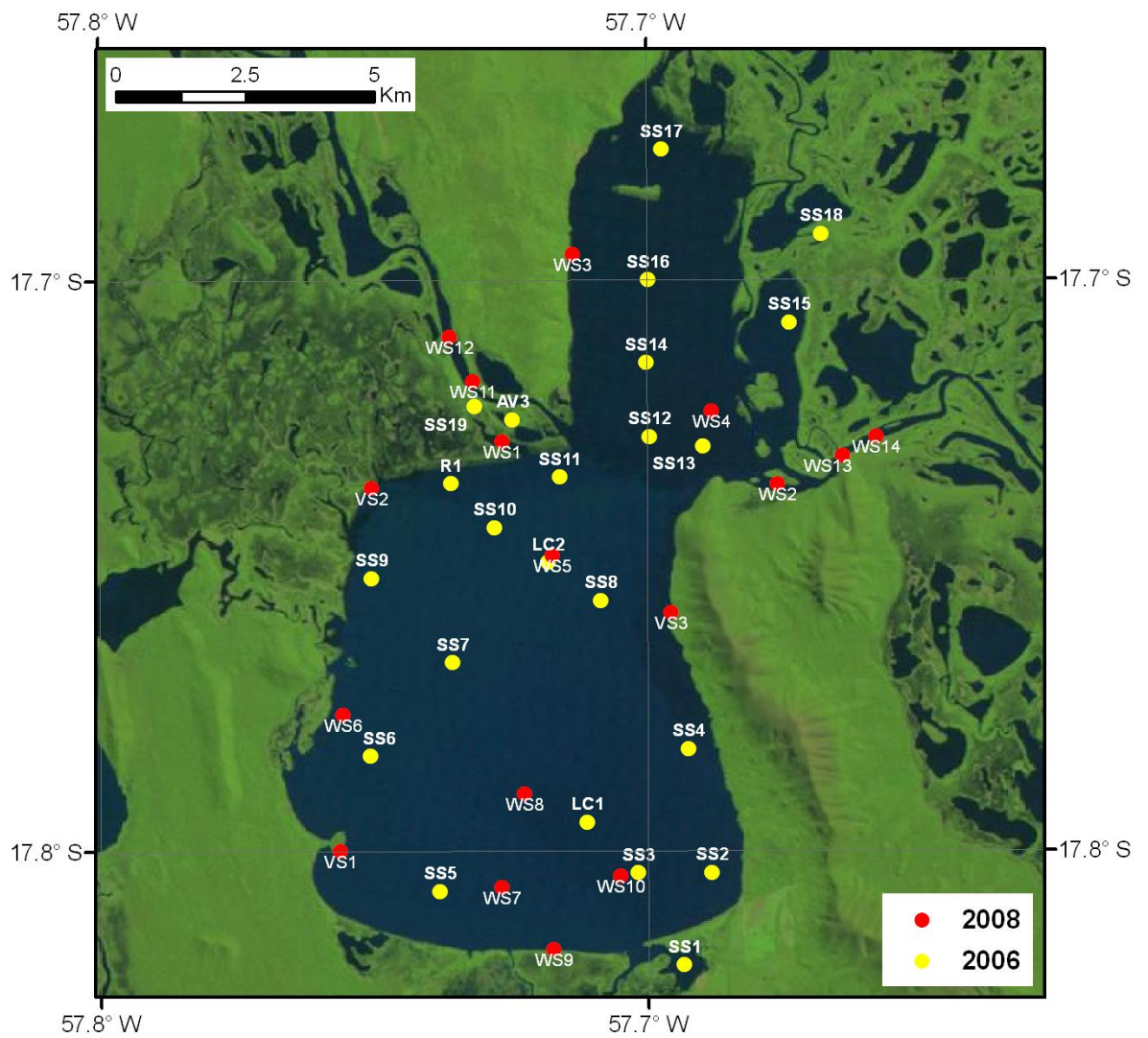


Figure II.6: Landsat image of LLG from July 2009 showing sample sites. Refer Table II.1 for water chemistry of 2006 and 2008 water and vegetation samples.

Sample No.	Site	Year sampled	Depth (m)	Temperature (°C)	Conductivity ($\mu\text{S cm}^{-1}$)	pH	PO ₄ (mg/L)	Cl (mg/L)	A _T (mg/L)	NO ₃ (mg/L)
WS1	North basin	2008	2.6	27.5	62	7.7	<1	10	40	0
WS2	North basin	2008	2.75	27.3	63	8.2	<1	10	35	0
WS3	North basin	2008	2	28.9	60	8.1	<1	10	35	0
WS4	North basin	2008	3.25	27.9	60	8.1	<1	10	35	0
WS5	South basin	2008	5.5	27.8	65	8.3	<1	10	35	0
WS6	South basin	2008	2.8	27.9	83	7.7	<1	10	40	0
WS7	South basin	2008	2.5	28.4	73	8.2	<1	10	40	0
WS8	South basin	2008	5.3	27.3	68	8.6	<1	10	40	0
WS9	South basin	2008	1.4	29.5	74	8.3	<1	10	40	0
WS10	South basin	2008	5.5	27.6	70	8.6	<1	10	35	0
WS11	River inflow	2008	4.6	28.2	65	9	2	10	40	0
WS12	River inflow	2008	3.7	27.7	64	9.1	<1	10	35	0
WS13	River outflow	2008	12.7	26.9	63	9.3	<1	10	35	0
WS14	River outflow	2008	4.9	26.9	63	9.3	<1	10	35	0
VS1	South basin	2008	N/A	28.4	55	9.8	N/A	N/A	N/A	N/A
VS2	South basin	2008	N/A	28.6	74	10	N/A	N/A	N/A	N/A
VS3	South basin	2008	N/A	28.7	68	9.7	N/A	N/A	N/A	N/A
LC1	South basin	2006	5.1	26.4	75	8	0	N/A	N/A	0

Sample No.	Site	Year sampled	Depth (m)	Temperature (°C)	Conductivity ($\mu\text{S cm}^{-1}$)	pH	PO ₄ (mg/L)	Cl (mg/L)	A _T (mg/L)	NO ₃ (mg/L)
LC2	South basin	2006	5.82	25.6	68	8	1.5	N/A	N/A	0
AV1		2006	0.62	26.9	81	7.7	0	N/A	N/A	0
AV3		2006	3.05	25.8	63	7.1	2	N/A	N/A	0
R1		2006	3.54	24.8	77	7.3	2	N/A	N/A	0

Table II.1: Water chemistry from all modern water and vegetation samples.

In 2008, a further thirteen water samples and three vegetation samples were collected from open water in the north and south basin and the river inflow/outflow. Samples were taken from the river inflow and outflow to determine whether the diatom assemblage composition in the river is distinct from the lake and if river inhabiting diatoms can be found in the surface sediments of the basin. This will highlight whether the river has an influence on the diatom species assemblage, as there can be great variability in habitat conditions in a river such as turbidity, nutrient concentrations and pH. When making palaeoenvironmental inferences, we can consider the influence of the River Paraguay on LLG by assessing how significantly diatoms deposited in LLG sediments reflect the diatom assemblages from the River Paraguay. It is possible there will be very little difference in the diatom assemblages in the lake centre and the river. A study conducted in Italy in a large lake which has varied lake bed morphology and sediment processes, a single sediment sample from the lake was similar to cores taken in other parts of the lake including the river mouth (Marchetto and Musazzi, 2001).

Water samples were taken by hand from the water column, 1 m down. Depth, water temperature, conductivity and pH were taken at the time of water sample collection. Water samples were tested for nitrate, phosphate, alkalinity and chloride, shortly after collection on the lake shore (Table II.1). As before, Lugol's iodine solution was added to preserve the algae.

2.3.2 Laboratory methods

2.3.2.1 *Particle size analysis*

Particle size analysis (PSA) was performed on surface sediments as a proxy for hydroconnectivity; a high or low energy environment connected to flooding and inwash of particles may have an affect on diatom species composition and also for

A diatom-based Late Quaternary precipitation record for lowland tropical South America lake level; grain-size fluctuations in sediment through time, particularly increases in sand sizes, may reflect low-level lake stands related to periods of drier and warmer climate. Conversely, decreases in sand content may reflect periods of wet climates (e.g., Alin and Cohen, 2003). For particle size analysis, samples were prepared following UCL laboratory methods (1999). Samples were air-dried overnight, crushed and sieved and then treated with dilute HCl and HNO₃ to remove carbonates and organic matter. A dispersal agent was mixed with the cleaned sample before being added to the coulter LS230 particle size analyzer.

2.3.2.2 *Diatoms*

Diatom sample preparation followed Battarbee (1986). Surface sediments were air-dried and then 0.5g was treated with dilute HCl and HNO₃ to remove carbonates and organic matter, respectively. Water samples from the 2008 field season were not treated with chemicals. Samples were simply evaporated onto a cover-slip, mounted onto a glass slide using Naphrax, and examined at 1000x magnification. A minimum of 400 diatom valves were counted per sample, and diatom abundance was calculated as a percentage relative to the sum. Sixty four taxa at the species and variety levels were encountered, representing 15 genera in total. Identification and nomenclature of cosmopolitan diatom species and varieties follows standard texts (Kützing, 1844; Krammer and Lange-Bertalot, 1986a,b, 1991a,b), whereas regionally-specific keys were used for taxa typical of tropical regions (i.e., *Eunotia camelus*, *E. didyma*) (Meltzeltlin and Lange-Bertalot, 1998; Rumrich and Lange-Bertalot, 2000). The diatom nomenclature used here remains unchanged from the source literature. Percent abundance of modern surface sediment samples and key diatom types are presented in stratigraphic plots, constructed using C2 (Juggins 2003) (Figure II.7 and Figure II.9).

2.3.2.3 *LLG lake depth calculations*

Figure II.2 is based on depth data taken with a Lowrance X-65 depth sounder in August 2008 from 270 points across the lake (Figure II.4). Lake depth was also taken using a plumb line from the lake in August of 2006 and 2008. To calculate the average difference in lake depth between 2006 and 2008, a lake depth coordinate from 2006 was compared to its 'nearest neighbour' coordinate and associated lake depth from 2008. This was applied to 6 sites that had the same coordinates for 2006 and 2008. The average difference of these 6 points is 0.84 (standard deviation 0.04).

2.3.2.4 *Multivariate analysis*

Ordination was performed on the diatom data to explore the primary environmental gradients influencing assemblage composition. Diatom species' abundance was calculated as a proportion of the sum of all identified species in each sample. Detrended correspondence analysis (Hill and Gauch, 1980) (DCA) was performed using the 'VEGAN' (Oksanen, 2010) package in the program R (R Development Core Team, 2007) on the relative percent abundance of the diatom species assemblage taxa in the 20 surface samples. To avoid rare taxa causing bias in the analysis, only species with an abundance of >1% in two or more samples were used. DCA was used in favour of correspondence analysis (CA) as DCA flattens the arch that CA creates on the second ordination axis and rescales the positions of the samples along an axis (González et al., 2008) Data were square-root transformed to downweight the dominant taxa. Proportional values were used in all cases because they stabilise the variance in the data (Birks and Gordon, 1985). Data was analysed using DCA to measure the gradient length in community composition. DCA ordination analysis exhibited long gradient lengths of more than 4 standard deviation units and so was deemed appropriate for analysing community variation (Legendre and Gallagher, 2001). For most environmental data with a wide range of variation, such as the modern data set from LLG, non-linear ordination methods such as DCA and CCA are most appropriate. PCA and RDA (linear methods) would

A diatom-based Late Quaternary precipitation record for lowland tropical South America suffice with datasets showing variation across a narrow range. DCA is an indirect form of analysis and this was applied to the diatom data sets only to highlight the community variation and diatom groups in the dataset which could be explained and interpreted by the current knowledge of the LLG environment.

Constrained correspondence analysis (CCA) (ter Braak, 1986) was performed on the water-borne diatom assemblages from LLG to constrain the species distribution by environmental variables. Whereas in the DCA, we first find the major compositional variation and then relate the compositional variation to observed environmental variation, in constrained analysis, most or all of the compositional variation is not displayed, only the variation that can be explained by the used environmental variables, or constraints is displayed (Oksanen, 2010). CCA is a direct rather than indirect form of gradient analysis that is used to directly assess the significance of a range of environmental parameters to explain the variance in the diatom assemblages. CCA is used because it is appropriate to indicate where species with narrow environmental niches can be seen as potential indicators or particular characteristics of an ecosystem. CCA has a particularly attractive feature in that species are ordered along the canonical axes following their ecological optima, allowing relatively easy ecological interpretation of species assemblages (Borcard et al., 2011). CCA is a weighted form of redundancy analysis (RDA) and it shares the same basic properties as correspondence analysis (CA), combined with those of constrained ordination. A gradient length larger than 4 indicates that some species have a unimodal response along the axis (ter Braak and Smilauer, 2002). CCA is based on a CA framework and has a better ability to handle unimodal responses (Oksanen, 2004).

The CCA is based on Chi-squared distances and performs weighted linear mapping. Data were square-root transformed prior to analysis in order to maximise the 'signal' to 'noise' ratio in the data and stabilise the variances (Prentice, 1980; Birks, 1995). The CCA analysis was also carried out using the *R* software package (*R*

A diatom-based Late Quaternary precipitation record for lowland tropical South America development core team, 2006). The main pattern on a CCA ordination plot shows how the environmental variables account for the variation in composition of the biological assemblages and, approximately, the distributions of species along each environmental variable (ter Braak and Verdonschot, 1995). By looking at the projection of a species point onto the axis of the environmental variable, the preference of a species to an environmental variable can be explored. This is because the order of the projected point corresponds approximately to the ranking of the species with respect to that environmental variable (Jiang et al., 2001).

2.4 Results

2.4.1 Fossil diatom species from surface sediments in LLG

The 2006 diatom data-set from surface sediment samples contains 49 diatom taxa present at >1% in two or more samples (Figure II.7). *Aulacoseira ambigua* var. *robusta* and *Aulacoseira ambigua* (Plate 1, on page 83) are the most abundant taxa in the majority of the samples (2 - 60%). To identify between the variety *Aulacoseira ambigua* and *A. ambigua* var *robusta* I used the description from a number of different texts including Kramer and Lange Bertalot (1991), Meltzeltlin and Lange-Bertalot (1998) and the European Diatom Database. From my own observation, the differences between the varieties I identified from LLG are as follows; *A. ambigua* var. *robusta* valves were larger than *A. ambigua*. The pores (areola) were larger and more evenly spaced in *A. ambigua* var. *robusta*. In *A. ambigua* the pores are smaller and are not in a straight line on the valve. *A. ambigua* var. *robusta* is most prevalent in samples from the centre and the south basin of the lake (SS1 – SS13 including the core site). Samples taken from the north basin of the lake (SS14 - SS19) are characterised by the presence of *Eunotia minor*, *E. camelus*, *E. bilunaris* as well as *Gomphonema contraturris* and *Amphora ovalis* (Plate 2, on page 84). Samples from the north basin also contain low numbers of *Aulacoseira distans* (2 – 10%). The presence of *Aulacoseira distans* is much greater (6 – 18%) in samples from the south basin and the centre of the lake (SS1 – SS13 including the cores site) than in the north basin with the exception of SS3 from the south basin where there is only 4%. *A. ambigua* does not demonstrate a strong preference for any particular part of the lake and occurs in high abundance in almost

A diatom-based Late Quaternary precipitation record for lowland tropical South America all samples, in particular the core site where it reaches a value of 60%. *Cyclotella stelligera* (Plate 1, on page 83) demonstrates a habitat preference for the south basin occurring in low abundance (1 – 5%) and in very low abundance (~2%) in two sites in the north basin (SS16 and SS14) and not at all in the other north basin sites.

The core sample has a distinct diatom assemblage from the other modern surface sediment samples. ~60% of the diatom assemblage is comprised of *Aulacoseira ambigua* whereas the other sediment samples from the south basin are dominated by *Aulacoseira ambigua* var. *robusta*. It is possible the assemblages differ, because the core sample was extracted from the top 0-1cm of a long core after it had been extruded for palaeoreconstruction analysis (see chapter 3) but the surface sediment samples were collected at a different time using a different method. The core sample is most likely to reflect the most recent core fossil assemblages, as there may have been an error in sampling the top 0-1cm and this sample is actually representative of the assemblage slightly further down the core where there has been more mixing of sediment material. The other surface sediment samples will reflect the most modern diatom assemblages in LLG.

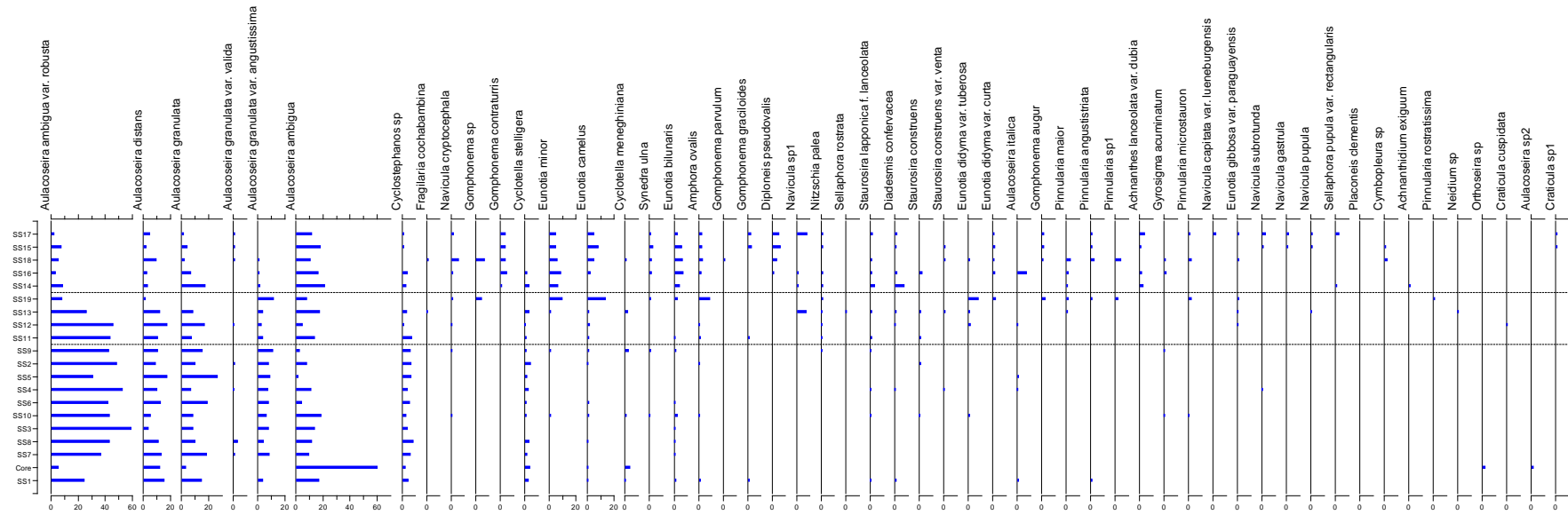


Figure II.7: Plot created in C2 (Juggins, 2003) to show diatom species percent abundance from surface sediments (SS) in LLG taken in 2006. 'Core' refers to the top 1cm of sediment taken from a sediment core in the centre of the southern portion of the lake. Refer to Figure II.6 for site locations.

Figure II.8 shows a DCA of 2006 surface sediment samples. The first two axes of the DCA revealed the main gradients formed by the diatom communities. Axis 1 explains 40% of the variance in the data and the sites from the north basin (SS13 - SS19) are plotting out separately from the sites from the south basin (SS1 - SS11 including the core site) with the exception of SS12 which is located at the intersection of the basins and is plotting out with the samples from the south basin. Species that have a very low presence in the assemblage are plotting out on the extremity of axis 2 (the very top and bottom of the plot (such as *Gomphonema sp.*, *Gomphonema parvulum*, *Eunotia didyma var tuberosa*, *Craticula sp.*, and *Brachysira superserians*) this could be because they are only present in one sample and therefore appear to have very specific ecological habitat requirements (only present in a particular part of the lake).

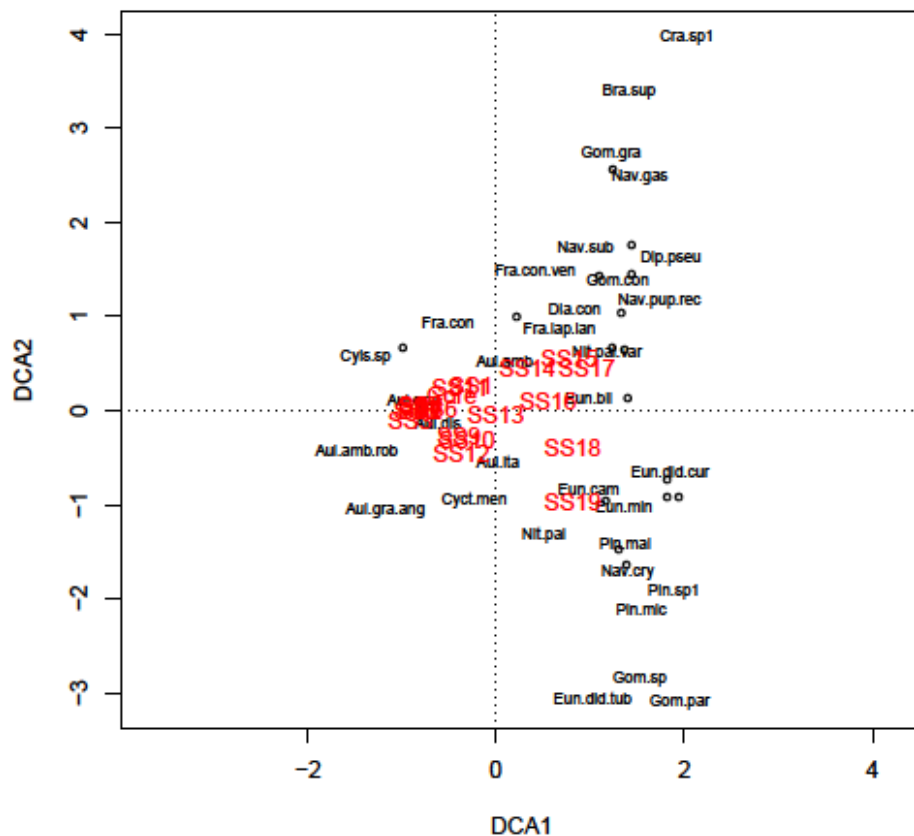


Figure II.8: Detrended Correspondence Analysis (DCA) of relative percent abundance of diatom taxa in LLG surface sediments from 2006. Refer to Figure II.7 for the relative percent abundance of

the taxa at each site. To display species more clearly, a priority argument was used in *R* to give labelling priority to species based on their abundance in the data-set. Other species that were not given priority are marked with a black circle. Abbreviations used for species names can be found in Table A.IV.1.

2.4.2 Diatom species from water and vegetation samples at LLG

The 2008 diatom data set from water and vegetation samples contains 61 diatom taxa present at >1% in two or more samples (Figure II.9). Three water samples from 2006 did not contain any diatoms. Nitrate and phosphate levels of LLG from water samples taken in 2008 were not detectable by the field testing kit. Any water chemistry that was not measurable was not used in statistical analysis. *Aulacoseira distans* (Plate 1, on page 83) is the most abundant species in the data set occurring in all of the samples (7 – 70%) and dominating the assemblage in samples from the south basin (WS5, WS6, WS7 and WS10). *A. ambigua* var. *robusta* (Plate 1, on page 83) is present in all samples and is abundant in most samples with the exception of two from the north basin (WS3 and WS4) and two from the river (WS11 and WS12). Samples taken from vegetation in the lake are characterised by the presence of *Gomphonema contraturris* (Plate 2, on page 84) which is not found in any of the water samples. *Fragilaria cochabambina* has high abundance in the vegetation samples (2 – 37%) and is also prevalent in two samples from the river and two samples from the south basin. It does not occur in the north basin. *Navicula cryptocephala* (Plate 2, on page 84) occurs in all samples from the north basin and the vegetation and has highest values of 9% and 10% from SS11 and SS12 taken from the river. However, it does not occur in any of the water samples from the south basin. *A. granulata* var. *angustissima* does not demonstrate a strong preference for any part of the lake but is most abundant in samples WS3 and WS4 from the north basin where it has values of 20% and 48%, respectively.

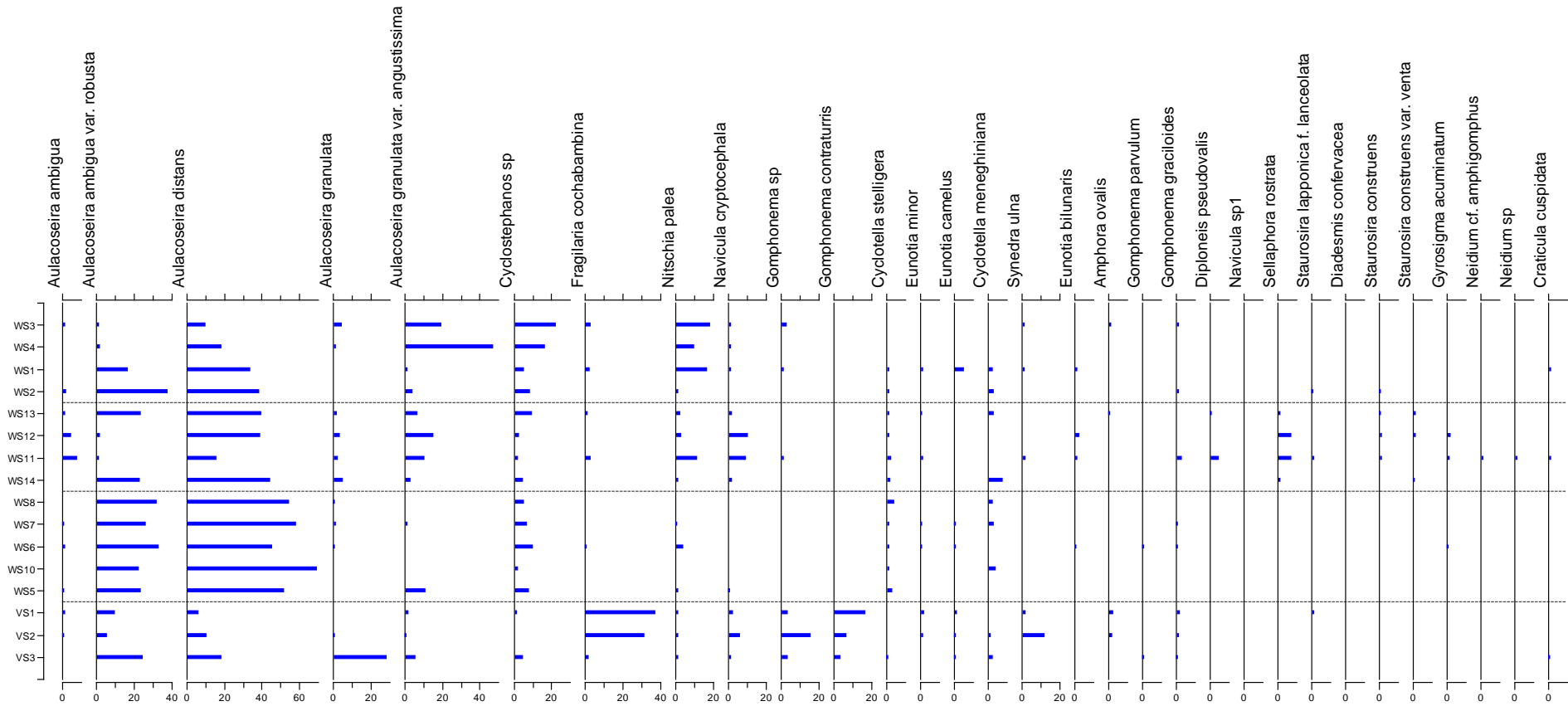


Figure II.9: Plot created in C2 (Juggins, 2003) to show diatom species percent abundance from water samples (WS) taken from 1 m down and vegetation samples (VS) in LLG taken in 2008. Refer to Figure II.6 for site locations

A DCA of water and vegetation sites taken in 2008 (Figure II.10) shows a pattern of community variation among the samples. Vegetation samples are positioned away from all the water samples on the positive side of axis 1 (Figure II.11). They are clearly separated from all of the water samples showing a different species compositional assemblage to the water samples. The river samples (WS11 - WS14) appear to be positioned along a gradient in the negative side of axis 2. All of the water samples from the south basin (WS5, WS6, WS7, WS8 and WS10) are positioned on the negative side of axis 1 and the positive side of axis 2. WS2 is also in this group.

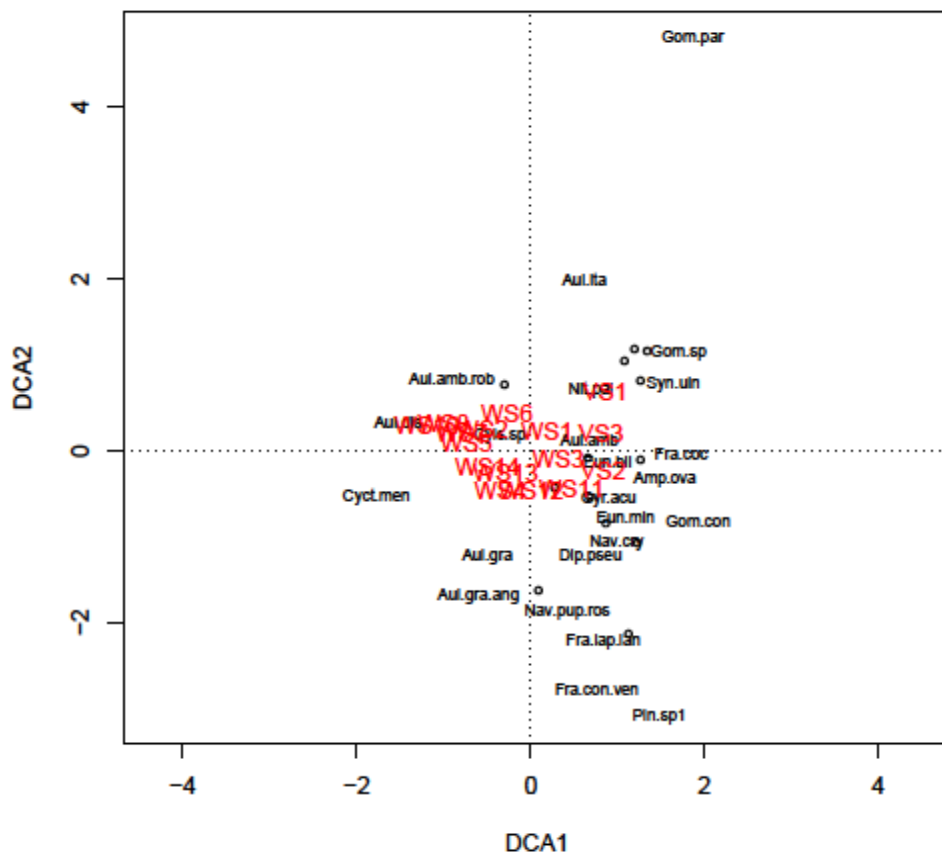


Figure II.10: DCA of relative percent abundance of diatom taxa in LLG water and vegetation from 2008. Refer to Figure II.9 for the relative percent abundance of the taxa at each site. To display species more clearly, a priority argument was used in R to give labelling priority to species based on their abundance in the data-set. Other species that were not given priority are marked with a black circle. Abbreviations used for species names can be found in Table A.IV.1

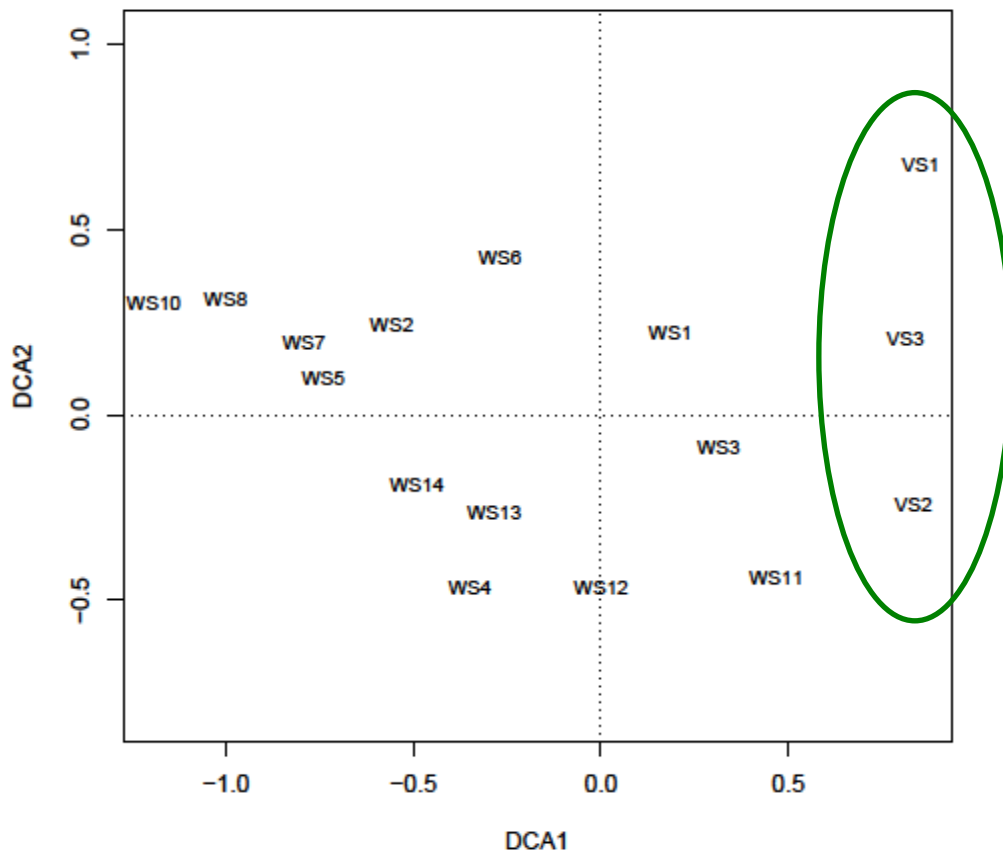


Figure II.11: Detrended Correspondence analysis showing the distribution of water and vegetation samples over axis 1 and 2 of the DCA. Vegetation samples (VS) are circled to highlight their distance from the other water samples (WS) reflecting strong difference in diatom assemblage composition in vegetation samples compared with water samples.

2.4.3 Relationships between diatom species assemblages and environmental variables

A linear regression between grain size and Axis 1 scores from the DCA biplot of the sediment samples was carried out (Figure II.12). There appears to be very little, if any, relationship between the diatom species assemblages and the particle size of the lake sediments. The correlation coefficient (r) was calculated to be 0.061 (sample size, $n=19$). A linear regression between grain size and depth (Figure II.13) also illustrated there is no relationship between these two variables ($r = 0.0008$). Therefore, particle

size analysis of the sediment surface samples from LLG does not reflect variations in diatoms species composition.

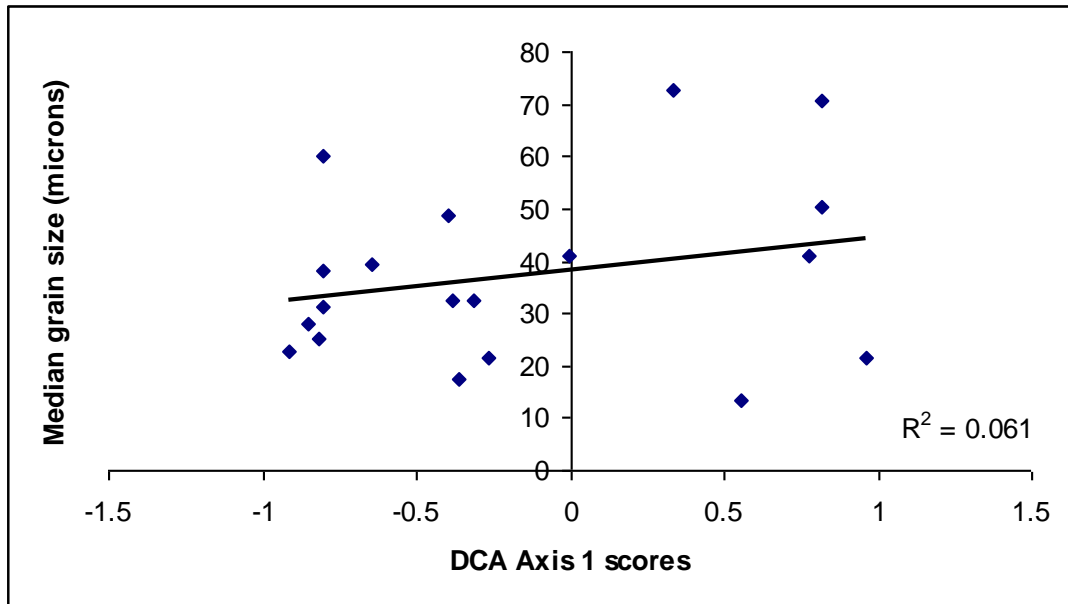


Figure II.12: Scatter plot to show relationship between average grain size of surface sediment samples and DCA axis 1 scores.

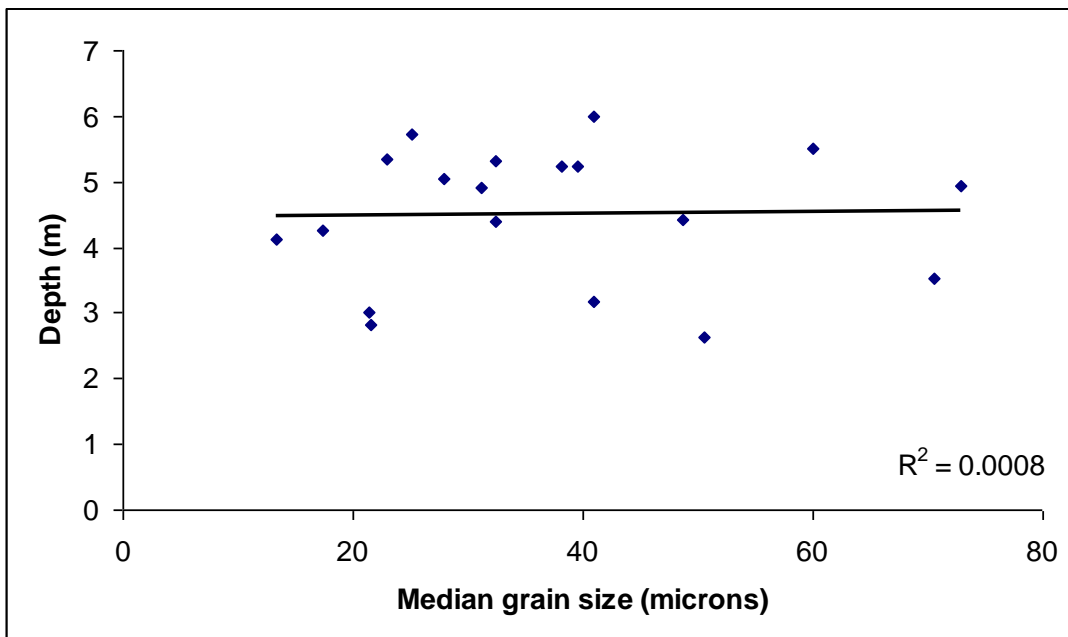


Figure II.13: Scatter plot to show the relationship between average grain size of surface sediment samples and depth.

A CCA was created to explore the relationship between environmental variables and species distribution of the 2008 water samples (Figure II.14). Multivariate analysis
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used 61 diatoms species in 13 water samples from 3 different aquatic environments of LLG; the north basin, the south basin, and the river inflow and outflow. Six environmental parameters are evaluated: pH, temperature, conductivity, alkalinity (AT), phosphate (PO_4) and depth. Water samples from 2008 only were used because it is known that vegetation samples show greater diversity in species assemblage than open water samples (Figure II.11 verifies this in LLG) and by exploring the environmental constraints on samples from the lake environment only, the results are not skewed by vegetation species assemblages and therefore a clearer picture of the lake environment is possible. In CCA, the eigenvalue of an ordination axis is used to show how much variance is accounted for by the variable assigned to that axis. In this analysis, the total inertia, which represents the total variance, is equal to 0.7 and the sum of all constrained eigenvalues is 0.4. CCA indicated that pH is the main factor that influences diatom distribution explaining the highest proportion of variation in the diatom data on axis 1. The cumulative percentage of variance for species-environment relationship was calculated. Axes 1 and 2 explain 45% of the variation in the datasets with the first axis (CCA1) explaining 31% and the second (CCA2) 14%. The angle between pH and depth parameters is very small suggesting a positive correlation between the two environmental gradients.

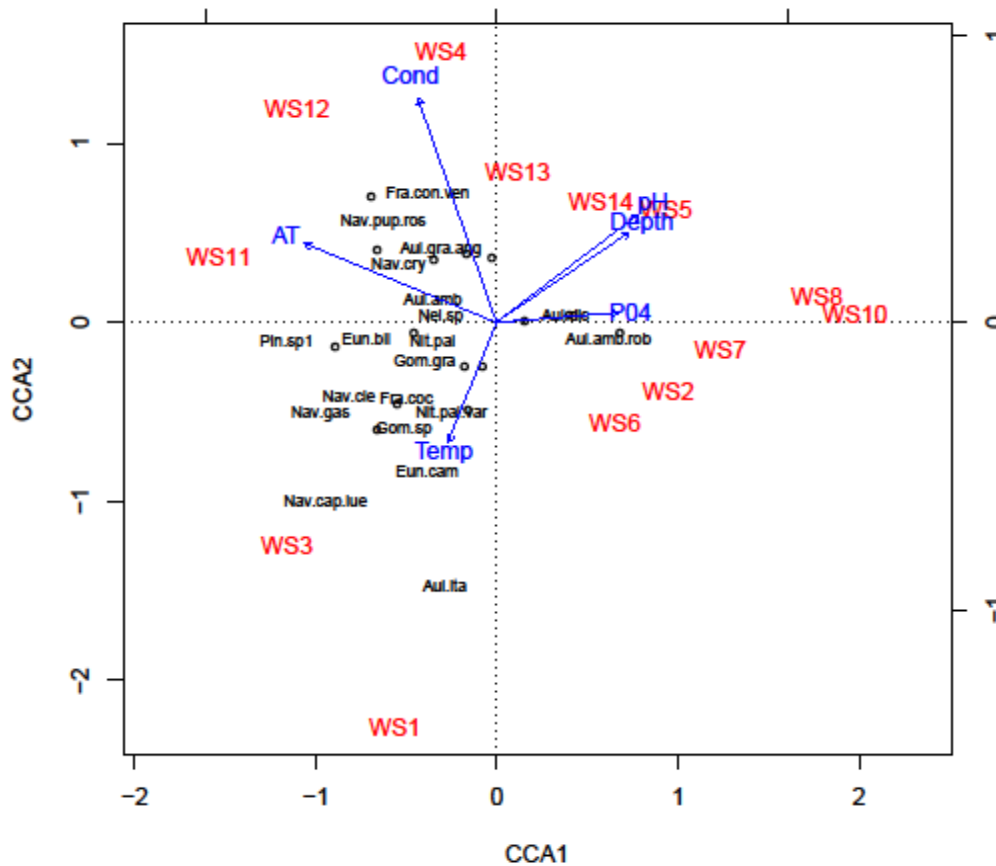
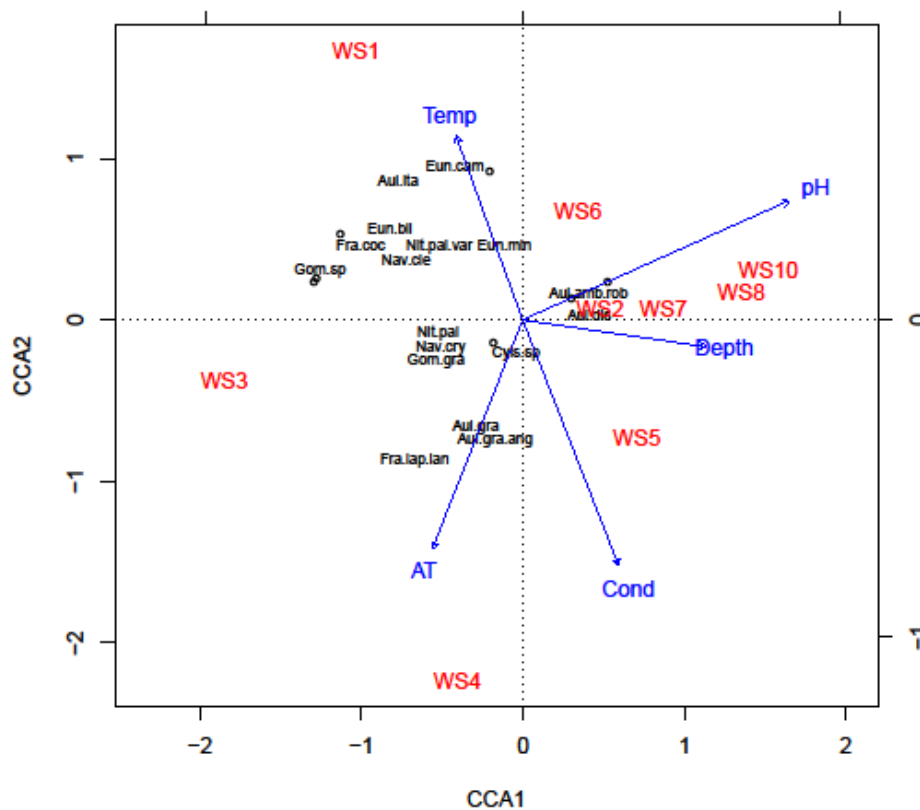


Figure II.14: Constrained Correspondence Analysis (CCA) ordination biplot showing the species (priority species) and environmental variables of 2008 water samples. Arrows indicate environmental variables and their length indicates the explanatory strength. The biplot indicates that pH and conductivity are the two variables that most influence the diatom distributions in LLG.

The ordination diagram (Figure II.14) displays species assemblages found in different areas of LLG; the deeper south portion, the shallow north portion of the lake, and the river course; the species assemblages differed between these different areas. All samples from the south basin (WS5, WS6, WS7, WS8 and WS10) and two from the river (WS13 and WS14) are positioned on the positive side of axis 1 along with typical planktonic and deep water species *A. ambigua* var. *robusta*, *Cyclotella meneghiniana*, and *Cyclostephanos* sp. *A. distans* is also found grouped with these planktonic species although not commonly described as preferring planktonic environments. Here, depth and pH have long vector lengths indicating these variables offer a strong explanation for constraining the species to these areas.

A further CCA was undertaken for the 2008 water samples for the lake environment only (Figure II.15). River samples were removed from analysis as for palaeoenvironmental reconstruction, an understanding of the aquatic environment of the lake ecosystem specifically is necessary to understand down-core changes. Therefore, a CCA of the lake samples of LLG would highlight the constraining variables on the diatom data. This CCA indicated that pH is the main factor that influences diatom distribution (CCA value of 0.84 on axis 1). The cumulative percent variance explained by the first two axes of the biplot is 63% with 40% variance explained by axis 1. Permutation test for all the constrained eigenvalues on the CCA



was 0.25.

Figure II.15: CCA ordination biplot showing the species (priority species) and environmental variables from 2008 samples from the lake environment only. Arrows indicate environmental variables and their length indicates the explanatory strength. The biplot indicates that pH and conductivity are the two variables that most influence the diatom distributions in LLG.

Water samples from the deeper, south basin of LLG (WS5, WS6, WS7, WS8 and WS10) are distributed on the positive side of axis 1 with the exception of WS2 which is towards the centre of the lake. All of the samples from the shallower, north basin (WS1, WS3 and WS4) are found on the negative side of axis 1. Axis one constrains most of the variability in the data and the site samples are distributed along this. Depth is closely correlated to axis 1 and therefore is strongly linked to the variance in the data. A simple linear regression of the pH and depth data was carried out (Figure II.16).

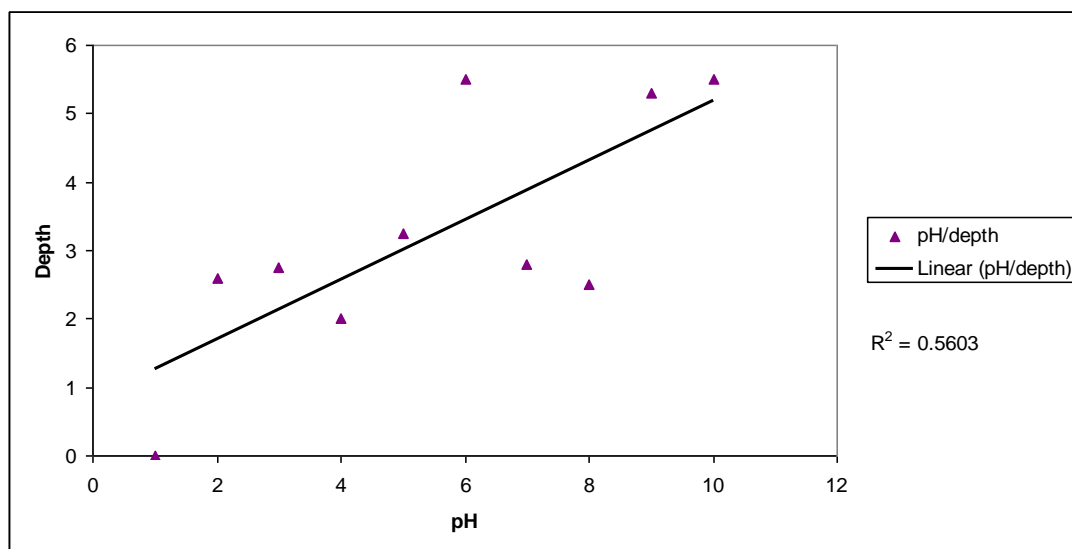


Figure II.16: Scatter plot to show relationship between depth and pH of 2008 water samples from the lake environment.

The correlation coefficient (r) is 0.75 (sample size, $n = 9$), confirming that pH and depth are positively correlated at the 5 % significance level (or 95 % confidence interval). From Figure II.16 (pH vs depth) it appears that as water depth increases, pH of the water samples increases. This could be because the deepest part of the lake (~6m) is located in the centre of the south basin and the south basin is enclosed by calcareous bedrock hills with calcareous soils (Hamilton, 2002). The samples from the South basin have a higher pH because in-wash and drainage from the surrounding hills makes the south basin slightly more alkaline than the north basin. Similarly to the previous CCA, typically planktonic diatom species are distributed among the sites from the deeper, southern portion of the lake on the positive side of axis one such as *A. ambigua* var *robusta*, *Cyclotella meneghiniana* and *C. stelligera*. *A.*

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distans is also found on the positive side of axis 1. *A. granulata* and *A. granulata* var *angustissima* are positioned in the negative part of axis 1 and 2 and appear to have some correlation with increasing alkalinity. Typically benthic and facultative planktonic species are mostly positioned on the negative side of axis one where the sites from the shallower, north basin are distributed. *Eunotia camelus* appears to be particularly correlated with increasing temperature.

2.5 Discussion

2.5.1 Diatom species assemblages in Laguna La Gaiba

In general, preservation of diatoms from modern LLG samples was very good. Chemical and physical processes that promote poor preservation are generally more common in saline lakes (Flower and Ryves, 2009). However, as the diatom assemblages from the water samples differ to the sediment surface samples, we must consider processes in LLG that will affect preservation. Water chemistry and physical limnology has been linked to diatom preservation; pH, salinity, temperature and ionic strength are all important factors (Ryves et al., 2006). Biological indicators such as bacterial dissolution and bioturbation can also alter taphonomic processes and affect preservation (Bidle et al., 2003). Physical characteristics of a lake can also be important such as water depth; during sedimentation over deeper water columns, dissolution of finer taxa can occur. In tropical, alkaline lakes, good preservation has been linked to the organic content of sediments (Hecky and Kilham, 1973).

The diatom flora from LLG is generally very similar to that found in other tropical regions. *A. ambigua* var. *robusta* and *A. distans* were found to be two of the most common and dominant species in LLG. *Aulacoseira ambigua* is commonly found in diverse environments from all over the world. In freshwater tropical South American and African lakes, *A. ambigua* and other *Aulacoseira* species are characteristic components of pelagic freshwater phytoplankton (Hecky and Kling, 1987; Kilham, 1990). However, the variety *robusta* is less commonly found although it has been identified in Quaternary records from the Pátzcuaro Basin, central Mexico (Metcalf

et al., 2007). In East Africa, ecological data has indicated that *Aulacoseira ambigua* var. *robusta* may indicate high silica levels and deep circulation as it is a heavy silicified diatom and has been found in deep, freshwater environments (Metcalf et al., 2007). As *A. ambigua* var. *robusta* is most abundant in the south basin in surface sediment and water samples at LLG, this suggests that in LLG environment this taxa prefer deeper lake conditions. *A. ambigua* and *A. granulata* var. *angustissima* was also found to be very abundant in both water and surface sediment samples from LLG. *Aulacoseira granulata* var. *angustissima* is a cosmopolitan diatom and is common in tropical lake. Van der Kaars (2001) described it as a Euplanktic diatom indicative of fresh open water in a lowland tropical lake in Indonesia. Abundance of *A. granulata* var. *angustissima* in surface sediment samples is high in the deeper, south basin of LLG but confusingly there is a much higher abundance in open water samples taken from the shallow northern basin. Therefore, *A. granulata* var. *angustissima* must be responding to an environmental variable other than depth. *Staurosira* spp. are also very common in tropical shallow lakes (Izaguirre and Vinocur, 1994; Mackay, 2007). In LLG they are mainly found in the north portion of the lake and the river channel suggesting that at LLG, *Staurosira* spp. favour a shallow, well mixed habitat. One unusual species of *Fragilaria* was found in the 2008 vegetation samples; *Fragilaria cochabambina* has previously only been found in a study by Morales et al. (2009) in a stream in the Bolivian cloud forest. All other taxa found in LLG are commonly found elsewhere in the tropics.

Percent abundance data from LLG surface sediments taken in 2006 show that the shallower north basin sites have a diverse species assemblages compared to the south basin sites. Species that characterise the north basin sites are *Eunotia camelus*, *E. bilunaris* and *E. minor*. *Eunotia* species are common in waters from the tropics (Velez et al., 2006) and are abundant in freshwater habitats. *Eunotia* is a large genus that comprises around 250 species (Van Landingham, 1969; Valenzuela Miranda, 2011) and 20% of the analyzed taxa from South American tropical environments belong to *Eunotia* (Metzeltin & Lange-Bertalot, 1998). *E. minor*, *E. bilunaris* and *E. camelus* are noted as being epiphytic diatoms in other studies from South America (Grunow in Chapter II Diatom ecology in the Pantanal wetlands of tropical South America

Van Heurck, 1881; Mills, 1934; Nascimento, 2010) and reflect a relatively shallow water level (1-3 m). *Gomphonema contraturris* and *Amphora ovalis* are also prevalent in samples from the north basin. The former is generally a eutrophic species (Lange-Bertalot, 1993) and needs higher nutrient concentrations and the latter is a benthic species. *Gomphonema contraturris* is a cosmopolitan taxa and is found to be abundant in Peruvian and Colombian rivers in phytoplankton samples (Vouilloud et al., 2010). In LLG, *Gomphonema contraturris* is found in sediment samples from the north basin and vegetation samples only. As *G. contraturris* has been previously noted as being prevalent in a lotic environment (Vouilloud et al., 2010), we can infer that the river has a large influence on the northern basin and sediments and diatoms may be deposited here. The species assemblage diversity is greater in samples taken from vegetation in 2008 than from open water. Particularly characteristic of the vegetation samples are *Gomphonema* spp. and *Aulacoseira* spp. *Gomphonema* species are found as epiphytes in other South American studies (Hassan et al., 2009, Nascimento et al., 2010).

Nitzscia palea is found in the north basin and the river at LLG and in smaller percentages in vegetation samples. Tapia et al. (2003) describe this species as an epiphytic, riverine diatom and has been found in lotic and vegetated environments in Lake Titicaca. Gasse (1986) describes *Nitzscia palea* as being both periphytic and planktonic freshwater diatom. In a tropical lake in Kenya, *Nitzscia palea* was found in periphytic, planktonic environment (Verschuren et al., 2000). In LLG it appears that *Nitzscia palea* favours a lotic environment. It's abundance in the north basin may be due to in-wash and influence from the River Paraguay and/or it's preference for a periphytic habitat. It also appears to be epiphytic in LLG as it is found in relatively low abundance in all vegetation samples.

The overall species assemblages in LLG from samples in 2006 are slightly different to those in 2008 which is to be expected as the availability of light, the mixing regime, water depth and nutrient availability are regulator factors of diatom biomass and composition in the Pantanal region (Oliveira and Colheiros, 2000; Loverde-Oliveira

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and Huszar, 2007). Both sets are dominated by *Aulacoseira* spp., particularly *A. ambigua* var. *robusta*, *A. distans* and *A. granulata* var. *angustissima*; however, the 2006 data set has a much higher abundance of *A. granulata* and also has a higher diversity of benthic, epiphytic and aerophilous species. This is unsurprising as the samples from 2006 were from mixed surface sediments and samples from 2008 were from the water-borne environment. Environmental factors will also have varied interannually, including (as mentioned previously) a difference in lake level at the time of testing between 2006 and 2008. (The lake level in 2008 was on average 0.84 lower than in 2006).

The modern diatom data set from LLG provides interesting ecological information about a lowland tropical lake in South America. The diatom data reveal a clear difference between species assemblages from different aquatic environments of LLG such as open water, vegetation and the river channel. The data also display a difference between samples taken in 2006 and 2008. Overall, assemblages from the south basin reflect a less varied, open water planktonic environment and assemblages from the north basin demonstrate a more diverse species assemblage, incorporating benthic, epiphytic and aerophilous taxa.

2.5.2 Environmental controls on diatom assemblages at LLG

As mentioned previously, water depths at LLG have high interannual variability (Figure II.3 adapted from Junk et al; 2006). At LLG, there was an average difference of 0.84 m between water depths taken in July 2006 and July 2008. The variation of water depths in LLG will have an effect on the diatom assemblages on an interannual basis as diatoms respond quickly to environmental change (Gasse et al., 1983). It may be misleading to make palaeoenvironmental inferences from modern water samples as a water sample is a 'snapshot' of the lake diatom assemblage, therefore caution should be exercised in quantifying the modern assemblage make-up of the lake in this way. In surface sediments, on the other hand, a sample may consist of sediments that have accumulated over a number of years and mixed slightly in settling

(Haworth, 1976). Therefore, the diatom assemblage will likely represent several years, or even decades of fossil taxa, giving a more general indication of diatom species assemblage and masking the 'noise' of the interannual changes. Studies have shown that surface sediment samples provide a good representation of the living plankton diatom communities in small lakes (Simola, 1977; Haworth, 1976, 1980; Battarbee, 1981). However a study of a large lake, Lake Malawi, Africa (Haberyan, 1990) found the living diatom assemblages to be distinctly different to the surface sediment samples likely due to sinking rate, dissolution, and winnowing of the diatoms before they reach the lake bottom. Although LLG is a much smaller lake, the same process may apply and we should therefore exercise caution when comparing fossil diatom assemblages to living water assemblages. Inferences about fossil diatom assemblages should be based on surface sediment samples as it is likely the same processes of dissolution and winnowing would have affected these diatoms in the lake in the past.

However, as there is more environmental information for the modern water samples in LLG it is important to know how these environmental variables affect the diatom assemblages. Therefore, water samples, along with the sediments samples are vital for our understanding of the modern lake environment and to assist in the interpretation of a palaeolimnological record from this lake.

The water samples from LLG highlighted that pH and depth explained most of the variation in the diatom data-set. Diatoms are well-known to respond sensitively to changes in pH (Battarbee et al., 1999) and diatoms as a proxy for pH has long been used in reconstructing past environments, for example for indicating changes in water acidification (Birks et al., 1990) or more recently, as a proxy for reconstructing climate change (Bigler et al., 2002). The CCA of environmental variables from the lake environment only and their influence on diatom assemblages revealed a close relationship between pH and depth indicated by the low angle between the vector arrows (Figure II.15). The relationship between depth and pH assumes these variables are independent, which they may not be due to the fact that when water levels rise or decline, corresponding changes in pH can occur (Wolin and Duthie, Chapter II Diatom ecology in the Pantanal wetlands of tropical South America

1999). Indeed, in other studies, water level changes have been reconstructed from diatom inferred-pH (Battarbee et al., 1999) and it was found that decreases in moisture (i.e. lake level) correspond with increases in humification and lower diatom-inferred pH. Therefore, even though both CCAs showed pH explained most of the variance in the diatom data, depth is also linked to this.

It is also important to know if the diatom assemblages from the surface sediment samples also reflect depth. The DCA of the surface sediment samples showed a clear separation between the north and south basin sites (Figure II.17) As there is limited environmental data related to the sediment samples (only depth) it is not possible to draw conclusions about the relationship between various environmental factors and their bearing on diatom assemblages. However, a relationship was found between lake depth and the DCA axis 1 scores ($R^2=0.53$) (Figure II.18), significant at 99.9% confidence interval, implying the surface sediment assemblages are also strongly constrained by depth. In conclusion, diatoms from LLG are a good indicator of water depth, thus analysis of diatom assemblages can be used to infer water level change.

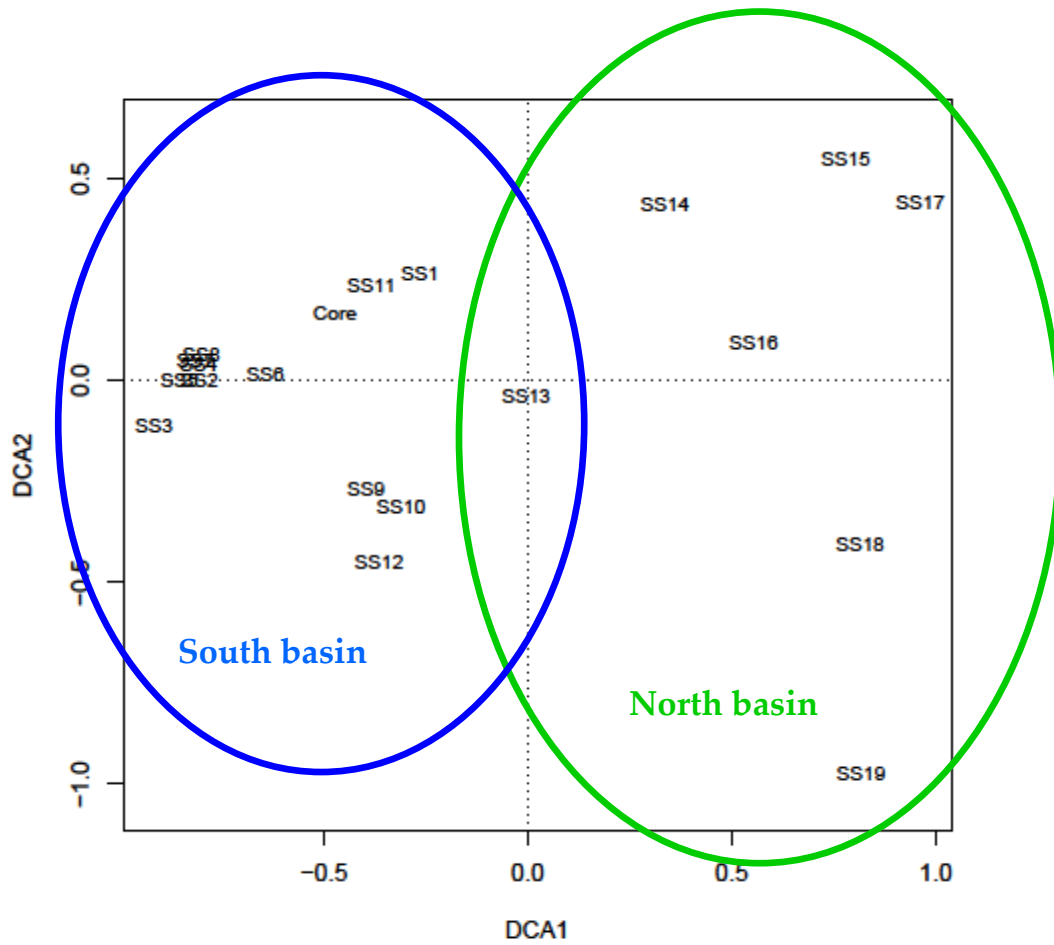


Figure II.17: DCA showing the distribution of surface sediment samples over axis 1 and 2 of the DCA. Green circle highlights samples that were taken in the north basin of LLG and the blue circle highlights samples that were taken in the south basin of LLG.

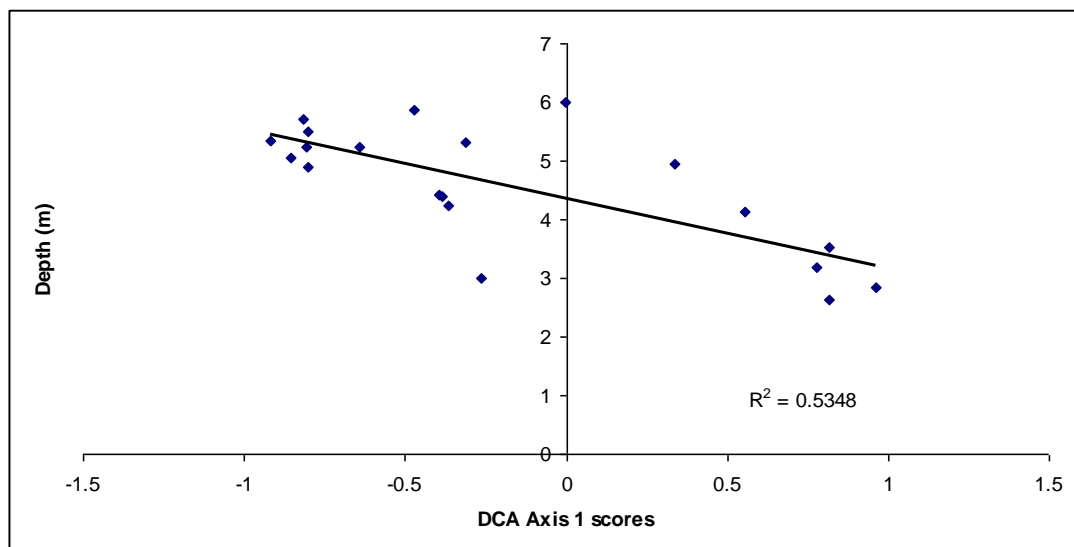


Figure II.18: Scatter plot to show the relationship between depth at surface sediment sample sites and DCA Axis 1 scores.

The results of the DCA of the sediment samples taken in 2006 allow qualitative assessment of the relationship between planktonic to non-planktonic ratios and water depth. Planktonic to non-planktonic ratios have often been used as an independent indicator of lake-level change in palaeoenvironmental reconstructions, but this is not always valid since the relationships can be complex and affected by other processes such as nutrient enrichment, chemical conditions, available habitat and light and changes in pH (Battarbee, 1991; Wolin and Duthie, 1999). In the 2006 data-set from the surface sediment samples from LLG the ratio technique is supported by the dominance of planktonic taxa in samples from the deeper, southern basin of LLG (Figure II.19) and non-planktonic forms dominate the shallower northern basin. In Figure II.19, SS1 which has high planktonic taxa abundance but is in a shallow environment as it is located in a small bay on the southern edge of LLG (Figure II.6, on page 53). Although it is shallow, the bay is connected to the south basin and the lake water washes in and out of the bay hence the sample was dominated by a planktonic assemblage. Similarly, SS14 located in the northern basin, sampled at a depth of 4.95m, has a predominately non-planktonic diatom assemblage. However this sample site is surrounded by shallower waters and so the overall assemblage is non-planktonic. This distribution of planktonic diatom assemblages in the deeper, southern portion of the basin and non-planktonic diatom assemblages in the shallower, northern portion of the basin is further evidence that modern diatom assemblages at LLG reflect water depth and therefore LLG is well suited for palaeoclimatic reconstruction with diatoms as a proxy for lake level change.

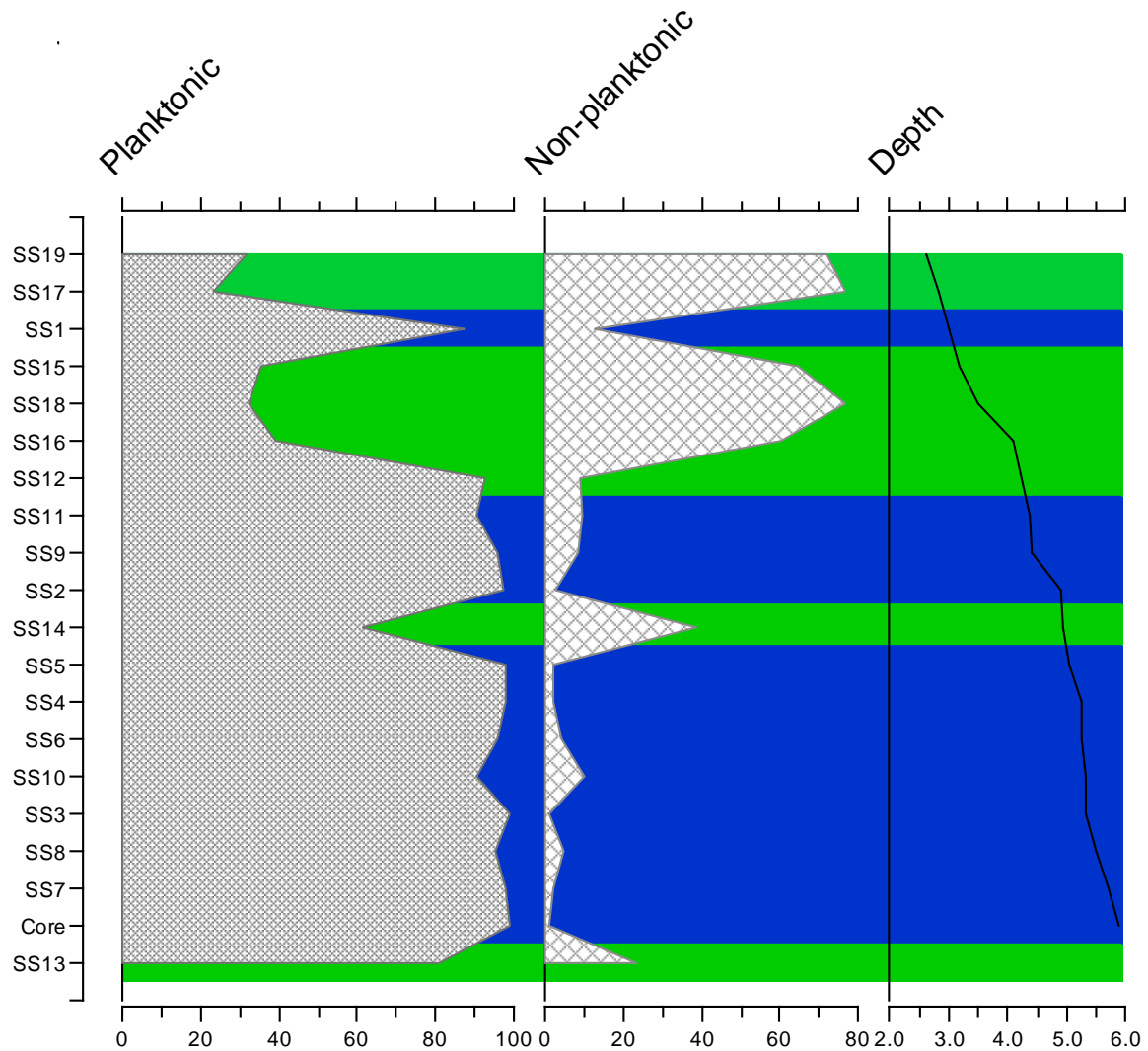


Figure II.19: Plot created in C2 (Juggins, 2003) to show planktonic to non-planktonic diatom assemblage ratio in sediment samples at different depths. Green shading indicates sites in the north portion of LLG while blue indicates sites in the south portion of LLG.

2.6 Conclusion

Diatoms in LLG respond sensitively to environmental variables, making them excellent bioindicators for inferring late Quaternary environmental change in the lowland tropics. Multivariate statistics indicated that pH and water depth are the most important factors that shape diatom communities. It is likely that the diatom assemblages found in LLG surface sediments are more reliable indicators of the overall modern environment than analysis of diatom assemblages from water samples because of their time averaging properties. Analysis of the sediment samples

from LLG revealed a clear distinction in the diatom assemblages between the northern portion of the lake and the southern portion with non-planktonic assemblages reflecting the shallow water of the northern portion and planktonic assemblages reflecting the deeper water in the southern portion. In conclusion, LLG provides a good setting for palaeoenvironmental reconstruction using diatoms as a proxy for past lake level changes and therefore to infer late Quaternary precipitation in lowland South America. This study also emphasises the potential for using this technique of using diatoms as a palaeo-tool in other lowland lakes in tropical South America.

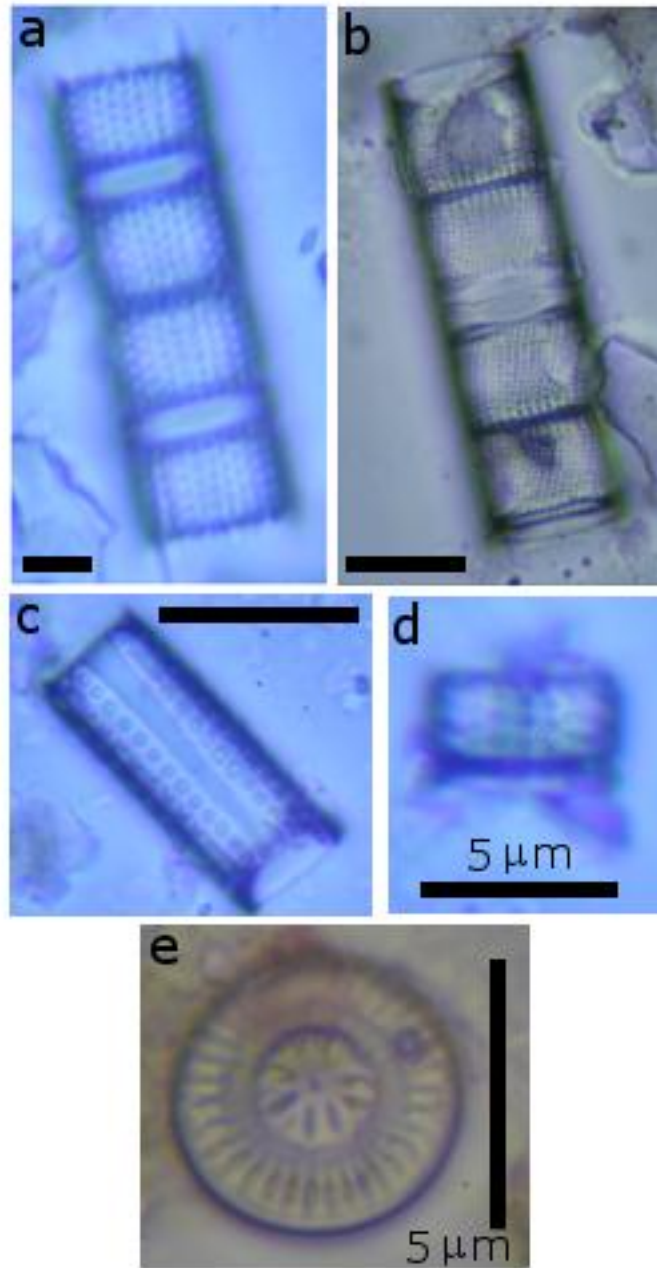


Plate 1. Key diatoms found in modern samples at LLG. Black scale bar = 10 μ m unless otherwise stated. a) *Aulacoseira ambigua* var. *robusta*, b) *Aulacoseira ambigua*, c) *Aulacoseira granulata*, d) *Aulacoseira distans*, e) *Cyclotella stelligera*.

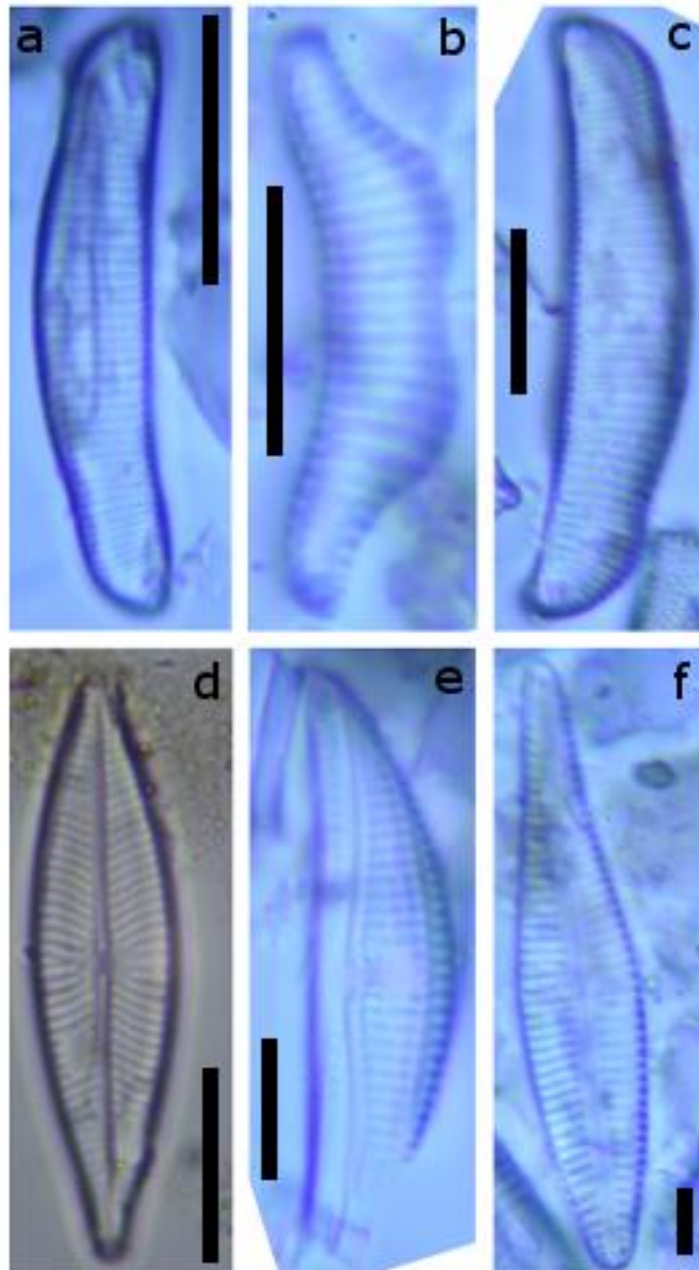


Plate 2. Key diatoms found in modern samples at LLG. Black scale bar = 10 μ m. a) *Eunotia minor*, b) *Eunotia camelus*, c) *Eunotia bilunaris*, d) *Navicula cryptocephala*, e) *Amphora ovalis*, f) *Gomphonema contraturris*.

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III. Reconstructing lake level change from a 20,000 yr diatom record in lowland Bolivia

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3.1.1 Abstract

This paper presents a 20,000 year history of precipitation in tropical South America using diatoms as a proxy for lake level change. The study site is Laguna La Gaiba (LLG) (17° 45'S, 57° 40'W) a shallow, broad lake situated along the course of the River Paraguay which runs along the western edge of the Pantanal, the world's largest wetland; located mostly in Brazil but extending into eastern Bolivia. Therefore, changing hydrological conditions at LLG likely reflect a regional signal. One hundred samples were taken from the sediment core extracted from LLG and analysed for diatoms producing a high resolution record. The diatom record revealed lower-than-present lake levels from 20.5 ka – 12.5 ka BP indicated by high abundance of benthic and facultative planktonic species. This is in contrast with records from the Bolivian Andes and coastal Brazil. Therefore, the precipitation cycle of lowland continental interior of South America is probably not driven by precessional forcing as previously suggested but is controlled by glacial-boundary mechanisms. A climatic shift marks the glacial-Holocene transition with high lake levels peaking at 12.2 ka BP during the North Atlantic Younger Dryas (YD) chronozone (GS-1 stadial, 12.9 – 11.6 cal. ka BP). Although lake levels do drop somewhat after 12.2ka BP the abrupt precipitation anomaly is not as pronounced as YD signals from other tropical South American sites. However, a possible YD signal in the continental interior of lowland tropical South America is a novel discovery. Another shift at 10 ka BP to planktonic species *Aulacoseira ambigua* var. *robusta* signals deeper water. The diatom signal throughout the Holocene suggests lake levels remain consistently high which contrasts with the evidence for early- mid-Holocene drying at LLG in the pollen record and also evidence for widespread mid-

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Holocene drying over tropical South America. I suggest this was due to a more
seasonal climate during the Holocene and/or lake levels not dropping low enough
to expose the littoral zone of the lake basin. Holocene lake levels were
unequivocally higher than during the late-glacial.

3.2 Introduction

Palaeoclimatologists and modellers have increasingly focused on the tropics as a potentially important driver of climate change because of the region's role in the Earth's energy budget and in regulating the water vapour content in the atmosphere. Also of importance is understanding global climatic teleconnections between the northern and southern hemisphere as understanding past climate history and making inter-hemispheric comparisons may make it possible to elucidate the dominant drivers responsible for climate, thus more accurate predictions for future climate change can be made. Global climate teleconnections generally refer to the linkage of seemingly unrelated climate anomalies over great distances and the essence of a teleconnection is that it allows a climatic event to affect the Earth system elsewhere (Liu and Alexander, 2007). This means there are climate interactions between different regions, adding greatly to the complexity of the climate system.

Detailed palaeoclimate studies are needed in tropical regions to better understand global climate change and the climate interactions between the northern and southern hemispheres. Glacial-interglacial climate studies from South America are concentrated in the central Andes (Baker et al., 2001a, 2001b) and along the Atlantic seaboard (Lea et al., 2003; Wang et al., 2004; Cruz et al., 2005). However, high resolution, well dated, palaeoenvironmental records from the lowland interior comparable to the records from the Andean and Atlantic records are lacking mainly due to low sedimentation rates and/or sedimentary hiatuses during the glacial period in lacustrine records (Ledru et al., 1998). The precipitation regime of lowland, tropical South America during the last glacial period and specifically the nature and timing of deglaciation across the last glacial-interglacial transition is still a matter for debate (Absy et al., 1991; van der Hammen and Absy, 1994; Hostetler and Mix 1999; Burbridge et al. 2004; Punyasena et al. 2008). Higher than present precipitation during the global last glacial maximum ~ 21 kyr BP (LGM) in the Andes and on the Brazilian coast exhibit a clear ~ 20 kyr cyclicity in precipitation in tune with the

A diatom-based Late Quaternary precipitation record for lowland tropical South America Earth's precessional cycle (Baker et al., 2001a; Wang et al., 2004; Cruz et al., 2005). It is thought that high summer insolation increased continental heating, steepening the land-sea thermal gradient, forcing the Intertropical Convergence Zone (ITCZ) southward, thereby strengthening the summer monsoon south of the equator in South America. Due to the climate linkages in these regions, along with evidence for closed canopy tropical forest in central Amazonia (Colinveaux et al., 1996; Bush et al., 2004) it is argued that they are representative of tropical South America, as a whole (Baker et al., 2001b). However, modelling studies have simulated decoupled Andean and lowland precipitation regimes for the LGM (Hostetler and Mix, 1999; Vizy and Cook, 2007). Therefore, high resolution palaeoclimate studies focusing on the precipitation regime of the continental lowland interior of South America is needed to validate the climate models.

As the quality and density of palaeo-records improves, global teleconnections linked to abrupt, millennial-scale events are being recognised. Ice cores retrieved from Greenland revealed that the climate of the North Atlantic region over the last glacial period was characterised by large abrupt climatic events that lasted several hundred years or longer (Dansgaard et al., 1993; Grootes et al., 1993). Heinrich events were also recorded in North Atlantic sediments (Heinrich et al., 1988; Broecker et al., 1992) which appeared to be connected with the climaxes of cooling cycles in the northern hemisphere (Bond et al., 1992, 1993). The Younger Dryas (GS-1 stadial) (YD) is expressed as an abrupt return to near-glacial conditions in the North Atlantic region between 12.9 and 11.6ka BP, occurring after an abrupt warming at 14.7ka BP (the Bølling-Allerød) and ending with a warming leading to the Holocene period (Rasmussen, 2006, Steffensen et al., 2008). The extent to which these high frequency climate fluctuations in the North Atlantic influenced climate in the southern hemisphere is still a matter for debate (Blunier et al., 1998, Markgraf and Seltzer, 2001; Sugden et al., 2005; Ackert et al., 2008).

Heinrich events have been recognised in records from the central Andes as 'wet' episodes. High lake levels in Titicaca and the Salar de Uyuni (Baker et al., 2001b; Placzek et al., 2006) and γ -radiation peaks in Salar de Uyuni (Baker et al., 2001b) between 16.6 and 14.1ka BP are attributed to Heinrich event 1 (H1). Wet events corresponding with H1 are also visible in stable isotope records off the north east coast of Brazil (Arz et al., 1998), speleothem growth phases in coastal Brazil (Salvador) (Wang et al., 2004) and a drop in $\delta^{18}\text{O}$ in speleothem records in Botuvera Cave, south east Brazil (Wang et al., 2007). The increase in precipitation in these regions is attributed to an anomalous southward shift in the ITCZ caused by cool sea surface temperatures (SSTs) in the North Atlantic, steeping the pole-to-equator thermal gradient and strengthening northeasterly trade winds. The cooling in the North Atlantic was caused by icebergs breaking off from glaciers and melting, thereby freshening the North Atlantic and altering the thermohaline circulation (Heinrich, 1988).

The YD (sometimes described as H0) is thought to have influenced precipitation regimes in tropical South America, Asia and Africa (Gasse, 2000, Yuan et al., 2004, Wang et al., 2004, 2007; Garcin et al., 2007). Pole-to-equator temperature gradients in the northern hemisphere, induced by reduced overturning circulation in the North Atlantic, is hypothesised to have pushed the mean position of the ITCZ southward (Dahl et al., 2005; Placzek et al., 2006). This is thought to have caused drying in the northern hemisphere tropics of South America and increased precipitation south of the equator. A YD signal indicated by higher precipitation has been recognised in well-dated reconstructions from tropical South America. 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 north east Brazil (Salvador) (Auler et al., 2004) and south east Brazil (Cruz et al., 2005; Wang et al., 2007).

Due to the lack of high resolution records from the continental interior of South America, it is unknown whether a precipitation anomaly occurred during the YD chronozone (GS-1 stadial, 12.9-11.6 cal. kyr BP) (Alley, 2000) or Heinrich events in this region. We would expect to see high lake levels, due to increased precipitation in the Pantanal as it is situated in the continental interior of South America, centrally located between the Altiplano and coastal Brazil, sites of increased precipitation during the YD chronozone and Heinrich events.

A continuous palaeoenvironmental record spanning the last ~ 45 kyr exists from Laguna La Gaiba (LLG), a large, shallow lake in the continental interior of the southern hemisphere tropics of South America (SHTSA) (Whitney et al., 2011). Whitney et al. (2011) show that during the last glacial period, the Pantanal wetlands, located in the continental interior of the SHTSA was drier and cooler than present. However, vegetation changes described by Whitney et al. (2011) can be difficult to interpret as the relationships between changes in temperature, precipitation and CO₂ and their effect on tropical plant communities are complex and poorly understood (Webb, 1986). It is therefore necessary to disentangle this synergistic relationship and a more accurate precipitation record is needed at this site to determine the influences on the precipitation regime in the lowland continental interior of South America. Furthermore, the resolution of the palynological record from LLG is not high enough to capture short-term, high frequency climatic fluctuations such as Heinrich events or the YD. It should be noted that no other tropical lowland terrestrial records from the interior have high enough sedimentation rates to capture these millennial-scale events. However it is likely that a high resolution diatom record may be able to highlight high frequency episodes in the late Quaternary and also capture the glacial-Holocene transition in greater detail. Diatoms have often been used as a proxy for lake level change in freshwater lakes (Metcalf et al., 1991; Bradbury, 1999; Fritz et al., 1999; Baker et al., 2001) and the analysis of diatom assemblages from a sediment core at LLG will enable inferences about past precipitation to be made.

Presented here is high-resolution diatom data to determine the nature and timing of deglacial and Holocene flooding periods from Laguna La Gaiba located in the Pantanal. Specifically, the aim is to i) ascertain whether the diatom record over the last glacial supports the 'dry' LGM suggested by pollen record at LLG, ii) determine whether there is any evidence of high frequency precipitation episodes particularly during Heinrich events and the YD chronozone, iii) define the timing and nature of the Pleistocene-Holocene transition at LLG and vi) ascertain whether the diatom record demonstrates a mid-Holocene aridity signal. This record is backed by particle size analysis, to shed light on the energy of the environment which may be related to changes in lake level (Alin and Cohen, 2003) and presented alongside the pollen evidence in order to compare and contrast the palynological record with the diatom record and to provide a continuous, multiproxy reconstruction spanning the LGM; unique in the lowland continental interior of South America. Analysis of modern diatom assemblages from LLG found there is a relationship with water depth at LLG (see chapter II), thereby allowing for the reconstruction of water level, and hence tracking the nature and timing of palaeoprecipitation change in the area from the last glacial period until present.

3.3 Study site

3.3.1 Physical setting

Laguna La Gaiba (17°45'S, 57°35'W, LLG), is a large shallow lake situated along the course of the river Paraguay which is hydrologically-linked to the seasonally-flooded Pantanal basin (Figure III.2). The Pantanal is the world's largest tropical wetland (~135,000km²) and is located in the lowland, continental interior of the SHTSA. The wetland occupies a tectonic depression between the Brazilian shield and the Andean foreland (elevation 80-120m asl) (Clapperton, 1993; Alho, 2005) and, together with the western Brazilian highlands, forms the headwaters of the River Paraguay. LLG is centrally situated between the Bolivian Altiplano, the site of

A diatom-based Late Quaternary precipitation record for lowland tropical South America palaeoclimate archives (Baker et al., 2001a, 2001b; Fritz et al., 2007, 2010) and coastal Brazil (Figure III.1).



Figure III.1: Map to show major sites of palaeoclimatic reconstruction in South America in relation to the study site LLG.

The Pantanal has a high capacity to retain rainfall, most of which falls in the austral summer when the South American Summer Monsoon (SASM) (Zhou and Lau, 1998) leads to intensive convective rainfall and causes a summer precipitation maximum, causing extensive flooding. Mean annual rainfall in the Pantanal is 1000-1700mm and is characterised by a 6 month dry season (Hamilton, 2002). Lake levels at LLG peak when summer monsoon rainfall drains from the low-lying terrain in the Pantanal region and adjacent Brazilian highlands, causing the river and its associated lakes to overflow (Alho et al., 1988; Alho, 2005). Additional rainfall can

A diatom-based Late Quaternary precipitation record for lowland tropical South America fall during the year when periodic cold air incursions from the south cause the temperature to drop (May et al., 2008).

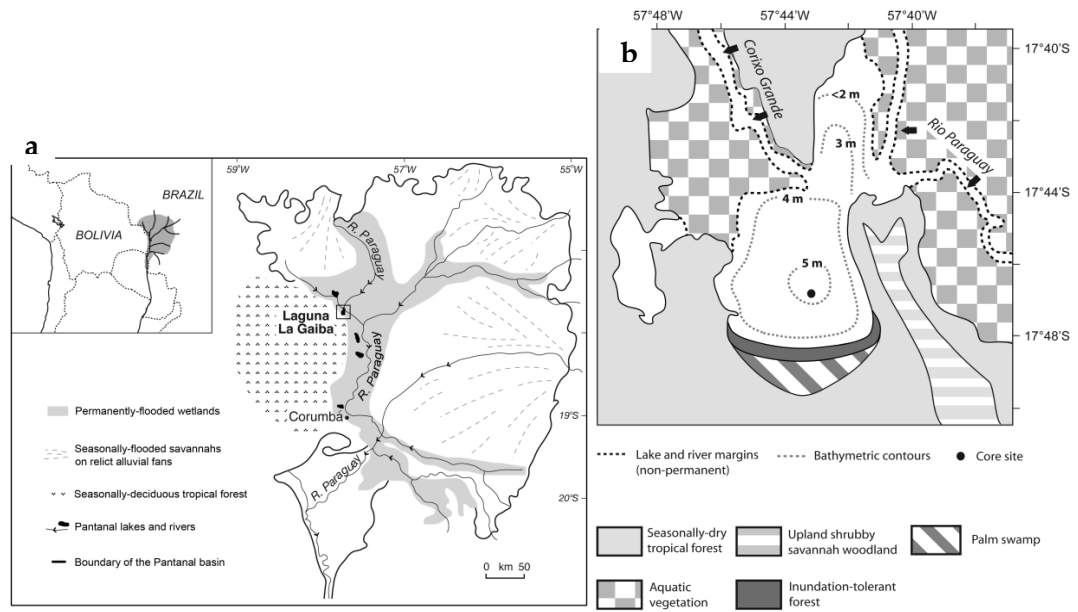


Figure III.2: (a) Location of the Pantanal basin and the study site, LLG located on the western edge of the Pantanal wetland and (b) Lake bathymetry of LLG and surrounding vegetation (courtesy of Whitney, 2009).

3.3.1.1 Limnology and Hydrology

Although LLG is an open-drainage system, it is climatically-sensitive and responds to climate variations over a regional area. LLG is intersected by the River Paraguay however, the southern part of the basin is bounded by hills and the northern part connects to the Pantanal wetland which means it is hydrologically-linked to the wetlands and therefore changes in water volume and water chemistry are reflective of an area $\sim 140,000\text{km}^2$ (Assine and Soares, 2004; McGlue et al., 2011). Diatoms in LLG respond to the changing water levels and species assemblages will reflect the planktonic:non-planktonic ratio (see modern diatom study in chapter II). There is further evidence that water level changes and river flow in the Pantanal and connecting river systems reflect climatically-forced precipitation changes. Collischonn et al. (2001) found that flow from the river Paraguay and changing water levels at a gauging station on the River Paraguay were linked to rainfall

A diatom-based Late Quaternary precipitation record for lowland tropical South America measurements across the Pantanal. Therefore, changing hydrological conditions at LLG are likely to reflect a broad pattern of precipitation change in the continental lowlands of SHTSA.

Maximum water depth in LLG varies from 4-6m. There are two distinct portions to the lake intersected by the River Paraguay. The northern part is shallower (~3m) and merges with the Pantanal wetlands on the east and the western margin is bounded by hills. The southern part of the lake is deeper (~4-6m) and is bounded on almost all sides by steep hills above the level of inundation. The basin is broad and flat. Very narrow beaches fringe the southern margin of the lake and mean there is only a very small littoral zone. The steep-sided hills bounding the southern basin mean any rise in lake level will be reflected in the diatom composition as the planktonic area of the lake increases. Aquatic grasses and water hyacinths (*Eichhornia* spp.) are present in the northwestern margin of the south portion of the lake and the eastern margin of the north portion of the lake. The lake is overall neutral-alkaline with the southern portion being slightly more alkaline than the northern portion. The average lake temperature in July is 28°C and the lake is well-mixed due to its large, shallow nature and strong winds (See chapter II for detailed modern water chemistry and Lake Environment).

In the analysis of modern diatom assemblages from LLG, a relationship was found between particular diatom species and lake depth (see chapter II). From lake water samples and surface sediments samples it was found that the deeper, south basin of LLG was dominated by *Aulacoseira* spp., *Cyclotella* spp., and *Cyclostephanos* spp. The shallow, north basin was dominated by *Eunotia* spp., *Navicula* spp., *Gomphonema* spp. and *Nitzschia* spp. Interestingly, there were only very few *Staurosira* spp., as they are generally common and widespread in the tropics and globally and are common in shallow waters (Battarbee, 1986) but what few there were, were associated with the shallow, north basin. Species diversity richness was greatest in 121, 122 the shallow, north basin. Drawing on the results from the modern diatom

A diatom-based Late Quaternary precipitation record for lowland tropical South America assemblages of LLG can assist in understanding the fossil diatom community. As the modern diatom assemblages show a relationship with water depth at LLG, it is an ideal site for reconstructing water level and hence tracking palaeoprecipitation change in the area through the late Quaternary. A preliminary study of diatoms from LLG revealed diatoms were present in the sediment core and generally well preserved until ~20 ka BP (Whitney et al., 2011). The diatom summary record resolution is very low and therefore a much higher resolution diatom record is needed at LLG to investigate potentially abrupt, high-frequency climate change.

3.4 Materials and methods

Down-core changes in diatoms assemblages and sediment grain size from a sediment core extracted from LLG were analysed to understand environmental changes through time.

3.4.1 Coring

In 2001, two, parallel, overlapping sediment cores measuring 5.6m and 4.8m were extracted by Mayle from a floating platform in the centre of the southern basin of LLG using a 'Colinvaux-Vohnout' drop-hammer modified Livingston piston corer (Colinvaux et al., 1999). A surface core measuring 110cm long and overlapping the Livingston core by 40cm, was extracted using a Perspex[®] tube and piston. It was extruded in the field and transferred into airtight plastic bags in consecutive 1cm slices. The Livingston cores were transported back the laboratory in their aluminium casing and extruded there. Parallel cores were correlated by magnetic susceptibility and cross-checked through analysis of pollen at zonal boundaries (Whitney et al., 2011), and the surface core was correlated to the consolidated sediments of the Livingston-extracted cores by loss-on-ignition at 550°C (Dean, 1974). See Figure III.7 for sediment stratigraphy.

3.4.2 Chronology

Eighteen AMS ^{14}C dates constrain the age-model for LLG (Figure III.3) which was made for the palynological study at LLG (for full details see Whitney et al., 2011). Analysis was carried out at NERC radiocarbon facility, East Kilbride, UK. 16 dates were obtained from well-preserved terrestrial plant macrofossils and 2 from non-calcareous bulk sediment. One anomalous date was rejected due to its young age possibly owing to contamination of the low carbon content of the sample material (Whitney et al., 2011). Unlike many lowland records (Ledru et al., 1998), sedimentation is uninterrupted across the LGM.

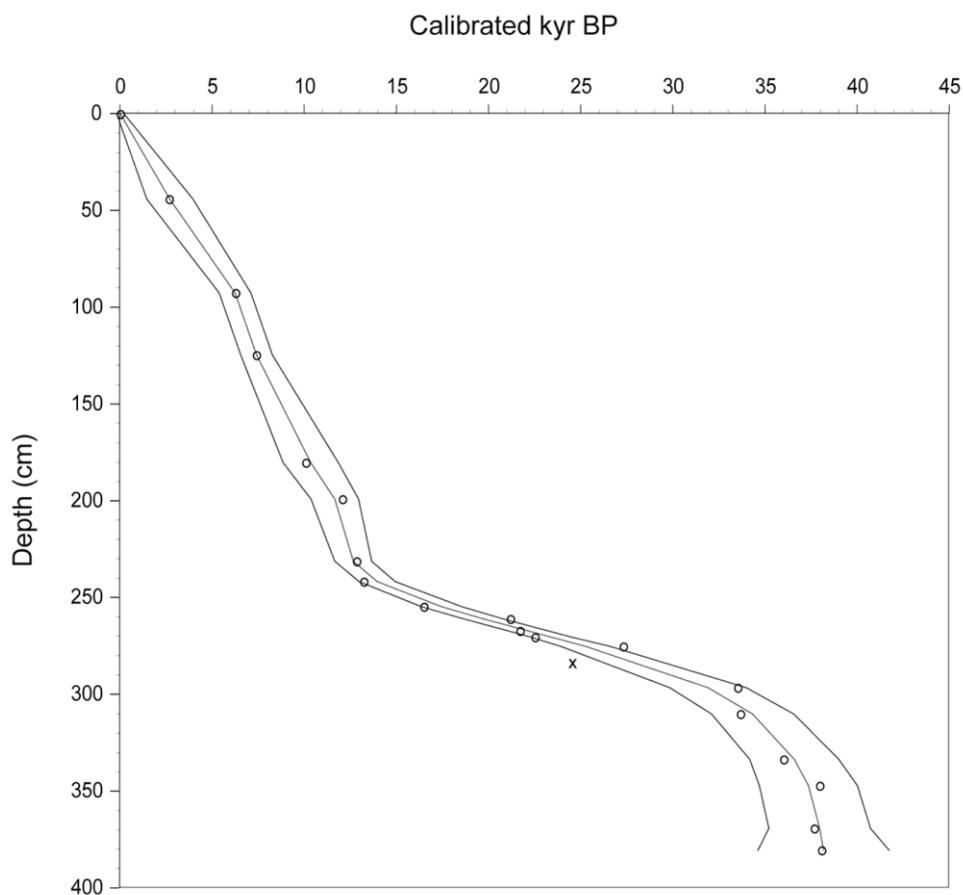


Figure III.3: The entire age-model for LLG based on 18 AMS ^{14}C dates and an assumed modern date for the uppermost 1 cm of sediment. Black outer lines represent 2-sigma error, and 'x' denotes the one outlying date rejected from the age-model. (Courtesy of Whitney et al. 2011)

Holocene	0 - 10,000 yrs BP	0.0175 cm/yr
Glacial-Holocene transition	10,000 - 12.5,000 yrs BP	0.0214 cm/yr
Late Glacial	12.5,000 - 20.5 yrs BP	0.0043 cm/yr
Glacial	20.5,000 - 40,000 yrs BP	0.011 cm/yr

Table III.1: Average sediment accumulation rates have been calculated based on age/depth data.

3.4.3 Diatom preparation and identification

The entire record initially was sampled at approximately 5000-yr intervals to gain an idea of diatom preservation. Once it was established that there were few diatoms remaining in the sediments after 20 ka BP, the sampling resolution was increased over the first 2.5m (0 – 20 ka BP). The Holocene was sampled at approximately 150-200-yr resolution, and the Late Glacial at approximately 400-yr resolution. The Late Glacial-Holocene transition was sampled at a higher resolution of 50-100-yr intervals to capture the high variability and abrupt changes in this period.

Diatom assemblages were analysed to infer lake level change (see above). A simplified method of inferring lake level from diatoms is to use the planktonic:non planktonic ratio (Wolin and Stone, 2010). An abundance of planktonic taxa in a sediment sample would suggest deeper water levels and an abundance of non-planktonic taxa would suggest shallower water levels. However, lake level reconstruction is not always as simple as using the planktonic:nonplanktonic ratio method as diatoms respond to other environmental variables such as pH, salinity, conductivity, nutrient availability, turbidity and temperature. Therefore, modern sampling results from LLG (see chapter II) was used for ecological interpretation of the diatom assemblages in the sediment core. However, non-analogue assemblages are frequent in fossil diatom studies and in these cases reference to other modern and fossil habitats from similar study sites are required.

Diatom sample preparation followed Battarbee (1986). Samples were air-dried and then 0.5g was treated with dilute HCl and HNO₃ to remove carbonates and organic matter, respectively. Samples were evaporated onto a cover-slip, mounted onto a glass slide using Naphrax, and examined at 1000x magnification. A minimum of 400 diatom valves were counted per sample, and diatom abundance was calculated as a percentage relative to the sum. Seventy two taxa at the species and variety levels were encountered, representing 15 genera in total. Only diatoms present at >1% in two or more samples were included in the stratigraphic plot. Diatom species displayed in the final species figure (Figure III.5) were the most prevalent diatoms in the species assemblage and were included because they were key diatom types in the environmental analysis. Zoning was carried out by using the software psimpoll. The method for obtaining the zone was 'optimal splitting by information content' (Bennett, 2011). Three different summary groups were identified to define zone boundaries and provide a framework for diagram description and interpretation. A full record of diatom species found in LLG sediment core is listed in Table A.IV.1

Identification and nomenclature of cosmopolitan diatom species and varieties follows standard texts (Kützing, 1844; Krammer and Lange-Bertalot, 1986a,b, 1991a,b), whereas regionally-specific keys were used for taxa typical of tropical regions (i.e., *Eunotia camelus*, *E. didyma*) (Meltzeltlin and Lange-Bertalot, 1998; Rumrich and Lange-Bertalot, 2000). The diatom nomenclature used here remains unchanged from the source literature.

3.4.4 Multivariate analysis

Ordination was performed on the diatom data from the core fossil assemblages to explore any patterns of community variation among the samples. Diatom species' abundance was calculated as a proportion of the sum of all identified species in each sample. Detrended correspondence analysis (Hill and Gauch, 1980) (DCA) was performed using the 'VEGAN' package in the program R (R Development Core Team, 2007) on the relative percent abundance of the diatom species assemblage

A diatom-based Late Quaternary precipitation record for lowland tropical South America taxa in the 100 core fossil samples and 20 modern surface samples. To avoid rare taxa causing bias in the analysis, only species with an abundance of >1% in two or more samples were used. Data were square-root transformed to downweight the dominant taxa.

3.4.5 Particle size analysis

Sediment particle size analysis was carried out to reflect changes in the processes and energy of sediment transport. Particle sizes are closely linked to turbulence, wave energy, and proximity to shoreline; increased grain sizes generally correspond to higher energy conditions of sediment production or transport, whereas decreased grain sizes indicate lower energies. Grain-size fluctuations in sediment through time, particularly increases in sand sizes, may reflect low-level lake stands related to periods of drier and warmer climate. Conversely, decreases in sand content may reflect periods of wet and cold climates (Alin and Cohen, 2003). Samples were prepared following (UCL laboratory methods, 1999). Samples were air-dried overnight, crushed and sieved and then treated with dilute HCl and HNO₃ to remove carbonates and organic matter. A dispersal agent was mixed with the cleaned sample before being added to the coulter LS230 particle size analyzer. This system measures volumetric grain sizes between 1-100 microns by analyzing in-situ the angle of refraction of a laser beam that is aimed through the container holding the sediment/dilutents.

3.5 Results and interpretation

Figure III.5 shows diatom species composition in the LLG sediment core. Figure III.7 is a summary diagram of palaeoclimate in lowland Bolivia inferred from a multiproxy study. The subheadings below refer to the diatom zones in Figure III.7 but detailed descriptions of diatom species changes are mentioned and reference to Figure III.5 should be made in these cases. In Figure III.7 diatoms were grouped in to planktonic, facultative planktonic, aerophilous, benthic and epiphytic taxa to

A diatom-based Late Quaternary precipitation record for lowland tropical South America highlight the changes in water level in LLG. Species were grouped by ecological preference with reference to texts such as Meltzeltlin and Lange-Bertalot (1998) and Rumrich and Lange-Bertalot (2000) and also with reference to LLG's modern diatom data set. For a full list of diatom species included in each group see Table A.IV.1.

3.5.1 Statistical comparison of fossil and modern diatom assemblages.

A DCA of the fossil sedimentary core samples (Figure III.8) revealed distinct separation of the diatom assemblages from the late glacial period (20.5 ka – 12.5 ka BP), the glacial-Holocene transition (12.5 ka – 10 ka BP) and the Holocene (10 ka BP to the present). This highlights the differences in the composition of the diatom assemblages throughout these different time periods. In particular, the diatom assemblages of the late glacial and the Holocene are completely different as there is no overlap with any of the samples along axis 1. A DCA of the fossil samples combined with the modern surface samples (taken in 2006, see chapter II) (Figure III.9) again shows clear community separation among the samples. The modern samples are positioned away from all of the fossil samples apart from a few samples in the Holocene. This is unsurprising as there are many diatom species that occur in the modern samples that do not occur in the fossil samples and vice versa. It is interesting to note that all of the modern samples however, are on the negative side of axis 1. Axis 1 explains most of the variance in the dataset and the vast majority of the samples from the Holocene are also positioned on the negative side of axis 1 which means that the modern assemblages have most in common with the Holocene assemblages. Another DCA was created which again show the fossil and modern diatom samples but only the species which occurred in both the fossil and modern assemblages were included in the DCA analysis (Figure III.10). This shows that all of the modern samples from the south basin are positioned on the negative side of axis 2 as are the majority of the samples from the Holocene. Therefore, the species composition of the assemblages from the deeper, south basin is most similar to the samples from the Holocene. The modern samples from the north basin are

A diatom-based Late Quaternary precipitation record for lowland tropical South America distinct from the samples in the south basin apart from samples 11, 12 and 13 which were all in the river inflow or outflow (see Figure II.6, on page 53).

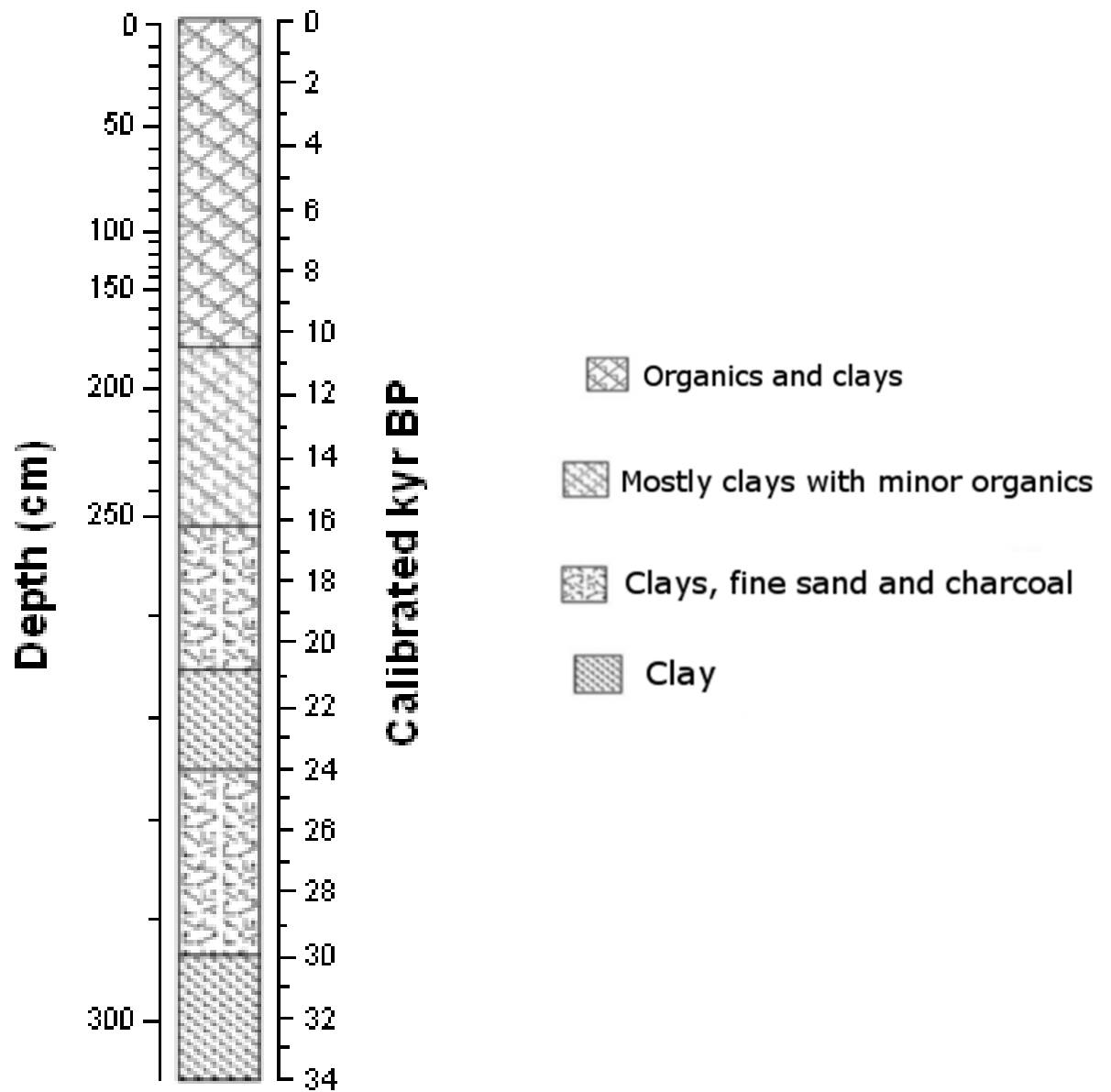


Figure III.4: Diagram to show sedimentary core with corresponding ages and depths.

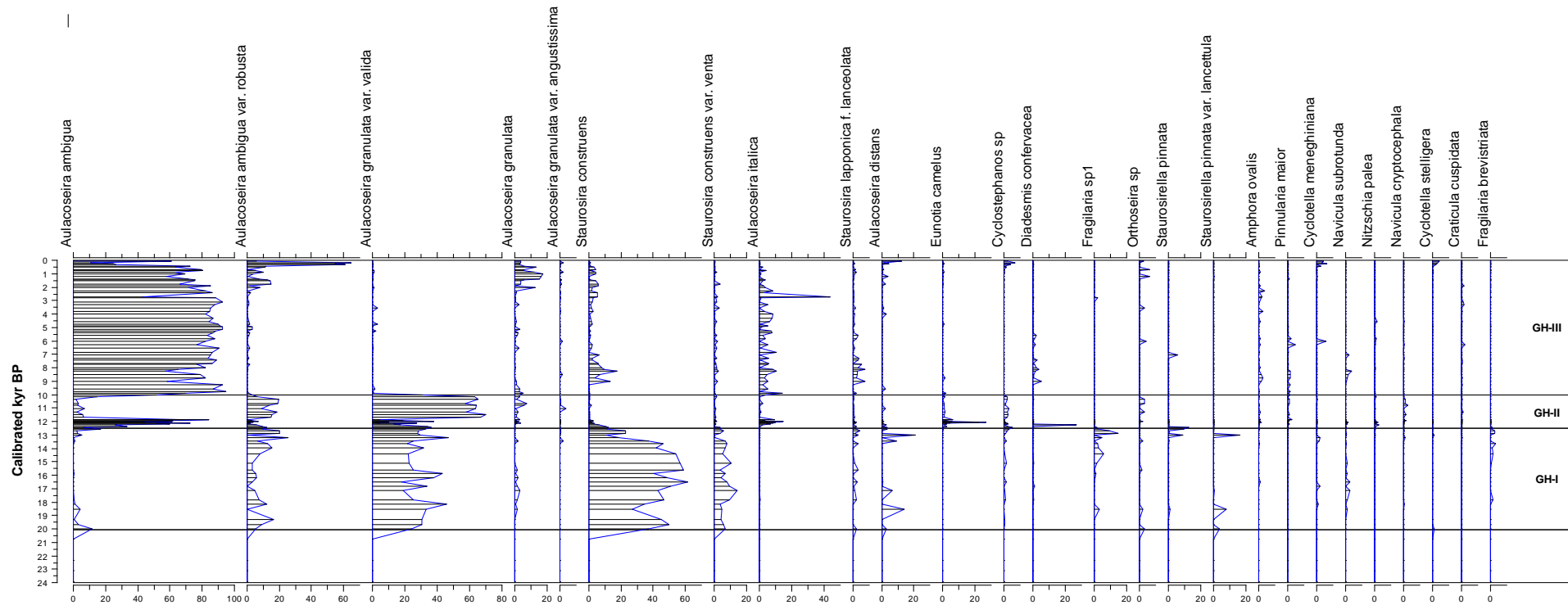


Figure III.5: Plot created in C2 (Juggins, 2003) to show diatom species percent abundance from LLG sediment core.

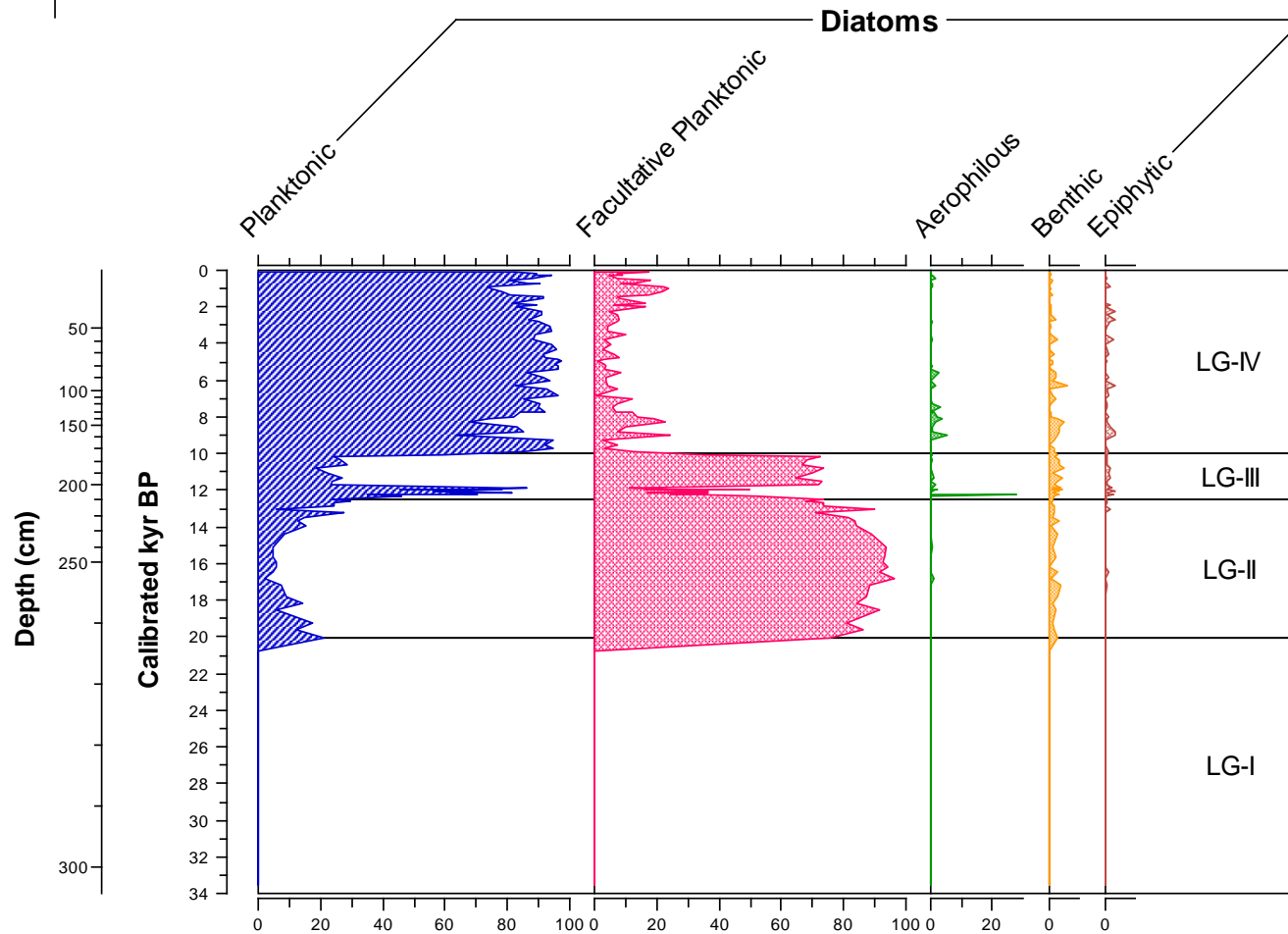


Figure III.6 Plot created in C2 (Juggins, 2003) to show a summary of diatom groups with corresponding depth and age axis.

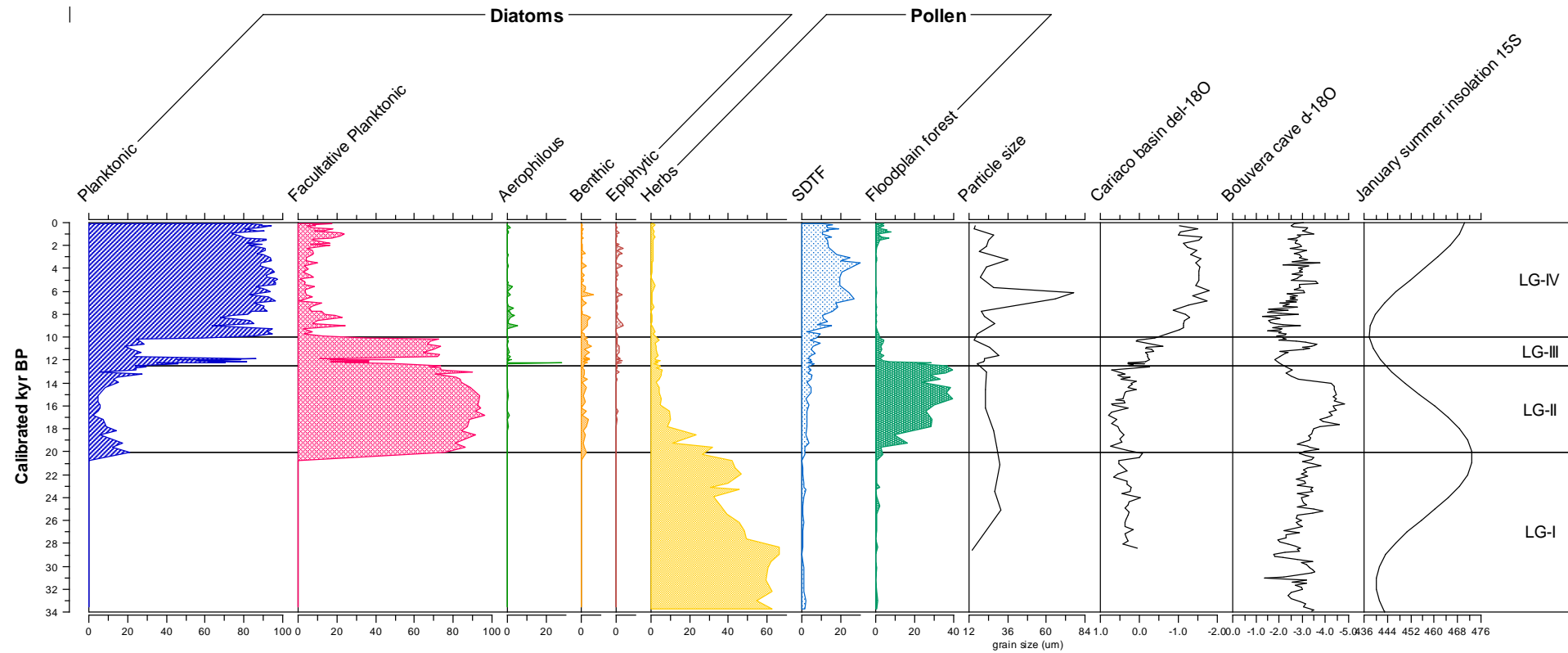


Figure III.7: Plot created in C2 (Juggins, 2003) to show a summary of multiproxy reconstruction at LLG. 5 categories of diatoms and 3 categories of pollen are included. Oxygen isotope data from the Cariaco basin (Peterson et al., 2000) and Botuvera cave (Wang et al., 2006) are also included for comparison. Also shown are January (austral summer) insolation (Berger and Loutre, 1991).

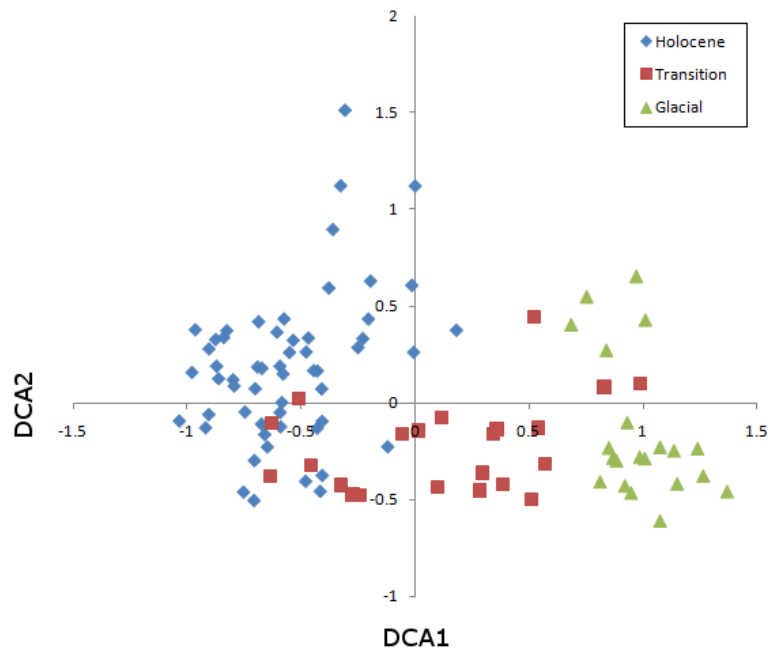


Figure III.8: De-trended correspondence analysis (DCA) showing the distribution of fossil samples from the sediment core over DCA axis 1 and 2.

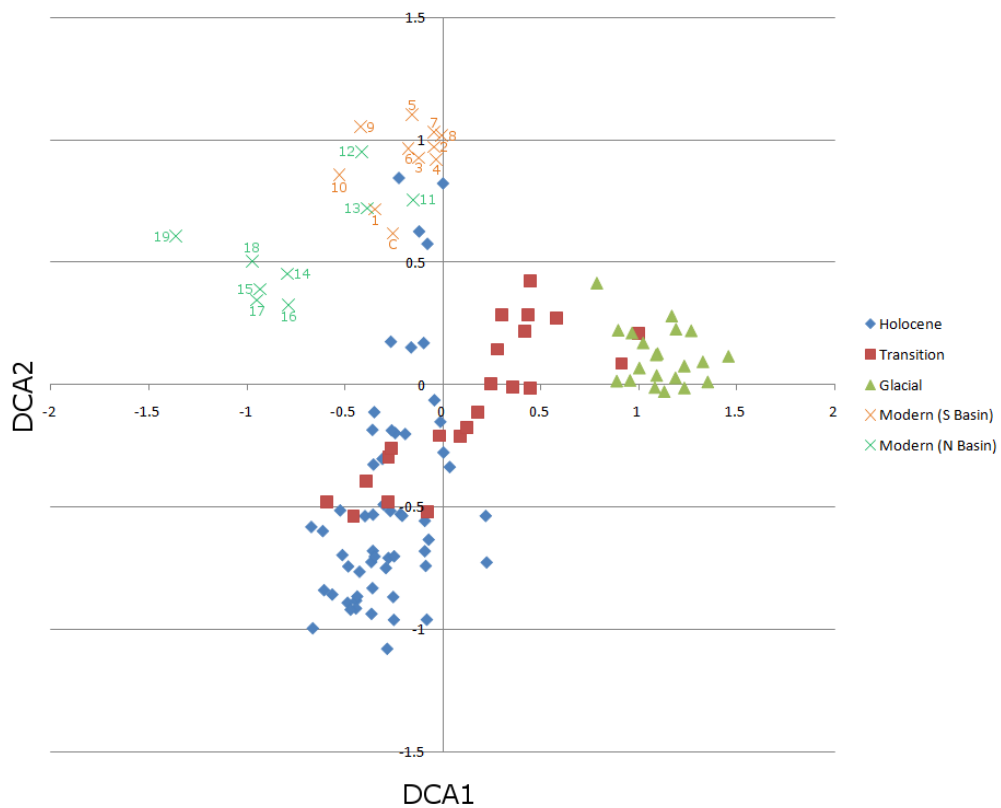


Figure III.9: DCA showing the distribution of fossil samples from the sediment core and modern surface sediment samples over DCA axis 1 and 2. Refer to Figure II.6 for modern sediment sample sites.

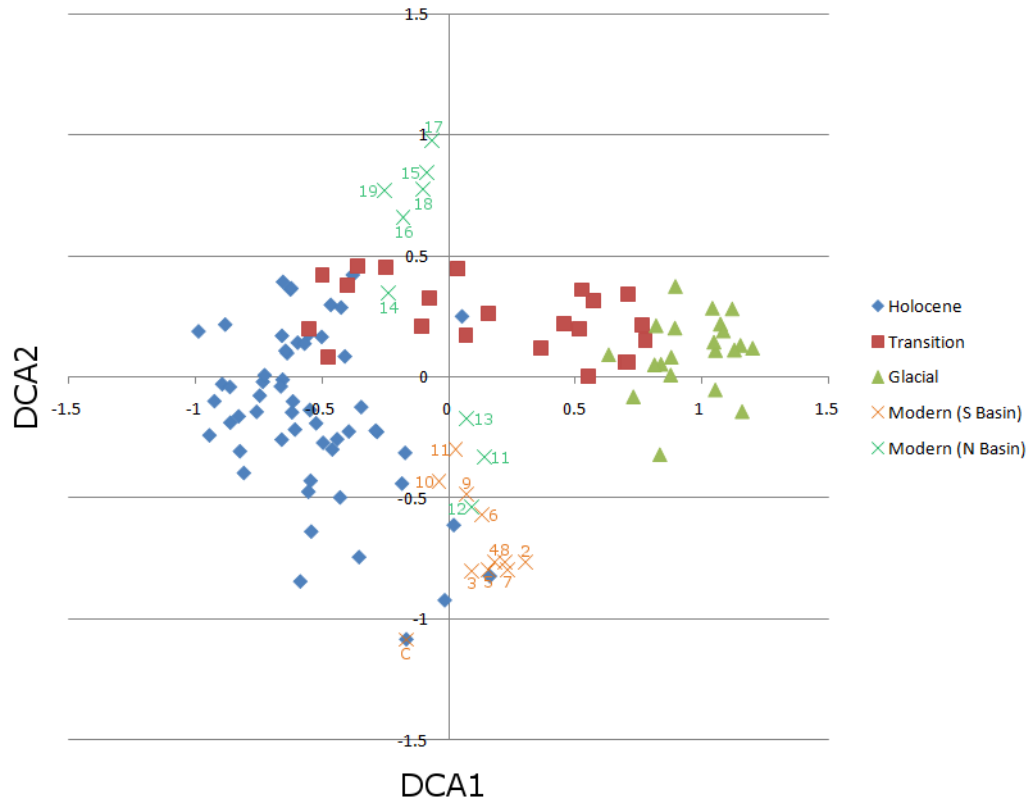


Figure III.10: DCA showing the distribution of fossil samples from the sediment core and modern surface sediment samples over DCA axis 1 and 2. Only diatom species which occurred in both the fossil core and modern assemblages were included in this analysis. Refer to Figure II.6 for modern sediment sample sites.

3.5.2 Chronology at LLG

The radiocarbon dated samples used to construct the age-depth model for the LLG core are fundamental in chronological interpretation of ecological changes at LLG. However, the availability of atmospheric ^{14}C content often complicates radiocarbon-based chronologies (Hajdas et al., 2003). One such change in the availability of ^{14}C is after 10,000 ^{14}C BP. The atmospheric $^{14}\text{C}/^{12}\text{C}$ ratio increased abruptly around 11,000 ^{14}C BP (a fast change in radiocarbon ages from 11,000 to $\sim 10,600$ ^{14}C BP) and then dropped over the next millennium, creating a radiocarbon plateau. The main cause has been suggested as being due to changes in ^{14}C fluxes between carbon reservoirs

A diatom-based Late Quaternary precipitation record for lowland tropical South America (Peterson et al., 2000). Therefore, the dates expressed in the following discussion must be viewed with caution, particularly in relation to dates during the Younger Dryas period (12.5 – 10.0 cal yr BP) when there was a radiocarbon plateau (Kitagawa and van der Plicht, 1998). The errors in the age-depth model also need to be taken into account (Figure III.3). Ages expressed in the following discussion are taken from the calibrated age-depth model by Whitney et al. (2011) and can be accurately compared against ages documenting changes in the pollen data set from the same LLG core. However, there will inevitably be uncertainty and error when comparing these dates to other palaeoclimatic studies and so suggestions of when climatic changes occur at LLG are tentative and should be viewed with caution as the nature of ^{14}C dating inherently includes errors.

3.5.3 LG-I. 560cm-263cm. Last glacial period; ~45ka BP – 20.5ka BP

The pollen record at LLG extends to approximately 45ka BP and from sedimentation rates and an age model from the core (Whitney et al., 2011). It is clear there was a lake present prior to the LGM through to the present day, but diatoms are not present in the record until ~20 ka BP (262cm). Prior to this there were two samples taken at 22.3 ka (268cm) and 23.1 ka BP (270cm) where a small number (<5) of fragmented diatoms were found. Ten further samples were extracted from the core from 23 ka – 41 ka BP which yielded no diatoms. A tentative suggestion for this lack of diatoms is extremely low lake levels at LLG at this time, combined with an extended dry period and evaporation, the lake may have been highly alkaline. Other studies have found that an absence of diatoms can be related to very low water levels combined with excess salinity or dissolution of biogenic silica in strongly alkaline solutions (Fritz et al., 1999). LLG obtains most of its silica from the adjoining Pantanal wetlands and from in-wash from the River Paraguay during the seasonal flood pulse (McGlue et al., 2011). If LLG was much shallower prior to 20 ka BP than it is today it is possible that the north portion of the lake was dry and the core site in the south portion was disconnected from the Pantanal wetlands and the

A diatom-based Late Quaternary precipitation record for lowland tropical South America River Paraguay. If this was the case, there would be very little silica input into LLG and therefore would create an uninhabitable environment for diatoms. Siliceous cell walls of the diatoms that did exist would be weak and unable to be preserved in the sediments (Martin Jezequel et al., 2000). Indeed, weakly silicified diatom valves are a common feature of Amazon records (Mikkelsen, 1997; Tapia et al., 2003). The absence of other siliceous organisms in the sediments prior to 20 ka BP supports this idea. Combining all the proxy evidence suggests low precipitation resulting in low lake levels to be a major component of the climate. Large, terrestrial plant macrofossils were found in the core sediments, indicating that the lake must have been somewhat smaller for the transport of the macrofossils (Whitney et al., 2011). This interpretation corroborated by the dominance of facultative planktonic diatoms in this period lead us to conclude that lake levels at LLG over the last glacial maximum were much lower-than-present.

3.5.4 LG-II. 263cm-229cm. Last glacial maximum and late glacial; ~20.5kyr to 12.5kyr BP

Diatom assemblages are dominated by facultative planktonic taxa consisting of mainly *Staurosira* species such as *Staurosira construens* (12% – 60%) and to a lesser extent, *Aulacoseira granulata* var. *valida* (19% – 45%) (Figure III.5) This is interspersed with small peaks of planktonic/facultative planktonic species *Aulacoseira granulata* var. *valida* particularly at 257cm, 250cm and 237cm (~ 18.1 ka, 15.9 ka and 13.2 ka BP according to age-depth model). Benthic species have low values throughout this zone (<4%). Other facultative planktonic taxa are present in higher-than-modern proportion but in low quantities including *Staurosira lapponica* f. *lanceolata*, *Fragilaria brevistriata*, *F. sp.* and *Navicula subrotunda*. Planktonic species *A. granulata* and *A. ambigua* and *Cyclostephanos sp.* are present in much lower-than-modern proportion in very low quantities (< 4%). Aerophilous and epiphytic taxa are negligible. Particle size remains low and steady throughout this period, consisting of silts and clays and getting slightly finer towards the end of the glacial period (Figure III.7). The fine

A diatom-based Late Quaternary precipitation record for lowland tropical South America particle size could be due to the isolation of LLG from the River Paraguay during the late glacial period combined with a weakened seasonal flood pulse; it is possible the high energy river was not transporting larger sediment particles to LLG as it does today (McGlue et al., 2011). The persistence of facultative planktonic and benthic diatoms throughout this period is concomitant with a shallower-than-present lake environment. Some fluctuations between planktonic and facultative planktonic taxa suggest there was some variation in water level throughout the late glacial or it is possible that the seasonality of the precipitation regime is reflected in the diatom record.

In shallow tropical freshwater systems, habitat characteristics are important in determining species composition (Metcalf, 1988). *Staurosira* spp. may dominate as a result of the penetration of the photic zone to the lake bottom which they inhabit (Bennion, 1995). However, these taxa have been shown to also dominate the plankton in highly turbid, shallow lakes (Fluin et al., 2007). *Staurosira* are able to form chains which allow them to be suspended into the photic zone, an advantage in shallow, turbid environments. They are also able to inhabit nutrient-enriched environments in the lake bottom (Sander van der Kaars, 2000). *Staurosira* spp. were more commonly found in the shallower, north basin in the modern samples from LLG (see chapter II). It is interesting that there is also a high abundance of what is typically thought of as a planktonic, deep water species; *Aulacoseira granulata* var. *valida* (Owen and Uthmaniyov, 1999, Cardoso and Marques, 2009). However, it is possible that this species variety prefers a more facultative planktonic environment. *Aulacoseira granulata* has been found in numerous studies from a tropical environments, particularly in East Africa (Gasse et al., 1989; Hubble and Harper, 2002; Stager et al., 2003; Ryner et al., 2007) and has been found to dominate the lake assemblage along with *Staurosira* spp. (Sander van der Kaars, 2000), indicating an open-water, relatively deep, possibly fluctuating lake level. High abundance of *Aulacoseira granulata* also indicates relative productivity within a lake. Indeed, in the modern diatom assemblages of LLG (chapter II), *Aulacoseira granulata* var. *valida* is

A diatom-based Late Quaternary precipitation record for lowland tropical South America present in the surface sediments of the shallow, north basin and when examined in constrained correspondence analysis (CCA) of the modern samples, it is found grouped with typically epiphytic and benthic diatoms. Therefore, for this study *Aulacoseira granulata* var. *valida* has been classified as a facultative planktonic diatom.

Diatoms associated with turbulence regimes can also be good indicators of water level change (Wolin and Duthie, 1999). The genus *Aulacoseira* is a particularly good example; it is a heavily silicified diatom with high sinking rates and its ecology requires turbulence to maintain its presence in the water column (Bradbury, 1975). During low water stages, increased turbulence corresponding with nutrient increases can favour this genus over other planktonic species. In Lake Malawi, *Aulacoseira* taxa are abundant in dry and windy conditions (Owen and Crossley, 1992). Although LLG is a much smaller lake than Lake Malawi, its southern basin is susceptible to wind-mixing as it is large and relatively shallow, where *Aulacoseira* species could take advantage of the slightly more nutrient rich, and more turbulent conditions. In a study from the south Pantanal floodplain, an abundance of *Aulacoseira granulata* and *Aulacoseira distans* was associated with falling water phases after flooding probably associated with greater mixing of the water column, due to climatological factors (Oliveira and Colheiros, 2000) as also observed by Train and Rodrigues (1998) in the Parana River. Therefore, it is likely that LLG was a shallow, turbid lake. This evidence, along with evidence of the expansion of the floodplain pollen assemblages provide clear evidence for low lake levels and therefore low precipitation in the Pantanal catchment during the late glacial period from 19.5 – 12.5 ka BP.

3.5.5 LG-III. 229cm-176cm. Late glacial and early Holocene; ~12.5kyr to 10kyr BP

The late glacial is characterised by an abrupt and dramatic short-lived increase in planktonic species *Aulacoseira ambigua* (85%) and aerophilous species (28%) peaking

A diatom-based Late Quaternary precipitation record for lowland tropical South America at ~12.2 ka BP (222cm) (Figure III.11). After this initial rise, aerophilous taxa drop to lower levels but are higher than the previous zone. Epiphytic species levels rise slightly over 12.5 ka– 11.3 ka BP but still remains low >3%. Benthic taxa rise slightly during this period to 10%. The occurrence of *Eunotia camelus* is distinctive in this zone and has a peak of 27 % between 12.1 ka and 12 ka BP (217cm-218cm) which coincides with a peak in *A. ambigua* and *A. italica*. There is also an abrupt peak in *Diadesmis confervacea* (27 %) at 12.3 kyr BP (225cm). Sediments consist mainly of clays with minor organics however at 11.0 ka (189cm) BP there is a change in the sediments to organics and clays and there is a small peak in particle size at 11.5 ka BP (196cm) (30.5µm).

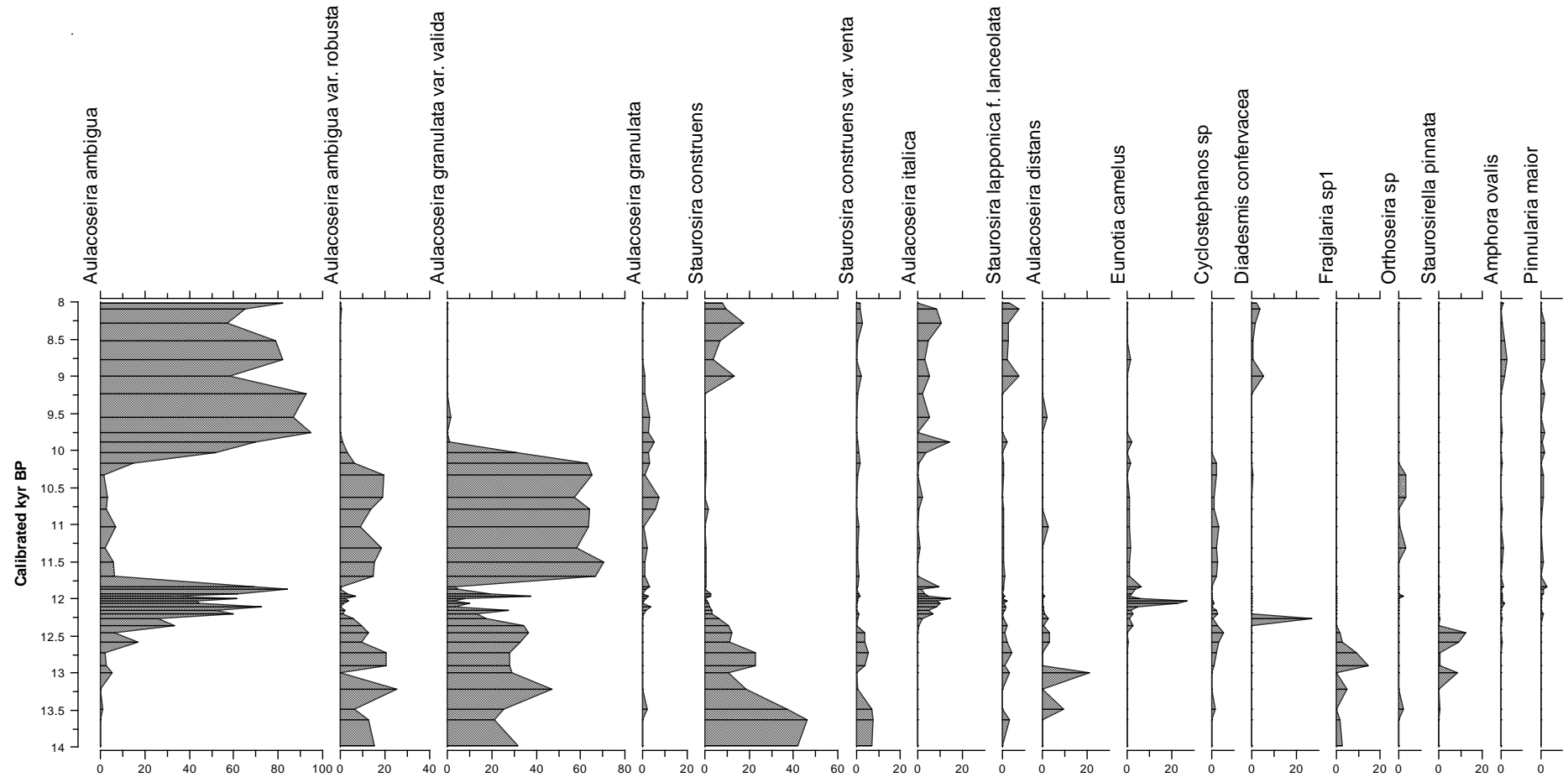


Figure III.11: Plot created in C2 (Juggins, 2003) to show key diatom species percent abundance from LLG sediment core from 14 ka – 8ka BP only.

A major switch from facultative planktonic dominated to planktonic dominated diatom assemblages indicates substantial hydrological change at the core site at 12.5 ka BP. The rising lake level is mirrored in the pollen record by an absence of floodplain trees (Whitney et al., 2011) indicating deeper, open water. The increased representation of planktonic taxa, particularly *Aulacoseira ambigua* and *Aulacoseira italica* suggests that changes in habitat, notably lake deepening, competitively advantaged *Aulacoseira* species. The lake level may have increased from prior to 12.5 ka BP as levels of *Staurosira* spp. have dropped dramatically from 13 ka BP. However at 12.2 ka BP, there is a large short-lived peak in *Aulacoseira ambigua*. The rise in planktonic diatoms also began slightly before the decline in floodplain forest at 12.5 ka BP, although it peaks at 12.2 ka BP. Rather than responding to planktonic:non-planktonic ratio changes, water level changes can be signalled by dominant planktonic forms which respond to physical or chemical variables (Wolin and Duthie, 1999). The shift from the coarser diatom form *Aulacoseira granulata* var. *valida* to *Aulacoseira ambigua* is difficult to interpret unequivocally. However, Kilham et al. (1986) argue that a switch between coarse-pored forms of *Aulacoseira* (e.g. *A. granulata* var. *valida*) and smaller forms (e.g. *A. ambigua*) are likely to result from changes in lake nutrient status. Kulikovskiy et al. (2009) also indicate that *Aulacoseira granulata* var. *valida* occurs in waters with higher nutrient status. Therefore, it seems that broad shifts from *Aulacoseira* species which are coarsely-areolated to those which have a high areole density in LLG may reflect lake deepening and an associated decrease in nutrient availability. However, this contradicts with a study by McGlue et al. (2011) on floodplain lakes in the Pantanal including LLG, which points to the importance of the flood pulse for nutrient and sediment delivery to the lakes. Another suggestion for the short-lived peak in *Aulacoseira ambigua* which could be due to a sudden increase in lake levels, but also to an increase in nutrients washed into the lake. However, I suggest that the diatoms at LLG first and foremost respond to LLG lake level changes as a study of the modern environment of LLG suggests *A. ambigua* is most strongly associated with the depth environmental variable and depth is the environmental variable that most explains the differences

A diatom-based Late Quaternary precipitation record for lowland tropical South America in diatom assemblages in LLG (see chapter II). It is possible that the switch to *Aulacoseira granulata* var. *valida* from ~11.8 - ~10.0ka BP (between 203-186cm) could have a stronger influence from the connection of the river to the lake than simple lake level change at LLG. To this end, it is possible that there was an abrupt and dramatic change to flooding at 12.2 ka BP that freshened the lake, deepening it and decreasing nutrient concentrations. The lake level stayed high until 11.7 ka BP (200cm) where it then dropped. The lake level from 11.7 ka BP – 10.0 ka BP was relatively shallow but higher than that of the late glacial from 20 ka BP to 12.5 ka BP. The higher-than-glacial lake level from 11.7 ka BP – 10 ka BP are indicated by the presence of planktonic species *Aulacoseira italica* and by negligible levels of the shallow water species *Staurosira construens*.

Coinciding with the peak in *Aulacoseira ambigua* at ~12.2 ka BP is a peak in aerophilous taxa such as *Eunotia camelus* and *Diadesmis confervacea* although *Diadesmis confervacea* peaks slightly earlier (~12.3ka BP) than the peak in *Aulacoseira ambigua* and *Eunotia camelus*. Aerophilous diatoms live exposed to the air or in very shallow water environments, often being associated with desiccation events (Bao et al., 1999), or dominant in areas that desiccate during the dry season (Nguetsop, 2004), suggesting that a increased flooding at 12.2 ka BP greatly increased the area of the lake, connecting the lake permanently to the Paraguay River and Pantanal wetlands. Aerophilous diatoms living on the previously dry lake shores and areas surrounding LLG would be washed into the lake. However, their high abundance in the fossil record would have been short-lived, reflecting the broad-scale and unidirectional nature of the flooding of low-lying terrain adjacent to LLG. *Diadesmis confervaceae*, which abundance accounts for the peak at 12.3 ka BP is an aerophilous diatom, (Velez et al., 2006; Spaulding and Edlund, 2009). However the reason for a peak in *Diadesmis confervaceae* occurring just before the major switch to *Aulacoseira ambigua* is uncertain. Following the peaks at 12.2 ka BP in planktonic diatoms, there is a small peak in particle size at ~12.0 ka BP. (Figure III.11). The sudden increase in planktonic diatoms, a peak in particle size suggesting a large influx of water into the

A diatom-based Late Quaternary precipitation record for lowland tropical South America southern portion of the basin and high sedimentation rates at this time (Figure III.3, on page 111) are all strong evidence in favour of increased flooding. I infer that this change to a wetter period permanently connected the River Paraguay and Pantanal wetlands to the southern part of LLG basin. Although facultative planktonic diatoms remain high throughout this period until 10.0 ka BP, the group is dominated by *Aulacoseira granulata* var. *valida* which is broadly considered a cosmopolitan freshwater taxa and is common in shallow lakes, rivers, and marginal regions of larger lakes (Kilham and Kilham, 1975). Although I have classified *A. granulata* var. *valida* as a facultatively planktonic diatom it requires more nutrients than *Staurosira* group (Stone et al., 2010); nutrients which may have been washed in with flooding at 12.2 ka BP and then sustained during higher precipitation and seasonal flooding until 10.0 ka BP. Therefore, its almost complete dominance of the assemblage between 11.7 ka and 10 ka BP suggests higher water levels than prior to 12.5 ka BP. I infer that LLG experienced frequent flooding from the River Paraguay, reflected by higher lake levels persisting at LLG from 12.5 ka– 10.0 ka BP ensuring water levels remained high enough for the deeper water and for *A. granulata* var. *valida* to thrive in LLG, marking the onset of a wetter Holocene climate in the South American lowlands.

3.5.6 LG-IV. 176cm-0cm. Holocene; 10kyr BP to present

A shift in diatom taxa from a dominance of *Aulacoseira ambigua* var. *robusta* and *Aulacoseira granulata* var. *valida* to *A. ambigua* (Figure III.5) at 10.0 ka BP signifies another episode of increased flooding. Lake levels then remain high throughout the Holocene, indicated by a dominance of deep water planktonic species *Aulacoseira ambigua* and *Aulacoseira italica*. The dominance of deep water diatoms throughout the Holocene reflects higher lake levels at LLG than in the late Pleistocene, which in turn suggests that flooding and precipitation in the Pantanal catchment was substantially higher. Facultative planktonic taxa vary slightly and have two peaks in the early Holocene at 9.0 ka (160cm) and 8.2 ka BP (145cm). At 10.0 ka BP,

A diatom-based Late Quaternary precipitation record for lowland tropical South America *Aulacoseira granulata* var. *valida* is replaced by *Aulacoseira ambigua*. *A. ambigua* is unequivocally a planktonic, deep water diatom (Bradbury, 1992).

At 9.5 ka BP (169cm), the abundance of planktonic taxa drops slightly and the abundance of facultative planktonic taxa increases. This is likely to indicate slightly lower lake levels from 9.5 ka – 7.5 ka BP (169-127cm). Aerophilous diatoms also increase between 9 ka and 7.5 ka BP although interestingly, there is no noticeable increase over this time in benthic taxa which suggests lake levels did not decrease to the extent where benthic taxa could flourish. *Diadesmis confervacea* occurs in the early Holocene (9 ka – 5.5 ka BP) but has minimal values throughout the late Holocene. From 7.5 ka BP to 2 ka BP (127cm-35cm) there is little variation in the diatom record and even then the fluctuations are between planktonic diatoms. Planktonic diatoms remain high, dominating the assemblage (up to 98%). This group is dominated by *Aulacoseira ambigua* which is also present in the modern samples, particularly the sediment samples where there is a slightly greater number of *A. ambigua* in the south basin samples than in the north basin. Levels of aerophilous taxa are negligible and benthic and epiphytic taxa remain low. This indicates stable mid-late Holocene lake level at LLG, with the exception of small fluctuations in planktonic and facultative planktonic taxa which may reflect seasonal lake level changes. At 0.2 ka BP (4cm) there is a switch from *Aulacoseira ambigua* to *A. ambigua* var. *robusta* (Figure III.12) which is the diatom species that dominates the modern surface samples in the south basin. Both *A. ambigua* and *A. ambigua* var. *robusta* species are deep water, planktonic species so the switch to the latter may be due to subtle changes in the environment that favours the variety *robusta*. There is a peak in particle size at 6 ka BP (11cm) with smaller fluctuations throughout the Holocene in comparison to unchanging particle size levels in the late Pleistocene. For the most part, the sediments consist of clays and silts. Greater fluctuations throughout the Holocene indicate more frequent high energy inputs of water or episodes of increased flooding associated with the connection of LLG to the River Paraguay, increasing sediment in-wash.

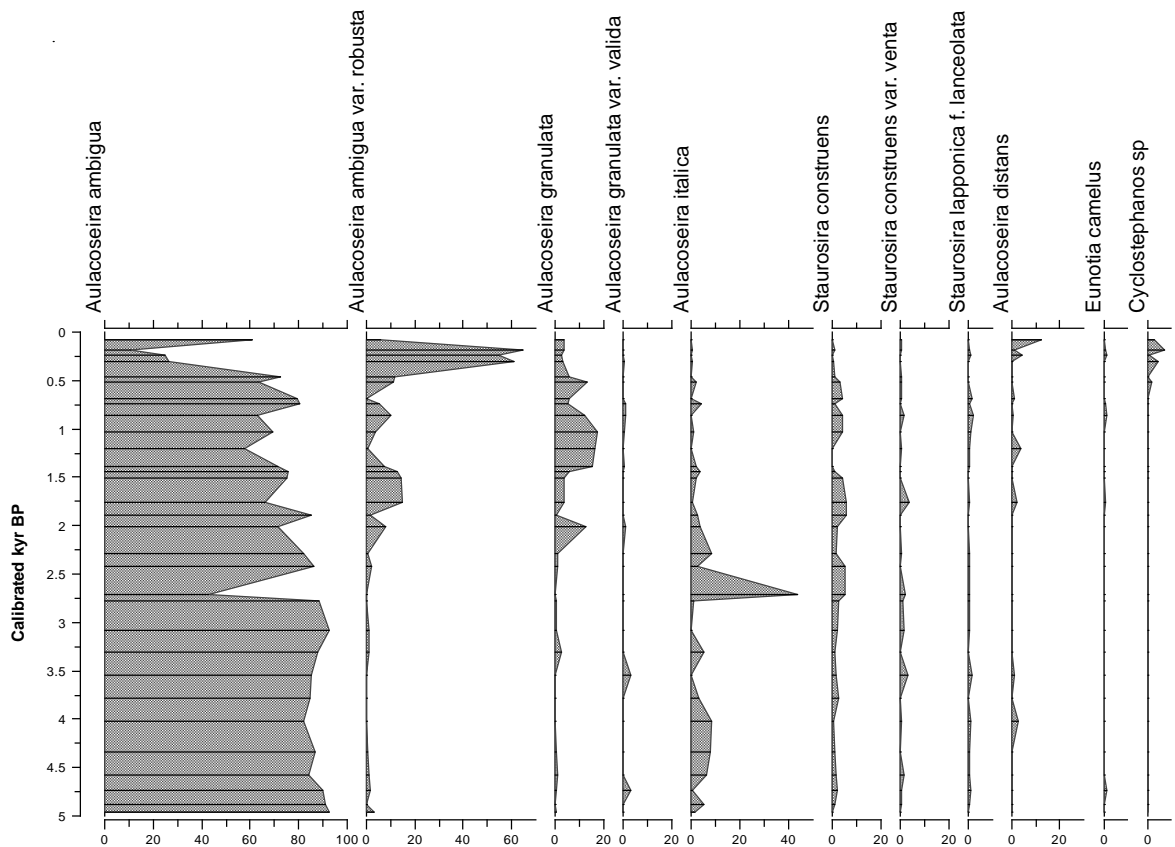


Figure III.12: Plot created in C2 (Juggins, 2003) to show key diatom species percent abundance from LLG sediment core from 5 ka BP to the present only.

3.5.7 Sediment stratigraphy

Sediment particle size is low during the late glacial which corresponds with sediments consisting of mainly clays. There is a small rise in particle size ~26ka BP when the sediments are characterised by clays, fine sands and charcoal. Overall, sediment particle size remains on average at 24µm until 12.8ka BP, where it then fluctuates throughout the Holocene to the present day. This does not correlate with a clear change in sediment stratigraphy at ~12.8ka BP, however I suggest that when LLG became permanently connected to the River Paraguay, a higher energy environment would have occurred. This may explain the fluctuating particle size in the Glacial-Holocene transition and through the Holocene. The fluctuating particle

A diatom-based Late Quaternary precipitation record for lowland tropical South America size could also be explained by the fact that sediments through the Holocene consisted of organics and clays. It is possible that the organic particles clumped together giving high peaks in particle size.

3.6 Discussion

3.6.1 Late Quaternary precipitation change at Laguna La Gaiba

The diatom record provides a continuous, high resolution record of water level changes at LLG from 20 ka BP to the present and is used to infer changing precipitation in the Pantanal basin. LLG is hydrologically linked to the Panatanal and River Paraguay and in turn, studies have shown that water level changes and river flow in the Pantanal and connecting river systems reflect climatically forced precipitation changes (Collischonn et al., 2001; Hamilton et al., 2006). We infer that the LGM and late glacial up to 12.5 ka BP was drier than present. This inference from the diatom record is also corroborated by the pollen record from LLG (Whitney et al., 2011). Further corroborating evidence for a dry LGM in lowland tropical South America are palaeoecological studies that have shown that glacial-age savannahs occupied the areas currently located within the boundaries of evergreen forest, indicating a drier glacial climate (Van der Hammen and Absy, 1994; Mayle et al., 2000; Burbridge et al., 2004). There is also evidence of sediment hiatuses and/or slow sedimentation rates from lacustrine records during the LGM that reflect drying lake basins which indicates lower-than-present precipitation (Ledru et al., 1998). This contrasts with diatom and fossil pollen records from the central Andes (Tapia et al., 2003; Fritz et al., 2003, 2007; Bush et al., 2004) and speleothem records from the Atlantic coast; NE (Wang et al., 2004) and SE (Cruz et al., 2005) Brazil, that suggest the LGM was wetter than present. These records exhibit a clear 20kyr precipitation cycle over the past 100-200kyr BP in tune with the precessional orbital cycle but at LLG, although a relatively short record in comparison, no precessional cycle pattern was found at LLG. A dry LGM at LLG contrasting with a wet LGM in the Andes supports a climate model generated to model precipitation over South America. This showed that annual rainfall was 25-

A diatom-based Late Quaternary precipitation record for lowland tropical South America 35% lower during the LGM than the present (Cook and Vizy, 2005). This was caused by a delayed onset of the South American monsoon. Since moisture inflow from the tropical Atlantic is the primary source of water for the South American monsoon, the model suggests cooler sea surface temperatures in the tropical Atlantic Ocean during LGM, weakening the South American Low-level Jet (SALLJ) and the 'Chaco low' and causing the delayed onset of the monsoon. This also increases moisture transport to the Altiplano via the Chaco low. Therefore we suggest that the precipitation in the continental interior of South America was influenced by LGM boundary conditions such as glacial ice extent in the northern hemisphere and cooler SSTs in the tropical Atlantic.

The high resolution of the diatom record allows detailed examination of precipitation and enables high frequency climate fluctuations to be captured. Peaks in planktonic diatoms through the late glacial (20.5 ka – 12.5 ka BP) suggest short-lived peaks in lake level. It is possible that these 'wet' periods in the mostly drier late glacial period reflect regional scale high fluctuation climatic events associated with the displacement of the ITCZ southward by a shutdown of the Atlantic meridional overturning circulation, a substantial cooling of the North Atlantic and an intensification of the northeasterly trade winds (Menviel et al., 2008). Increased precipitation at 15.9 ka BP at LLG may be part of Heinrich event-1, where an increase in precipitation during Heinrich events has been recorded in palaeoclimate records from southern South America (Baker et al., 2001; Jennerahn 2004; Wang et al. 2004, 2007). However, the peak at 15.9 ka BP is not anomalously high compared with the other wet episodes through the late glacial at LLG that do not appear to be associated with other continental climate anomalies. So I tentatively suggest this positive precipitation anomaly may be associated with H1 but also this wet episode and the other small peaks in precipitation throughout the late glacial period may be associated with more local fluctuations in precipitation.

One of the most studied climatic events in the late Quaternary is the Younger Dryas (GS-1 stadial = 12.9 to 11.6 cal. ka BP, terminology of Björck et al. 1998) (YD) which is thought to have induced aridity in the northern hemisphere tropics of South America and increased precipitation south of the equator (Dahl et al., 2005). The diatom record is characterised by a two abrupt shifts in diatom species dominance over the glacial-Holocene transition between 12.5 ka and 10 ka BP. I infer that rapid flooding took place centred over 12 ka BP, deepening the lake level substantially over this period. The planktonic diatom assemblages in LLG show particularly high abundance and dominate the assemblage from 12.5 ka to 10 ka BP with an abrupt change in climate beginning at 12.5 ka BP and climaxing with flooding at ~12.2 ka BP with water levels remaining high until 11.8 ka BP. This increase in flooding is mirrored in the pollen record as it is inferred that lake levels remained lower than present until 12.2 ka BP when flooding eliminated the seasonally-inundated floodplain forest (Whitney et al., 2011). However, a YD anomaly is not captured in the pollen record from LLG; the shift from floodplain forest to seasonally dry tropical forest (SDTF) is unidirectional and Whitney et al. (2011) inferred that at 12.2 ka BP, lake levels rose and then remained high. Due to the high resolution of the diatom record and the identification of taxa to species level, we can identify that the period of increased flooding was short-lived. From 12.5 ka -11.8 ka BP, lake levels were high but then dropped to where the facultative planktonic species *Aulacoseira granulata* var. *valida* could thrive but lake levels were too deep for the persistence of *Staurosira* taxa. I infer that this flooding increased the area of LLG and permanently connected the lake to the Paraguay River and the Pantanal wetlands. This inferred increase in precipitation from 12.5 ka BP agrees with high precipitation found in Titicaca and the Salar de Uyuni (Baker et al., 2001b; Placzek et al., 2006) and of travertine growth, indicative of running water in northeast Brazil (Salvador) (Auler et al., 2004) during the YD chronozone. A YD signal is also captured in an oxygen isotope record from the Botuvera cave in subtropical southern Brazil (Cruz et al., 2005). In the Cariaco basin, off the coast of Venezuela, an increase in $\delta^{18}\text{O}$ values signifies a dry, cold, climate (Lin et al., 1997). Therefore, the record at LLG is

A diatom-based Late Quaternary precipitation record for lowland tropical South America consistent with the theory that the ITCZ was forced southward caused by reduced overturning circulation in the North Atlantic, decreasing precipitation in the northern hemisphere and increasing precipitation in the southern hemisphere (Wang et al., 2004; Yuan et al., 2004). Although the LLG record highlights high lake levels at 12 ka BP, within the YD chronozone, the lake levels remain high throughout the Holocene. Although it is clear that lake levels do not return to the lowstand that persisted throughout the late-glacial until 12.5 ka BP, after 11.8 ka BP they do drop somewhat reflecting a potential YD-like signal. It is uncertain whether this anomalous wet period is responding to North Atlantic climate forcing like the records in the Altiplano and coastal Brazil as the return to drier conditions after the YD in these regions is attributed to a northward shift of the ITCZ, as resumed heat transport to the North Atlantic restored the interhemispheric thermal gradient after the YD. There is clearly an interesting shift in the environment at LLG to allow for the abrupt expansion of *Aulacoseira ambigua* species and I infer this period of flooding may be a YD signal which is a novel discovery in the lowland continental interior of South America.

Another abrupt change in climate occurs at 10 ka BP where lake levels rapidly rise, possibly caused by a strengthened flood pulse, but stay at high levels throughout the Holocene to the present day. The dramatic shift in conditions at LLG is not apparent in the pollen record at LLG but it does signal the beginning of a rise in seasonally dry tropical forest (SDTF) which is indicative of a slightly drier climate (Whitney et al., 2011). A major climatic or precipitation shift at 10 ka BP is not recognisable in any other palaeoclimatic records from tropical South America although an erosional anomaly recorded in palaeo-sols from the Andean Piedmont in south Bolivia is indicative of flooding caused by a change in seasonality (May et al., 2008). Therefore I suggest that the abrupt switch to deep water, planktonic diatoms is associated with a competitive response in the diatom community. *Aulacoseira ambigua* is a seasonal blooming diatom (Wolin and Stoermer, 2005; Bradbury et al., 2004). Its strong, seasonal bloom may have coincided with change to

A diatom-based Late Quaternary precipitation record for lowland tropical South America a more seasonal climate at 10 ka BP (May et al. 2008), giving *Aulacoseira ambigua* the competitive edge needed for its survival. Sustained higher lake levels throughout the Holocene were also ideal for its dominance. *A. ambigua* have also been associated with being a warmer water diatom (Bradbury et al., 2004) therefore lending further support to a moister, warmer Holocene. Sustained higher lake levels throughout the Holocene were also ideal for its dominance.

The diatom record from 10 ka BP to the present indicates the climate of the Holocene is characterised by higher precipitation than the late-glacial. Unlike the pollen record at LLG, the diatoms do not demonstrate a mid-Holocene drying. There are small fluctuations in the planktonic diatoms through the Holocene, indicating fairly stable high lake levels but there is no pronounced drop in planktonic species throughout this period. This contradicts the widespread evidence of early-mid Holocene drying (Mayle et al., 2000; Burbridge et al., 2004; Mayle and Power, 2008) across tropical South America and also evidence of early-to-mid-Holocene drying from the pollen record at LLG (Whitney et al., 2011). Mid-Holocene aridity has been recognised in studies of sediment cores on the Bolivian Altiplano, mainly from lake Titicaca. Lake levels were lowest between 8 ka and 5.5 ka BP (Baker et al., 2001), indicated by a dominance of benthic species. Therefore, it appears that the diatom record does not respond to the precession-paced seasonal insolation changes, influencing the latitudinal migration of the ITCZ and the strength of the SASM (Cruz et al., 2009). However, due to the strong evidence of mid-Holocene aridity over the SHTSA (Cross et al., 2000; Mayle et al., 2000; Baker et al., 2001; Bradbury et al., 2001; Freitas et al., 2001; Fritz et al., 2001; Muhs and Zarate, 2001; Wolfe et al., 2001; Mourguiart and Ledru, 2003; Burbridge et al., 2004; Iriarte, 2006) it is probable that the lack of a mid-Holocene aridity signal may be due to the nature of diatom ecology rather than as evidence against precessionally forced aridity in the lowland tropics. One reason for the appearance of a mid-Holocene drying in the pollen record and not the diatom record is that the wet season (austral summer) in SHTSA may have been drier and longer than usual, but (austral) winter

A diatom-based Late Quaternary precipitation record for lowland tropical South America precipitation increased. A significant change in seasonality reverts back to summer precipitation from 10 ka BP have been inferred from palaeosol analysis in the Andean Piedmont (May et al. 2007). This can be explained either by cold air incursions (Servant and Servant-Vildary, 2003) or by intensified south east trade winds bringing moisture advection. May et al. (2008) also report a decrease in annual precipitation related to the change in seasonality. Therefore at LLG, drought-tolerant/adapted SDTF community increased but overall average annual precipitation remained the same or decreased slightly and therefore lake levels remained high, allowing planktonic taxa to continue to flourish. This suggestion is supported by the fact that during the mid-Holocene there was no increase in floodplain forest taxa (Whitney et al., 2011) (Figure III.7) which may be expected if lake levels dropped, exposing a wider area of floodplain for the seasonally inundated forest to inhabit. The change in seasonality can be explained by a weakening and/or abrupt northward shift of the SASM/SACZ which has been recorded in speleothem records in south east Brazil (Cruz et al., 2005, 2006; Wang et al., 2006) probably related to the reorganisation of the atmosphere and oceanic circulation during the late Glacial-Holocene transition. Another possibility for the lack of a mid-Holocene drying signal in the LLG diatom record is that the steep-sided nature of the lake basin means that a small reduction in lake levels would not expose the underlying floodplain and therefore there would be no substantial increase in the littoral zone for littoral diatoms to flourish (Figure III.13) hence the persistent planktonic diatom signal through the Holocene. From this evidence, I infer that Holocene climate in this region is characterised by higher precipitation than the late-glacial period and the Pleistocene-Holocene transition. While the diatom record I present here does not support the strong evidence of mid-Holocene drying in SHTSA, it does not necessarily refute the idea. For example, it is possible that a transition to a more seasonal precipitation regime during the early Holocene could have maintained lake levels during a period of increased drying in the region.

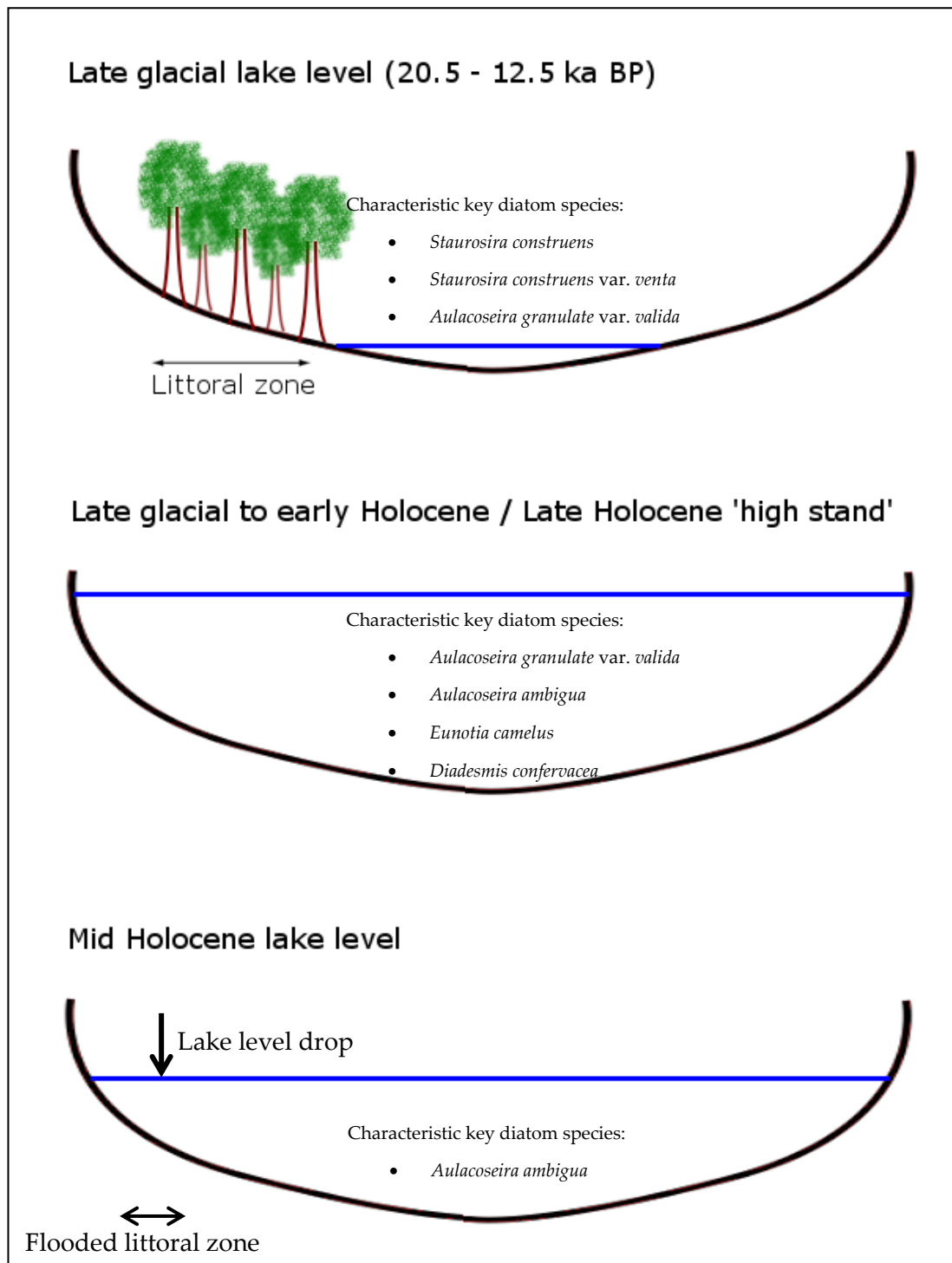


Figure III.13: Schematic diagram to show the possible changes in lake level at LLG from 20.5 ka BP to the present.

3.7 Conclusion

The high temporal resolution of the record at LLG provides a unique insight into the pattern of precipitation in the interior of SHTSA, the climate of which has been previously extrapolated from Andean records (e.g. Titicaca). Two major shifts in climate and diatom assemblage define the glacial-Holocene transition in the Pantanal basin. Lake levels were low over the LGM and through the late glacial in contrast with records from the tropical Andes and the Atlantic seaboard in Brazil. The region was drier than present until the beginning of the YD chronozone, at which increased precipitation in the Pantanal basin caused a switch to higher seasonal flooding and for LLG to be permanently connected to the River Paraguay and Pantanal wetland. Although the diatom record highlights a particularly wet period centred over 12.2 ka BP, the drop in lake levels after the peak is not as pronounced as it is in Andean and coastal sites. The lake levels stay relatively high. However, I infer that LLG did experience a precipitation anomaly during the YD chronozone but not to the same extent as other sites in tropical South America. The Holocene is marked by high lake levels from 11.8 ka BP, dominated by planktonic species from 10 ka BP and lake levels remain high through to the present in contrast with records from the Andes and Brazil that show mid-Holocene drying. However, I infer the lack of a diatom signal to be due to strong seasonality in the Pantanal region and/or the lake basin shape. It is unclear whether Heinrich events are reflected in the LLG record as the interpretation of the diatom signal at the time is uncertain and the temporal resolution is too low. In conclusion, precipitation changes in the continental interior of South America during the Pleistocene do not appear to be associated with precessionally forced summer insolation as has been previously suggested by extrapolated climate records from the Andes and NE and SE Brazil but precipitation events can be explained changes in glacial boundary conditions such as Atlantic sea-surface temperatures. Therefore latitudinal shifts and changes in the intensity of the South American Summer Monsoon played a dominant role in controlling the hydrological and environmental conditions in the lowland continental interior of South America. However, the precessional cycle had

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an influence over the climate regime during the Holocene as it is likely LLG
experienced early- mid-Holocene drying in-line with a northward shift of the ITCZ.

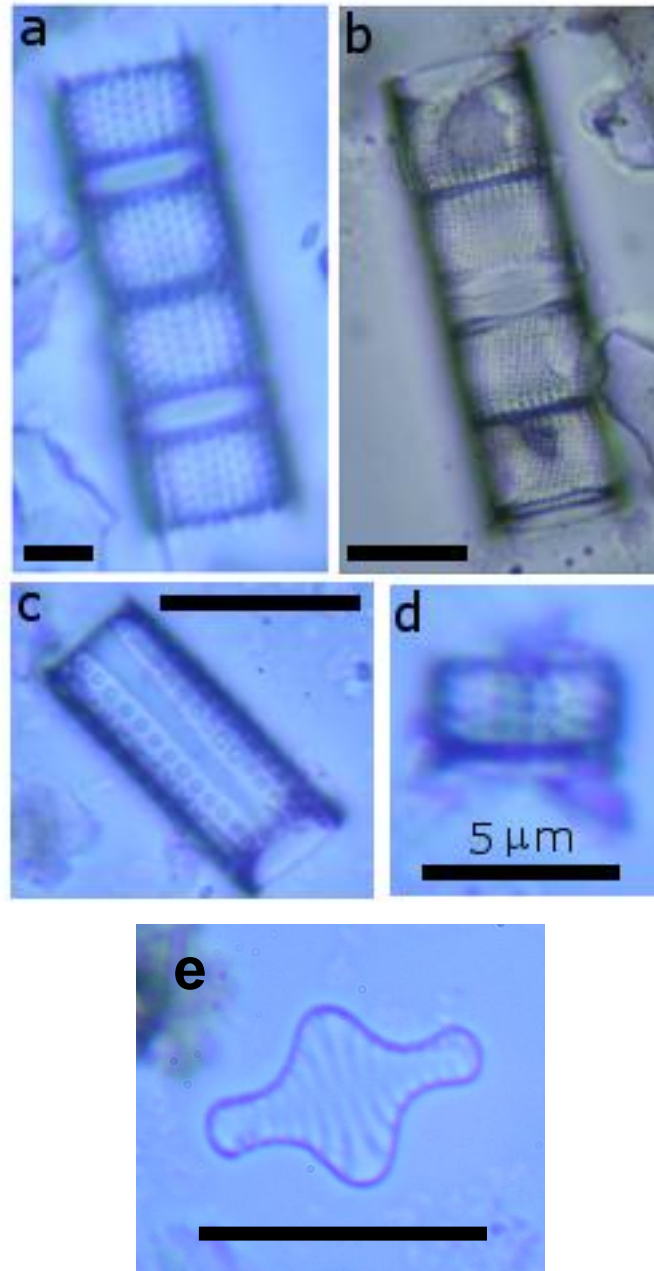


Plate 3. Key diatoms found in modern samples at LLG. Black scale bar = 10μm unless otherwise stated. a) *Aulacoseira ambigua* var. *robusta*, b) *Aulacoseira ambigua*, c) *Aulacoseira granulata*, d) *Aulacoseira distans*, e) *Staurosira construens*.

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IV. General Discussion

This study has allowed the detailed reconstruction of lake level change from the last glacial period (20.5 ka BP) to the present day. The use of diatoms as a palaeoenvironmental proxy has highlighted a precipitation record and detail within the reconstruction such as high-frequency, millennial scale events that is not visible from a previous pollen record alone due its lower sampling resolution. This thesis has substantially contributed towards the knowledge of diatom communities in a lowland tropical lake and the understanding of palaeoclimatology in tropical South America. Examined in detail below is how this thesis contributes towards two broad research themes: (i) diatoms as a proxy for lake level change in the lowland tropics and ii) moisture pattern over the southern hemisphere tropics of South America (SHTSA) from 20.5 ka BP to the present. Finally, I discuss the broader implications of this thesis and possible future work

4.1 Diatoms as a proxy for lake level change in lowland tropical SA

The modern diatom study (see chapter II) from Laguna la Gaiba (LLG) provides an understanding of intra-site diatom ecology and community variability in a lowland tropical lake. Water and surficial sediment samples were analysed in order to relate variations in diatom community structure to environmental variables, specifically depth, pH, conductivity and water chemistry. A study of the modern diatom environment was necessary as a) the study site for palaeoenvironmental reconstruction was previously unexplored for diatom analysis and b) to explore whether diatoms could be used as a proxy for lake level change. Given the hydrological links between lake level in LLG and mean annual precipitation in the Pantanal basin and the adjacent western Brazilian highlands (Collischonn et al., 2001; Hamilton, 2002), past variations in lake level could be used to infer past precipitation over a large part of the continental interior of SHTSA. As the study site

A diatom-based Late Quaternary precipitation record for lowland tropical South America was in the little-studied tropical lowlands of South America, it was necessary to understand the modern environment before palaeoenvironmental reconstruction to i) explore whether diatoms at LLG responded to variations in lake level, ii) understand the environmental variables and lake hydrology that may also affect diatom assemblages, and iii) identify the modern diatom ecology of the lake for use as an ecological reference in palaeoenvironmental reconstruction. Diatoms were used in the reconstruction at LLG as they can be excellent indicators of past environmental change as they respond sensitively to conditions prevailing in different aquatic environments and the diatom composition of an ecosystem is related to its size, depth and turbidity among other factors (Gasse et al., 1983). They reproduce rapidly and due to their siliceous cell walls they can be readily preserved in the sediment record and can be identified to at least species level (Cohen, 2003; Moser et al., 1996). The modern diatom record from LLG revealed that the diatom assemblages, particularly from surface sediments generally reflected the varying water level, therefore confirming that LLG provides a good setting for palaeoenvironmental reconstruction, using diatoms as a proxy for past lake level changes.

The diatom flora from LLG had many species which are found in other tropical areas in South America (from reviews of Metzeltin and Lange-Bertalot (1998, 2007) and Rumrich et al. (2000)) such as *A. ambigua* var. *robusta* and *A. distans*. These species were found to be two of the most common and dominant species in LLG. *Aulacoseira ambigua* is commonly found in diverse environments from all over the world. In freshwater tropical South American and African lakes, *A. ambigua* and other *Aulacoseira* species are characteristic components of pelagic freshwater phytoplankton (Hecky and Kling, 1987; Kilham, 1990). Only one unusual species, *Fragilaria cochabambina*, was discovered at LLG and to my knowledge has only been recorded in one other modern diatom study in the Bolivian cloud forest on the Eastern Cordillera of the Andes (Morales et al., 2009). However, the modern diatom assemblage from LLG was distinct from other modern diatom studies in South

A diatom-based Late Quaternary precipitation record for lowland tropical South America. For example, in tropical north east Brazil, a diatom study from the shallow Caco Lake was composed of mainly benthic and epiphytic forms such as *Pinnularia gigas*, *Frustulia rhomboids*, and *Encyonopsis krasskei*. The only species this lake had in common with LLG was *Eunotia Camelus* and *Eunotia monodon* (Nascimento et al., 2010). In other lakes in equatorial Columbia, Peru and Brazil, many endemic species of *Encyonema*, *Encyonopsis* and *Gomphonema* were found (Vouilloud et al., 2010), none of which had the same species as found in LLG. On the other hand, both the water and surface samples at LLG contained *Aulacoseira granulata* which is a common species in tropical regions and has been found in modern studies from lakes in lowland Columbia (Velez et al., 2005) from lowland fluvial systems, Argentina (O'Farrell, 1994) and on the Bolivian Altiplano (Baker et al., 2001a; Tapia et al., 2003). Although the modern assemblage at LLG contained tropical species only found in South America, such as *Eunotia camelus*, there are also a high percentage of cosmopolitan species such as *Aulacoseira ambigua* which has been found in diverse environments all over the globe including Arctic rivers in Canada (Stewart et al., 2005). In conclusion although the diatom assemblages of LLG have not been previously documented, and studies of the tropical lowlands are few and far between, endemic species were not found in the modern dataset. The species assemblages at LLG point to a mixed assemblage of common tropical and cosmopolitan species.

The modern data set for LLG was invaluable as an ecological reference for the reconstruction of the fossil data set as many of the most dominant species in the modern set were recognisable as key species in the fossil record, enabling habitat ecology comparisons to be made. However, the modern data set contained more diverse species assemblages than the fossil record. This could be because there has been some fracturing and/or dissolution of some species that are less heavily silicified (Battarbee et al., 2005) or that the present day environment is ecologically different to past environments. There are also some species that are found in the fossil record that do not occur in the modern assemblages for example, *Staurosirella*

A diatom-based Late Quaternary precipitation record for lowland tropical South America *pinnata*, *F. brevistriata* and *Craticula cuspidata*. This is likely due to the fact that the fossil record captures a much greater range of environmental variations that contribute to species composition such as changes in precipitation, temperature, nutrient supply and vegetation cover. Caution must be exercised when using a simple planktonic: non planktonic ratio for water level reconstruction as other environmental and hydrological variables will affect the diatom composition (see chapter II). Therefore, in the palaeoenvironmental reconstruction I combined knowledge from the modern data set at LLG with reference to the diatom habitat preference from various tropical palaeoecological reconstructions (such as Fritz et al., 2003; Tapia et al., 2003; Velez et al., 2005, 2006; Metcalfe et al., 2002, 2007).

There is considerable scope for improving the floristic study of modern diatoms in the Pantanal region and for investigating further environmental effects on diatom assemblage composition. It was not possible during this study to collect samples during the wet season however it would be interesting to see how the diatom assemblages differ and if they respond annually to the rise in lake levels. I would expect to see changes in the species composition at different stages of the seasonal cycle. For example, just before the summer monsoon rains the lake would likely have low lake levels. It would be interesting to see whether this would increase the amount of benthic and/or littoral diatoms in the species composition. During the wet season when lake levels were increasing and also after the flood water has reached LLG from the Pantanal (~4 months after the wet season rains) when the lake levels are at the highest stage, it is possible the nutrient availability in the lake would increase as in-wash from the Pantanal would bring vegetation and organic matter which also may affect the dominant species. A recent study of lowland lakes in the Pantanal including LLG has shown that LLG obtains most of its silica from the adjoining Pantanal wetlands and from in-wash from the River Paraguay during the seasonal flood-pulse (McGlue et al., 2011) which is likely to affect diatom assemblage composition on a seasonal basis. Also of interest would be to determine whether any dominant species had strong seasonal blooms. A study of the algal

A diatom-based Late Quaternary precipitation record for lowland tropical South America community in the Pantanal basin found that the seasonal alternations between the wet (flooding) and dry season had an effect on the macrophyte vegetation, which in turn influenced the water chemistry (De-Lamonica-Freire and Heckman, 1996). During the periods of rising and falling water levels, called *enchente* and *vatante*, respectively, high concentrations of dissolved nutrients are liberated into the water when the terrestrial species are drowned under the flood water and, alternatively, when the aquatic species die off as the water dries up (De-Lamonica-Freire and Heckman, 1996). Although this Pantanal study is of the whole algal community and my study is focused on diatoms, it gives an indication of how seasonal alternations may affect diatom assemblage composition and in turn may shed more light on whether seasonal changes are reflected in the fossil record. The fossil record at LLG could not be sampled at a high enough resolution to track seasonal changes, but it is possible that the record could highlight a change in the strength of seasonality. Nevertheless, the modern diatom study at LLG provides the only record of diatom composition for the lowland continental interior of South America that is combined with a fossil diatom reconstruction and highlights the value of diatoms as a proxy for lake level change at this site. Most importantly, however, the relationship between lake depth and diatom assemblages allows us to disentangle an important climatic variable from the host of environmental parameters that shape tropical ecosystems, adding a new dimension to, and bolstering the multiproxy record at LLG.

4.2 Moisture pattern over the SHTSA from 20 ka BP to the present

The radiocarbon dated samples used to construct the age-depth model for the LLG core are fundamental in chronological interpretation of ecological changes at LLG. However, the availability of atmospheric ^{14}C content often complicates radiocarbon-based chronologies (Hajdas et al., 2003). Therefore, the dates expressed in the

A diatom-based Late Quaternary precipitation record for lowland tropical South America following discussion must be viewed with caution, particularly in relation to dates during the Younger Dryas period (12.5 – 10.0 cal yr BP) when there was a radiocarbon plateau (Kitagawa and van der Plicht). The errors in the age-depth model also need to be taken into account (Figure III.3). Ages expressed in the following discussion are taken from the calibrated age-depth model by Whitney et al. (2011) and can be accurately compared against ages documenting changes in the pollen data set from the same LLG core. However there will inevitably be uncertainty and error when comparing these dates to other palaeoclimatic studies and so suggestions of when climatic changes occur at LLG are tentative and should be viewed with caution as the nature of ^{14}C dating inherently includes errors.

4.2.1 The last glacial precipitation regime

It is of particular interest to characterise the climate of South American tropical lowlands at the LGM because the atmospheric convection centred over the Amazon basin plays a central role in understanding climate conditions of South America. At present, there are no clear conclusions about the moisture patterns in the SHTSA at the LGM. A general consensus exists that the LGM climate was $\sim 4^{\circ}\text{C}$ colder than today (Betts and Ridgway, 1992; Stute et al., 1995; Bush et al., 2001; Seltzer et al., 2002; Whitney et al., 2011). However, the moisture patterns over South America are still widely debated, particularly for the Southern tropics.

An hypothesis dealing with glacial boundary forcing was suggested by Peterson et al. (2000) and Haug et al. (2001) among others. This proposed that a southerly mean position of the ITCZ coincided with cooler North Atlantic sea surface temperatures, strengthened winds and observed increased precipitation in the southern tropics (Arz et al., 1998; Jennejahn et al., 2004; Wang et al., 2004; Jaeschke et al., 2007). The reverse pattern is observed in the northern hemisphere tropics (Peterson et al., 2000; Peterson and Haug, 2006). Currently, moist conditions at the LGM in the Andes and as far as southern Brazil are explained by a strengthening of the SASM and

A diatom-based Late Quaternary precipitation record for lowland tropical South America southward shift of the ITCZ caused by glacial boundary forcing mechanism. By extension, it is argued that Amazonia, the current source of moisture for the Andes, would have experienced higher precipitation during the LGM. Evidence of a 'wet' LGM in lowland Amazonia include travertine growth, indicative of running water, in the currently moisture deficient Caatinga region of Brazil (Auler et al., 2004; Wang et al. 2004, 2007) and in central, equatorial Amazon there is evidence of closed-canopy forest reflective of a cool, moist climate (Colinvaux et al., 1996, 2000).

Precessional forcing is believed to be the dominant influence over the precipitation regime in tropical South America. During high summer insolation peaks, there is a steepened contrast between land and sea temperatures which increases the strength of the summer monsoon (Baker et al., 2001a). Precessional forcing of tropical climate has been demonstrated in Andean (Hooghiemstra et al., 1993; Baker et al., 2001b; Fritz et al., 2004) and lowland regions (Auler et al., 2004; Bush et al., 2004; Wang et al., 2007). Palaeoclimate modelling has supported the theory of precessionally-forced precipitation (Clement et al., 2004) demonstrating that regional hydrological change in the tropics over glacial-interglacial cycles is more sensitive to the precessional cycle than to changes in boundary conditions (CO₂ concentrations, ice volume, temperature). High summer insolation in the precessional cycle over the LGM is hypothesised to be the cause of increased precipitation on the Bolivian Altiplano (Baker et al., 2001a,b; Fritz et al., 2004, 2007) and in coastal Brazil (Wang et al., 2004). Rainfall from the South American summer monsoon (SASM) originates as convective moisture over Amazonia. Moisture from the Amazon basin is currently advected into Andean regions and carried to the Pantanal basin. The exit of the SASM is the south-southwesterly mid-latitude flow forming the South Atlantic convergence zone (SACZ), which brings precipitation to south-eastern Brazil. Therefore, it would be expected that the Pantanal also located in the southern hemisphere would have had similar-to-present precipitation levels during the LGM. However, this study reveals that the Pantanal basin experienced drier-than-present conditions over the LGM and during the last glacial period until the glacial-

A diatom-based Late Quaternary precipitation record for lowland tropical South America Holocene transition (20 ka– 12.5 ka BP). This indicates that precessional forcing is not the dominant influence on the climate of this region.

Using atmospheric general circulation models (AGCMs), Chiang et al. (2003), and Chiang and Bitz (2005) suggested that precipitation asymmetries over tropical latitudes can be produced by the displacement of the ITCZ which is caused by the expansion and contraction of land and sea-ice during the LGM or millennial events. Therefore, palaeo-evidence for a dry climate at the LGM in tropical lowland South America would suggest that something other than insolation forcing at the time of the LGM, forcing the ITCZ southward, is at play and other mechanisms must have been working to create dry conditions at LLG. Drying during the last glacial period has also been recognised over tropical South America in vegetation studies that record regions that are now covered by rainforest that were savannah occupied (Van der Hammen and Absy, 1994; Mayle et al., 2000; Burbridge et al., 2004) and also Assine and Soares (2004) found evidence of aeolian activity in the Pantanal which also implies a dry late-glacial period. However, the record from Laguna La Gaiba is unique: it is a high resolution, well dated, continuous record of lake level change which highlights a precipitation regime over the continental lowlands of the SHTSA as the changing hydrological conditions at LLG are reflective of a broad, regional signal representing >140,000km². A mechanism involving a delayed onset of Amazon convection during austral spring could explain the paradox of a drier Amazon synchronous with a wetter Andes over the last glacial period (Vizy and Cook, 2006); 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 (Cook and Vizy, 2007). However due to the connection between the exit of the Amazon moisture towards south east Brazil via the SACZ, if the delayed onset of Amazon convection was the cause of drought in the Pantanal, you would expect to see the same pattern in SE Brazil, but LGM records from SE Brazil clearly show a wet LGM (Cruz et al., 2005, Wang et al., 2007). There is still a paucity of records from tropical

South America and from the records that exist it is clear that the precipitation regime over the last glacial was complex. Further palaeoclimatic proxy studies combined with climate models are needed in this region to fully understand the climate forcing in South America over the last glacial.

4.2.2 High frequency climate fluctuations

Due to the high temporal resolution and identification of diatom taxa to species level in the LLG diatom record, it is possible to identify abrupt, high frequency precipitation episodes in the lowland tropics. It is important to document the exact timing of abrupt climate changes, whether they lead or lag the northern hemisphere, and the nature of the abrupt change. This would make it possible to attribute them to the various forcings, as both summer insolation and millennial scale events are thought to impact precipitation and moisture transport over the tropical Andes and the Amazon basin (Seltzer et al., 2000; Baker et al., 2001b). As mentioned previously, longer-term fluctuations in palaeo-rainfall over the Andes and coastal Brazil have been attributed to summer insolation forced by the Milankovich ~23ktr precession cycle however, other climate forcing has an effect on a smaller scale. Indeed, off the Venezuelan and Brazilian coast, there is no clear match between summer insolation and SST (Arz et al., 1998; Lea et al., 2003; Waldeab et al., 2006) or hydrological records (Arz et al., 1998; Peterson et al., 2000; Jennerjahn et al., 2004). Instead, in these records, SST and hydrological variations are dominated by millennial-scale events, such as Heinrich-events.

4.2.2.1 Is there evidence of Heinrich events at LLG?

A fluctuation in *Aulacoseira granulata* var. *valida* in the sedimentary record at LLG may signal a rise in precipitation at 15.9 ka BP, which could reflect an abrupt millennial-scale event. However the peak at 15.9 ka BP is not anomalously high compared with the other wet episodes through the late glacial at LLG (such as at 18.2 ka and 13.2 ka BP) that do not appear to be associated with other continental

A diatom-based Late Quaternary precipitation record for lowland tropical South America climate anomalies. So I tentatively suggest this positive precipitation anomaly may be associated with Heinrich event 1 but also this wet period and the other small peaks in precipitation throughout the late glacial period may be associated with changes in the intensity of the flood pulse that are not connected with millennial-scale climatic forcing. Heinrich (H) events are characterised in North Atlantic sediments by horizons with increased Ice Rafted Debris (IRD) concentrations. They occurred quasi-periodically with a spacing of 5000–14,000 yrs (e.g., Heinrich, 1988; Broecker, 1994). Sediment cores from the IRD belt suggest a common age for H1 (the last major event occurring at the onset of the deglaciation) between 16 ka and 17.5 ka BP (e.g., Bond et al., 1999; Bard et al., 2000; Grousset et al., 2001; Rohling et al., 2003; Hemming, 2004 and McManus et al., 2004).

Precipitation anomalies corresponding with H1 have also been recognised in records from the central Andes as 'wet' episodes (Baker et al., 2001a; Baker et al., 2001b; Placzek et al., 2006) between 16.6 ka and 14.1 ka BP and also in north east and south east Brazil (Arz et al., 1998; Wang et al., 2006; Wang et al., 2007). It is difficult to compare the timing of this precipitation anomaly with evidence for a precipitation anomaly during H1 in other areas in South America as the chronological control on the records through this period is quite poor. For example, Auler et al. (2004) found evidence for speleothem growth phases in north east Brazil between 14.2 ka and 16 ka BP but the record is not well constrained and Wang et al. (2006) find sediment hiatuses throughout the record from Botuvera cave, SE Brazil from 17 ka – 11 ka BP so the dating through this period that encompasses H1 is not accurate. Although the dating of the sedimentary record at LLG is good, the chronological control through the late glacial could be improved and so there is error around the dating of the precipitation peak at 15.9 ka BP. As discussed previously, precise dates are difficult to pin-point in the chronological record as the errors in the age-depth model can be substantial (~800 yrs). Therefore, it is not possible to compare synchronicity between records in the tropics of South America

A diatom-based Late Quaternary precipitation record for lowland tropical South America at H1 and the evidence from LLG is not strong enough to unequivocally state the presence of precipitation anomaly associated with H1.

4.2.2.2 Is there evidence of a Younger Dryas precipitation anomaly at LLG?

The record from LLG is an area devoid of high resolution records and therefore provides a unique insight into the precipitation regime in the continental lowlands of South America. The record from LLG reveals two major shifts in climate and species assemblage over the glacial-Holocene transition. Abrupt change in the diatom community and mirrored in the vegetation indicates a increased seasonal flooding centred at 12.2 ka BP, reflective of increased precipitation in the Pantanal basin, that signifies the start of the higher lake levels through the Holocene than in the late Pleistocene. At LLG, the flooding anomaly and high precipitation, from 12.5 ka – 11.8 ka BP, is short-lived (~700yrs) and although the lake levels remain high through the Pleistocene-Holocene transition and throughout the Holocene, there is clearly an anomalous episode centred over 12.2 ka BP where precipitation levels are particularly high. What is clear is that a high precipitation anomaly at LLG, chronologically occurs directly within the Northern Hemisphere YD chronozone (GS-1 stadial, 12.9-11.6 cal. ka BP).

The Younger Dryas (YD) is a short-lived but significant cold climatic reversal was first described in Scandinavia (Mangerud et al., 1974). The formalized YD expression is used; this has been defined by the synchronisation of dates from the North Atlantic region that recorded the abrupt change in climate, as advised by the INTIMATE group (Lowe et al., 2008). Therefore the YD = 12.9 – 11.6 cal. ka BP GS 1: Greenland stadial 1. The event is most pronounced in the Northern hemisphere. During this time, summer insolation was high and glaciers that had been retreating experienced significant re-advance and some areas that had been deglaciated saw the re-establishment of glacier ice (MacLeod et al., 2011). The general majority view

A diatom-based Late Quaternary precipitation record for lowland tropical South America is that the YD was caused by a slowing down or cessation of the North Atlantic thermohaline circulation (Clark et al., 2001).

A YD precipitation anomaly has also been recognised in several well-dated palaeoclimate reconstructions from tropical South America however the exact nature of the YD in South America has not been quantified as the climatic response may vary geographically in timing and the type of change that occurs. The records demonstrate a general pattern of increased precipitation south of 10° S and decreased precipitation north of 10° N. Many records from the northern hemisphere and within 10° S of the equator demonstrate increased aridity during the YD (Arz et al., 1998; Van't Veer et al., 2000; Seltzer et al., 2000; Maslin and Burns, 2001; Peterson and Haug, 2006; Ledru et al., 2006; Jacob et al., 2007). There is a paucity of records for the southern hemisphere tropics, and these records are primarily in the Andes or in coastal regions. However, there is a pattern of higher precipitation from the records from latitudes lower than 10° S (Baker et al., 2001a; Auler et al., 2004; Cruz et al., 2005; Placzek et al., 2006; Wang et al., 2007).

The change to a wet period at LLG within the North Atlantic YD chronozone at LLG is evidence for increased precipitation which is concurrent with other records from the southern hemisphere. This suggests that the precipitation regime in the lowland tropics was dominated by the influence of the cold climatic reversal in the North Atlantic where the thermohaline circulation slowed, weakening Atlantic meridional overturning circulation (AMOC). This forced the ITCZ southward, altering the precipitation regime in South America and in particular, intensifying the monsoon in the southern tropics (Dahl et al., 2005).

Overall, the diatom record shows a precipitation rise beginning at 12.5 ka BP, which is consistent with diatom and geochemically inferred precipitation change on the Altiplano (Baker et al., 2001a, 2001b), and travertine growth in coastal Brazil (Auler et al., 2004; Wang et al., 2004). Although there was anomalously high precipitation

A diatom-based Late Quaternary precipitation record for lowland tropical South America at LLG during the YD chronozone, indicated by a clear short-lived change in the diatom community, the post-YD drop in lake levels was not as severe as at other sites in tropical South America (Baker et al., 2001a, 2001b; Auler et al., 2004; Wang et al., 2004), where dry conditions return after the YD.

4.2.3 The Holocene precipitation regime

The abrupt shifts in diatom species assemblage over the glacial-Holocene transition at LLG indicate a shift to lake levels substantially higher than that of the late Pleistocene. I infer the onset of the Holocene as from 11.8 ka BP following the anomalous peak from 12.5 ka – 11.8 ka BP when higher precipitation in the Pantanal catchment caused higher lake levels in LLG. Both the diatom and pollen records indicate wetter conditions from the glacial-Holocene to the present. From 12.2 ka BP the pollen and diatom records are in agreement about high precipitation however, from 10 ka BP the proxy records from LLG tell conflicting stories. The diatom reconstruction shows an abrupt shift to the highest lake levels in the record at 10 ka BP whereas a gradual decrease in precipitation is inferred from the pollen record (Whitney et al., 2011). However, I infer that the abrupt community change in diatoms from facultative planktonic to planktonic was triggered by another flood pulse at 10 ka BP where the lake levels then remained high and the environment favoured the domination of planktonic species *Aulacoseira ambigua*.

The vegetation record at LLG reflects a steady increase in seasonally dry tropical forest (SDTF) taxa from 10 ka BP which is demonstrative of a drier and/or more seasonal climate in the early- to mid-Holocene (Whitney et al., 2011). During the mid-Holocene, the SDTF taxa peaks at 6.4 ka BP adding to the evidence for mid-Holocene drying (see Whitney et al., 2011 in Appendix B. for detailed pollen description). However, this drying cannot have been as severe as in the late Pleistocene as the planktonic diatom levels remain high and there is no recurrence

A diatom-based Late Quaternary precipitation record for lowland tropical South America of floodplain forest from 12.2 ka BP which is indicative of relatively high lake levels. Therefore, the proxy records at LLG appear to be conflicting. The pollen record indicates a reduction in precipitation from 10 ka – 3 ka BP but the diatom record indicates lake levels remained consistently high throughout this period. However, there is a small increase in facultative planktonic species *Staurosira construens* and *Staurosira laponica* from ~9.5 ka – 7.5 ka BP coinciding with a small drop in planktonic species which may represent a drop in lake levels over this time.

The diatom record at LLG shows little change in the species composition from the mid-Holocene to the present which indicates stable lake levels. However, the pollen record at LLG identifies rising precipitation records from the mid-Holocene to the present, with deeply flooded conditions being reached at 1.4 ka BP (Whitney, PhD thesis, 2009) which is also demonstrated in the diatom inferred reconstruction at Lake Titicaca (Baker et al., 2001b). The difference between the pollen record at LLG combined with the diatom reconstruction at Titicaca indicating higher precipitation, and the diatom record from LLG showing stable lake levels could be because the established planktonic diatom community throughout the Holocene was stable and indicative of deep, open water but does not recognise further lake level rise. The vegetation response over the Holocene may have been stronger than the diatom record as warming temperature, combined with the precipitation regime afforded more dramatic vegetation changes whereas the diatom community is unlikely to have responded to the temperature and is more sensitive to variations in lake levels change (see chapter II), and therefore precipitation.

Several Holocene palaeoclimatic studies in tropical South America indicate a drier climate during Early and mid-Holocene (Absy et al., 1991; Salgado-Labouriau et al., 1997; Ledru et al., 1998; Behling and Hooghiemstra, 2000; Freitas et al., 2001; Siffedine et al., 2001; Abbott et al., 2003; Cordeiro et al., 2008). A wetter climate and higher river discharge has been recorded in the northernmost region of South America by the geochemical composition of the Cariaco basin sediments (Haug et

A diatom-based Late Quaternary precipitation record for lowland tropical South America al., 2001). The wet conditions in the Cariaco basin can be explained by a northern position of the ITCZ during the early- to mid-Holocene (Haug et al., 2001). A drier palaeoclimate in the early- to mid-Holocene in tropical South America has been interpreted as being due to a northward shift of the ITCZ in response to lower summer insolation at that time (Martin et al., 1997; Mayle et al., 2000; Marchant et al., 2001). This is hypothesised to have increased precipitation in the northern hemisphere and reduced precipitation in the southern hemisphere tropics of South America. It is possible that unlike the severe mid-Holocene aridity demonstrated in Lake Titicaca (Baker et al., 2001b) and Laguna Bella Vista (located 610km NW of LLG) (Burbridge et al., 2004; Punyasena, 2008), the reduction in precipitation at LLG was not as severe. The relative abundance of key SDTF taxa from LLG corroborates this (Whitney, PhD thesis, 2009).

Although it was originally suggested by Whitney et al. (2011) that the vegetation in the lowlands of SHTSA reflected drying in the early- to mid-Holocene, it is possible that the vegetation responded to increased seasonality at the onset of the Holocene (May et al., 2007) rather than an average annual decrease in precipitation. Ledru et al. (1996) and De Oliveira (1992) suggested the early Holocene (9.5 ka to 5.0 ka BP) was characterised by a marked seasonal pattern and higher temperatures in southeastern Brazil and a palaeoclimate model shows reduced rainfall from December to April (summer) and slightly increased precipitation from September to November (winter) in tropical South America in the mid-Holocene (Silva Dias et al., 2009) which may support the hypothesis of relatively stable levels of total precipitation throughout the Holocene, allowing lake levels at LLG to remain high. Evidence from the Pantanal suggests that during the Pleistocene-Holocene transition, “the modern Pantanal wetland was established, the drainage system was reorganized, and some temporary channels became permanent rivers” (Assine and Soares, 2004). Also, along with a change to more humid conditions came the individualisation of lake systems from 10.2 ka BP (Bezerra, 1999). This may have had a substantial effect on the lake levels at LLG as the lake was permanently

A diatom-based Late Quaternary precipitation record for lowland tropical South America connected to the Pantanal River, sustaining higher-than-Pleistocene lake levels throughout the year. Another possibility for the persistence of planktonic taxa through the Holocene may be that the steep-sided nature of the lake basin at LLG allows a large area of open water and very little space for a littoral zone when lake levels are high (Figure III.13, on page 139, chapter III). Therefore, even if lake levels did drop slightly in response to mid-Holocene aridity, the drop was not substantial enough to expose a large littoral area for the expansion of benthic and littoral diatoms. This is corroborated by the fact that there is no recurrence of riverine vegetation in the Holocene (Whitney et al., 2011), further evidence to suggest that the Holocene aridity in the continental lowlands of South America was not as severe as during the glacial period.

The importance of a multiproxy reconstruction, particularly over the Holocene period at LLG is clear. Examination of the diatom record alone would have led us to believe that lake levels were high throughout the Holocene, indicated by consistently high levels of planktonic diatom species and there was no indication of lake levels dropping. Examination of the pollen record alone inferred there is clear evidence of early –to-mid-Holocene drying, indicated by the expansion of certain SDTF types. However the multiproxy reconstruction suggests that it is likely the lowlands of South America may have experienced a change in seasonality starting at 10 ka BP and that lake levels may have dropped in response to a reduction in precipitation, but not to the level of the late-glacial lowstands.

The gradual increase in precipitation from the mid-Holocene to the present is indicated in the vegetation record (Whitney, PhD thesis, 2009) and although it is not clear there was a rise in lake levels from the diatom record, this trend is also inferred from a diatom record in Lake Titicaca (Baker et al., 2001b). This would suggest that precipitation over the lowland continental interior of South America was influenced by the precessional cycle variations in (austral) summer precipitation from the mid-Holocene to the present, strengthening the SASM and bringing more moisture to

A diatom-based Late Quaternary precipitation record for lowland tropical South America (Baker et al., 2001b; Cruz et al., 2005; Mayle and Power 2008).

I suggest that the precipitation regime during the Holocene of the continental interior of tropical South America was i) influenced by the precessionally-forced insolation changes during the Holocene but the response of the vegetation and diatom communities suggest the influence was not as strong in this region compared to the Altiplano and coastal Brazil ii) the diatom community was not dramatically affected by the mid-Holocene drying that is apparent in the vegetation record and at other sites in South America, however there is evidence of a possible drop in lake levels from 9 ka - 7 ka BP, iii) the mid-Holocene to present increase in precipitation was not strongly reflected in the diatom record. Therefore, it is difficult to determine from the Holocene diatom record alone whether the precipitation regime was influenced by summer insolation changes or other climate forcing. However, considering the full multi-proxy record from LLG and the strong evidence of a mid-Holocene aridity in the SHTSA, it appears that the precipitation regime in the lowland continental interior of South America is linked to precession-paced seasonal insolation changes influencing the strength and latitudinal migration of the ITCZ and monsoon (Cruz et al., 2009).

4.3 Broader implications and future work

There is still scope for exploring the role of diatoms as tool for palaeoenvironmental reconstruction at Laguna La Gaiba and in the whole of the Amazonian lowlands. Due to the time constraints in the field, the number of modern samples taken from the lake environment was limited. An increased number of diatom and environmental variable samples from a more diverse range of aquatic environments at LLG and in other lakes situated along the River Paraguay, for example from the littoral zone, vegetation and stone scrapings would provide more complex knowledge of the modern diatom communities and their relationship with the

A diatom-based Late Quaternary precipitation record for lowland tropical South America physical and chemical environment (Hassan et al., 2009). This information could then be used as training sets for transfer functions that could be applied to the fossil assemblages in the sedimentary sequence. Diatoms have highly resolved temporal sensitivity and therefore the assemblage composition in different seasons may differ dramatically as hydrological conditions along with nutrient concentrations, light availability and the amount of vegetation are just a few other variables that are likely to change (Wolin and Duthie, 1999). An advantage of using transfer functions and also taking samples in different seasons is that analogues for past conditions are more likely to be apparent and therefore there would be less reliance on using ecological data from other study areas. In this study I have used modern diatom assemblages as an analogue for fossil reconstruction which provides qualitative estimates of ecological conditions in the fossil record. A training-set for the modern diatom counts and associated ecological data would provide a quantitative approach to palaeoenvironmental reconstruction at LLG. The data set would be used to calibrate a transfer function that quantitatively describes the relationship between species and ecological conditions. An additional benefit is that the transfer functions can be applied to other assemblages to derive quantitative estimates of key ecological variables such as pH, temperature, depth, salinity, location etc... The use of transfer functions is also important for evaluating the likely reliability of ecological reconstructions (Kumke et al., 2004). Transfer functions have been used to indicate lake level change. Fritz (1990) developed a transfer function for the quantitative reconstruction of salinity change using diatom surface sediment assemblages and associated water-chemistry data from a Great Plains lake in North America. Fluctuations in the balance between evaporation and precipitation result in changes in lake level and the concentration of dissolved salts, and diatoms are sensitive indicators of salinity in closed basin, saline lakes. Fritz (1990) found the transfer function was in good agreement with historical records. Although transfer functions would provide mathematically robust analysis of diatom assemblages, there are often deviations from the expected empirical values (Fritz,

A diatom-based Late Quaternary precipitation record for lowland tropical South America (1990). A better understanding of diatom physiological ecology in lowland tropical lakes is imperative before transfer functions can be applied to LLG.

Climatic interpretations of fossil diatom assemblages from a palaeoreconstruction are likely to be more accurate when compared with modern assemblage analogues from the same site (Nascimento et al., 2010), for example, unexplained changes in diatom composition at LLG, such as the switch between *Aulacoseira granulata* var. *valida* and *Aulacoseira ambigua*, which may be related to seasonal changes in precipitation, would be clarified with further study of the modern environment by implementing higher temporal resolution sampling regime of the modern data set in order to resolve any change in seasonality that may affect diatom blooms or composition in the diatom signal.

However, the full potential for diatoms to track precipitation change at LLG has yet to be applied to the existing record. There is further scope for increasing the resolution of the analysis over high frequency, abrupt events such as Heinrich events. Currently, it is unclear whether the positive peaks in deeper-water diatoms during the late glacial period at 18.2 ka and 15.9 ka BP are associated with climatic events or just 'noise' in the record. The last glacial was marked by large and abrupt climate variability in the form of Dansgaard-Oeschger (D-O) cycles and Heinrich events (Bond et al., 1992; Alley, 1998). The North Atlantic Heinrich events have been shown to occur at a global scale (Voelker et al., 2002), and indeed are visible in records from the central Andes (Baker et al., 2001b; Placzek et al., 2006) and north east (Arz et al., 1998) and south east (Wang et al., 2007) Brazil. However, there are no high resolution records in the lowland continental interior of tropical South America that capture these abrupt episodes. Considering the sedimentation rate at LLG through the late glacial it would be possible to sample the core at a resolution of ~150 years which would highlight whether the inferred increases in precipitation were abrupt, anomalous changes in climate. Another key aspect of identifying key events in the LLG sedimentary core is defining the timing of the climatic change.

The core is currently well-dated but further radiocarbon analysis to improve the age-chronology would help enormously in constraining abrupt events such as the possible H1 event and the precipitation event during the Younger Dryas chronozone. High stratigraphic resolution and improved chronology of the sedimentary core at LLG would shed light on the extent that North Atlantic climate events had on the precipitation regime in the lowland interior of the SHTSA and whether there is synchronicity in the timing of these events with the Andes and coastal Brazil.

4.4 Conclusions

The original aims of the two journal style chapters are detailed below along with the key findings of each chapter. General conclusions of the thesis as a whole and how the research contributes to the overall picture of South American tropical palaeoclimatology are briefly presented after the conclusions of the focused chapters.

Chapter II focused on the modern diatom environment at Laguna La Gaiba and I aimed to determine the environmental controls on species assemblage composition. A key goal of this research was to ascertain whether diatoms from LLG can be used as a tool for palaeoenvironmental reconstruction, specifically as a proxy for lake level change. Key findings include:

- The modern diatom community at LLG is comprised of a mixed assemblage of common tropical and cosmopolitan species.
- Depth is a major constraining variable on the diatom assemblage composition at LLG, which is particularly evident in the sediment surface samples.
- Diatoms can be used as a proxy for lake level change at LLG and this study has highlighted the potential for application of diatoms in

A diatom-based Late Quaternary precipitation record for lowland tropical South America palaeoenvironmental reconstruction at other sites in the lowland tropics of South America.

Chapter III focused on precipitation change from the last glacial maximum to the present. In particular, I attempted to determine whether there is evidence of precipitation anomalies during abrupt, millennial-scale events. Key findings include:

- Dominance of facultative planktonic and benthic species in the fossil record indicated that LLG was drier than present from the last glacial maximum to 12.5 ka BP.
- A positive precipitation anomaly occurred during the Younger Dryas chronozone although lake levels remained relatively high after 11.8 ka BP. The two-stepped precipitation anomaly at the late glacial-Holocene transition also included another episode of increased flooding at 10 ka BP which coincided with a switch to a more seasonal climate in the Pantanal basin.
- A small positive precipitation anomaly at 15.9 ka BP occurs during the time of Heinrich event 1 but it is not certain whether this is linked to a high frequency climatic event.
- The Holocene diatom assemblages are marked by a dominance of planktonic species implying high lake levels throughout the Holocene. I infer that precipitation during the Holocene was higher than the late glacial but a mid-Holocene drying in the lowlands of tropical South America is masked by the continuous presence of planktonic species.

The general conclusions of this thesis that furthered understanding of late glacial-Holocene climate change in tropical South America are as follows:

- The dry climate of lowland tropical South America in the late-glacial from 20.5 ka – 12.5 ka BP contrasts with well-dated record from the central Andes and NE and SE Brazil that demonstrate a wetter-than-present LGM in tune

A diatom-based Late Quaternary precipitation record for lowland tropical South America with the precessional cycle. Therefore, it is more likely that the climate of lowland tropical South America was dominantly influenced by global glacial-interglacial cycles.

- There is a positive precipitation anomaly at LLG from 12.5 ka – 11.8 ka BP that falls within the YD chronozone and is in agreement with other tropical South American records that suggest an anomalously wet climatic episode was caused by a brief southern shift of the ITCZ in response to weakening of the Atlantic Meridional Overturning Circulation. 11.8 ka BP signals the onset of the Holocene in the continental interior of SHTSA.
- The precipitation cycle was broadly similar to other sites in tropical South America and experienced slightly lower precipitation in the early- to-mid-Holocene. Although the increased precipitation from the mid-Holocene was not detected in the diatom record it appears the Holocene was linked to precession-paced insolation changes that influenced the strength and latitudinal migration of the ITCZ.
- Overall, the precipitation cycle in the lowland continental interior of South America was dominated by the influence of global glacial-interglacial cycles but on a secondary level was also influenced by the precession cycle. The continental interior of SHTSA also appears to be influenced by high frequency northern hemisphere climatic changes.

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A. Appendix

A.1 Diatom complete species list

<i>Species name</i>	<i>Authority</i>	<i>Shortened name</i>
<i>Achnantheidium exiguum</i>	Grunow	Ach.exi
<i>Achnanthes lanceolata</i> var. <i>dubia</i>	Grunow in Cleve & Grunow, 1880	Ach.lan.dub
<i>Amphora ovalis</i>	Kützing	Amp.ova
<i>Aulacoseira ambigua</i>	Grunow in Van Heurck	Aul.amb
<i>Aulacoseira ambigua</i> var. <i>robusta</i>	(Grunow) Simonsen	Aul.amb.rob
<i>Aulacoseira distans</i>	(Ehrenberg) Simonsen	Aul.dis
<i>Aulacoseira granulata</i>	(Ehrenberg) Simonsen	Aul.gra
<i>Aulacoseira granulata</i> var. <i>angustissima</i>	(O. Müller) Simonsen	Aul.gra.ang
<i>Aulacoseira granulata</i> var. <i>valida</i>	(Hustedt) Simonsen	Aul.gra.val
<i>Aulacoseira italica</i>	(Ehrenberg) Simonsen	Aul.ita
<i>Brachysira superserias</i>		Bra.sup
<i>Craticula cuspidata</i>	(Kützing) D.G. Mann ex Round et al. (1990)	Cra.cus
<i>Craticula</i> sp. <i>unknown1</i>		Cra.sp1
<i>Cyclostephanos</i> sp.	Round ex Theriot, Håkansson, Kociolek, Round & Stoermer 1987	Cyls.sp
<i>Cyclotella meneghiniana</i>	Kützing	Cyc.men
<i>Cyclotella stelligera</i>	Cleve and Grunow	Cyc.ste
<i>Cymbopleura</i> sp.	Krammer	Cym.sp
<i>Diadesmis confervacea</i>	Kützing(1844)	Dia.con
<i>Diploneis pseudovalis</i>	Hustedt 1930	Dip.pse
<i>Diploneis</i> sp. <i>unknown</i>	Ehrenberg (1844)	Dip.sp

<i>Species name</i>	Authority	Shortened name
<i>Encyonema silesiacum</i>	(Bleisch in Rabenhorst) D.G. Mann(1990)	Enc.sil
<i>Eunotia bilunaris</i>	(Ehrenberg) Mills	Eun.bil
<i>Eunotia camelus</i>	Ehrenberg	Eun.cam
<i>Eunotia circumborealis</i>	Lange-Bertalot & Norpel	Eun.cir
<i>Eunotia didyma</i> var. <i>curta</i>	Hustedt ex Zimmerman	Eun.did
<i>Eunotia didyma</i> var. <i>tuberosa</i>	<i>Eunotia didyma</i> . Grunow. var. <i>tuberosa</i> . Hustedt	Eun.did.tub
<i>Eunotia gibbosa</i> var. <i>paraguayensis</i>	Hustedt	Eun.gib.par
<i>Eunotia minor</i>	(Kützing) Grunow in Van Heurck(1881)	Eun.min
<i>Fragilaria brevistriata</i>	Grunow in Van Heurck, 1885	Fra.bre
<i>Fragilaria capucina</i>	Desmazières Bremerton	Fra.cup
<i>Fragilaria cochabambina</i>	Morales sp. nov.	Fra.coc
<i>Staurosira construens</i>	(Ehrenberg) Grunow	Fra.con
<i>Staurosira construens</i> var. <i>venta</i>	(Ehrenb.) Grun. in Van Heurck 1882	Fra.con.ven
<i>Staurosira lapponica</i> f. <i>lanceolata</i>	Hustedt	Fra.lap.lan
<i>Staurosirella pinnata</i>	Ehrenberg 1843	Fra.pin
<i>Staurosirella pinnata</i> var. <i>lancettula</i>	(Schumann) Hustedt in A. Schmidt et al. 1913	Fra.pin.lan
<i>Gomphonema augur</i>	Ehrenberg(1840)	Gom.aug
<i>Gomphonema contraturris</i>	Lange-Bertalot & Reichardt	Gom.con
<i>Gomphonema graciloides</i>	F.Hustedt	Gom.gra
<i>Gomphonema parvulum</i>	Kützing(1849)	Gom.par
<i>Gomphonema</i> sp.	Ehrenberg 1832	Gom.sp
<i>Gyrosigma acuminatum</i>	Kützing	Gyr.acu
<i>Navicula capitata</i> var. <i>lueneburgensis</i>	(Grunow) Patrick in Patrick & Reimer 1966	Nav.cap.lue
<i>Placoneis clementis</i>	Grunow	Nav.cle
<i>Navicula cryptocephala</i>	Kützing 1844	Nav.cry

<i>Species name</i>	<i>Authority</i>	<i>Shortened name</i>
<i>Navicula gastrula</i>		Nav.gas
<i>Navicula moralesii</i>		Nav.mor
<i>Sellaphora pupula</i>	Kützing, 1844	Nav.pup
<i>Sellaphora pupula</i> f. <i>rostrata</i>	Hustedt	Nav.pup.ros
<i>Sellaphora pupula</i> var. <i>rectangularis</i>	(Gregory) Cleve & Grunow	Nav.pup.rec
<i>Navicula subrotunda</i>	Schumann	Nav.sub
<i>Naviculadicta</i> sp.	Lange-Bertalot in H. Lange Bertalot & G. Moser, 1994	Navdicta
<i>Neidium</i> cf. <i>amphigomphus</i>		Nei.amp
<i>Neidium</i> sp.	Pfitzer (1871)	Nei.sp
<i>Nitzschia granulata</i>	Grunow	Nit.gra
<i>Nitzschia palea</i>	(Kützing) W. Smith	Nit.pal
<i>Orthoseira</i> sp. <i>unknown</i>	Thwaites (1848)	Ort.sp
<i>Pinnularia angustistriata</i>	D. Metzeltin & K. Krammer	Pin.ang
<i>Pinnularia maior</i>	(Kützing) Rabenhorst	Pin.mai
<i>Pinnularia microstauron</i>	(Ehrenberg) Cleve 1891	Pin.mic
<i>Pinnularia rostratissima</i>	Metzeltin & K. Krammer	Pin.ros
<i>Sellaphora</i> sp.	Mereschkowsky, 1902	Sel.sp
<i>Surirella</i> sp.	Turpin, 1828	Sur.sp
<i>Synedra ulna</i>	(Nitzsch) Ehrenberg 1836	Syn.uln

Table A.IV.1: Complete list of diatom species found in modern samples and fossil core samples from LLG. Also included are species abbreviations used in ordination figures.

A.2. Diatom species groups

Planktonic	Facultative Planktonic	Aerophilous	Benthic	Epiphytic
<i>Aulacoseira ambigua</i>	<i>Aulacoseira distans</i>	<i>Diadesmis confervacea</i>	<i>Diploneis</i> sp. unknown	<i>Achnantheidium exiguum</i>
<i>Aulacoseira ambigua</i> var. <i>robusta</i>	<i>Fragilaria brevistriata</i>	<i>Eunotia bilunaris</i>	<i>Navicula capitata</i> var. <i>lueneburgensis</i>	<i>Achnanthes lanceolata</i> var. <i>dubia</i>
<i>Aulacoseira italica</i>	<i>Fragilaria capucina</i>	<i>Eunotia circumborealis</i>	<i>Placoneis clementis</i>	<i>Amphora ovalis</i>
<i>Cyclostephanos</i> sp	<i>Fragilaria cochabambina</i>	<i>Eunotia didyma</i> var. <i>curta</i>	<i>Navicula cryptocephala</i>	<i>Eunotia minor</i>
<i>Cyclotella meneghiniana</i>	<i>Staurosira construens</i>	<i>Eunotia didyma</i> var. <i>tuberosa</i>	<i>Navicula gastrula</i>	<i>Gomphonema augur</i>
<i>Cyclotella stelligera</i>	<i>Staurosira construens</i> var. <i>venta</i>	<i>Eunotia gibbosa</i> var. <i>paraguayensis</i>	<i>Navicula moralesii</i>	<i>Gomphonema contraturris</i>
<i>Orthoseira</i> sp. unknown	<i>Staurosira lapponica</i> f. <i>lanceolata</i>		<i>Sellaphora pupula</i>	<i>Gomphonema graciloides</i>
	<i>Staurosirella pinnata</i>		<i>Sellaphora pupula</i> f. <i>rostrata</i>	<i>Gomphonema parvulum</i>
	<i>Staurosirella pinnata</i> var. <i>lancettula</i>		<i>Sellaphora pupula</i> var. <i>rectangularis</i>	<i>Gomphonema</i> sp.
	<i>Gyrosigma acuminatum</i>		<i>Navicula subrotunda</i>	<i>Synedra ulna</i>
	<i>Nitzschia palea</i>		<i>Naviculadicta</i> sp.	
	<i>Eunotia camelus</i>		<i>Nitzschia granulata</i>	
	<i>Aulacoseira granulata</i>		<i>Pinnularia angustistriata</i>	
	<i>Aulacoseira granulata</i> var. <i>angustissima</i>		<i>Pinnularia maior</i>	
	<i>Aulacoseira granulata</i> var. <i>valida</i>		<i>Pinnularia microstauron</i>	
			<i>Pinnularia rostratissima</i>	
			<i>Neidium</i> cf. <i>amphigomphus</i>	
			<i>Neidium</i> sp.	

Table A.IV.2: Diatom species groups referred to in Figure III.7

B. Appendix

B.1 A 45 kyr palaeoclimate record from the lowland interior of tropical South America.