Human and climate impacts on tropical Andean ecosystems

Thesis

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Human and Climate Impacts on
Tropical Andean Ecosystems

A thesis presented for the degree of Doctor of Philosophy
by
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THEESIS CONTAINS
CD/DVD
Population growth and predicted global climate change are applying new, and increasing, pressure to mountain environments, but the consequences of these changes upon the biodiverse and vulnerable Tropical Andean ecosystems are poorly understood. This thesis explores past human-climate-ecosystem interactions using multi-proxy palaeolimnological investigations (fossil pollen, spore, charcoal and Chironomidae (midges); elemental abundance, colour spectra and magnetic susceptibility) of two sites in the eastern Bolivian Andes (Lake Challacaba and Laguna Khomer Kocha Upper) over the last c. 18,000 years. During the deglaciation and Holocene, ecosystems were exposed to varying climatic stress levels, and pressures imposed by the development of human cultures.

Examination of preserved ecological assemblages, including the first assessment of subfossil central Andean Chironomidae, reveals ecosystem sensitivity to changes in temperature, moisture, fire regime, lake level, nutrients and salinity. Charcoal analysis from Laguna Khomer Kotcha Upper reveals changes in burning at c. 14,500, 10,100 and 6,400 cal yr BP. Concomitant palynological shifts shows climatically controlled fire regime was a transformative agent of Andean vegetation, particularly for the threatened, high elevation, *Polylepis* woodlands. Pollen and geochemical data from Lake Challacaba indicate two periods of aridity (c. 4,000–3,370 and 2,190–1,020 cal yr BP), these broadly correlated to El Niño/Southern Oscillation variations. Increased *Sporormiella* abundance after c. 1,340 cal yr BP indicate changes in trade-route use and agricultural practices; demonstrating human adaptation to environmental change and interconnectivity to Tiwanaku and Inca civilizations.

The long-term response of the terrestrial and aquatic ecosystems, reconstructed from these lakes, has provided insights into how Tropical Andean ecosystems may respond to future changes in temperature, precipitation and human interference. The palaeoenvironmental data has implications for conservation management; it indicates that spatial and temporal variations in site sensitivity, exposure and resilience should be
assessed, and that planting strategies should mimic the present day natural patchy
distribution of *Polylepis* woodlands.
First of all I wish to thank my supervisors Will Gosling, Angela Coe and Steve Brooks for their encouragement, guidance and support over the past three and a half years. I just hope I manage to retain even a faction of all the knowledge they have imparted. Will without doubt warrants special thanks. Not only are you an excellent supervisor, but also one of the few scientists who somehow is able to see the big picture in the midst of all the hundreds of thousands of pollen grains, charcoal fragments, and chironomid remains. Above this, you are also the person who first introduced me to Bolivia; albeit via a plate of gherkins, phony police and U.S. customs officials. I hope your first experiences of supervision have not put you off future students.

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I confirm that following chapters have been previously published or submitted for publication.

Chapter 4, “Four thousand years of environmental change and human activity in the Cochabamba Basin, Bolivia”, has already been published separately as the following journal article:

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Four thousand years of environmental change and human activity in the Cochabamba Basin, Bolivia.
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Journal of paleolimnology (Submitted April 20, 2011; Under review 27 April, 2011)

Signed: ...........................................  Date: ........................................
1.1) The Tropical Andes

The highly diverse ecosystems of the elevated Tropical Andes are vulnerable because of increasing human occupation of the area and predicted future climate change (Cincotta et al., 2000; Malcolm et al., 2006; Myers et al., 2000). Narrow vertical species ranges in high elevation sites (>2000 metres above sea level (m asl)) means that even small variations in temperature and precipitation can result in considerable species movement. The sensitivity and diversity of Tropical Andean vegetation, together with the complex topography of the Andean valleys and ridges, typically of elevations 2500–4500 m asl, allows continuous montane forests to be separated from grassland and bare rocky peaks by just a few tens of kilometres laterally. Despite the relative short lateral and vertical distances, the adjustment of vegetation zones and community composition is restricted by increasing human impact on the landscape, through land acquisition, conversion to agriculture and increasing grazing pressures. It is clear that the current status of the ecosystems in the region are under threat and in need of careful conservation and management, especially when the ability of species and communities to shift with changing climatic conditions is so severely limited today. However, in order to provide information useful for conservation purposes, a robust understanding of an ecosystem’s response over longer timescales than historical observations is required.

This thesis traces Tropical Andean ecosystem adjustments since the last glacial period, 18 thousand years before present (ka), using the sediment record from two lakes in the eastern Bolivian Andes. The response of vegetation and lake systems to climatic changes and shifts in human population dynamics, has been used to improve our understanding of the threats to this biodiverse region, allowing the importance of controlling factors and the spatial and temporal scales they operate on to be assessed. This examination of past human and climate impacts in the Tropical Andes provides evidence of how these ecosystems may react to future predicted changes (see Section 1.3 for specific objectives).
1.1.1) Geographical location and setting

The Tropical Andes biodiversity hotspot spans an area of 1,500,000 km² from Venezuela in the north to Argentina in the south (Figure 1.1; www.conservationinternational.org). The hotspot covers elevations from as low as 500 m asl and follows the tropical portion of the Andes mountain chain, the longest continental range in the world, extending ~8000 km through the continent of South America (Murray et al., 2010). Uplift of the Andes is in association with the convergence and subsequent subduction of the Nazca tectonic plate under the South American plate, and has resulted in the highest plateau on Earth today that is formed at a noncollisonal plate boundary (Gregory-Wodzicki, 2000; Montgomery et al., 2001). The uplift history of the Andes Cordillera (mountain chain/range) is varied and complex along its length (see Hoorn et al., 2010), but the Central Andes domain is considered to have been <30% of its current elevation by c. 25–14 million years ago (Ma) (Gregory-Wodzicki, 2000; Lamb and Hoke, 1997).

Figure 1.1 Extent of the Tropical Andes biodiversity hotspot within South America and the major atmospheric features of the climate system. ITCZ = Intertropical Convergence Zone, SALLJ = South American Low Level Jet, SACZ = South Atlantic Convergence Zone. Data sourced from Mittermeier et al. (2004) and Sylvestre (2009).
Chapter 1) Introduction

The Central Andes encompasses southern Ecuador through to northern Argentina and Chile and marks the segment of greatest orogenic volume along the entire length of the Andean Cordillera (Mamani et al., 2010). The southern Peruvian and Bolivian portion of the Central Andes, the Central Andean orocline (\(\sim 13^\circ S - 28^\circ S\)), forms the widest section of the orogenic belt at up to \(\sim 750 \text{ km}\) across (Graham, 2009). Throughout Bolivia the Andes consists of four physiographic provinces, from west to east these are: the Western Cordillera (Cordillera Occidental), the Altiplano, the Eastern Cordillera (Cordillera Oriental) and the Subandean (Arce-Burgoa and Goldfarb, 2009; see Figure 1.2).

The Eastern Cordillera, which forms the back-arc region of the Bolivian Andes, reaches greater than 5000 m in elevation. The Eastern Cordillera mainly consists of Ordovician age geological material, 488.3–443.7 Ma (Tawackoli et al., 1996). More recent successions of Devonian (416–359 Ma) and Cretaceous through Neogene (145–2.5 Ma) age rocks are also present, including; shale, siltstone, limestone, sandstone, slate, and quartzite (Arce-Burgoa, 2009).

Within the Eastern Cordillera, the Cochabamba Basin is a large flat expanse of fluvio-lacustrine Quaternary deposits, and is the study location for this thesis (see Section 1.4 for detailed description). The extent of basin is easily distinguished from the steep topography of the Eastern Cordillera mountain ranges (Figure 1.2).
Figure 1.2 A) Digital shaded relief map (SRTM data; 90 m grid resolution) of Bolivia. B) Elevation cross-section of line A–B. Corresponding physiographic provinces and Cochabamba Basin, the study area for this thesis, is shown (black box).
1.1.2) Modern ecology

The Tropical Andes is the richest and most biologically diverse region on earth (Killeen et al., 2007). 45,000 plant and 3,300 vertebrate species have been documented within the boundaries of the Tropical Andean hotspot, including 6.7% and 5.7% of the global endemism in plants and vertebrates respectively (Myers et al., 2000). The high biodiversity is attributable to the variety of habitats encompassed by the hotspot as well as its extremely heterogenous topography (Foster et al., 1994).

Of all locations in the Tropical Andes, the eastern slopes, where moist air from the Amazon collides with the barrier of the Andean Cordillera, are the most biologically diverse (Killeen et al., 2007). In just the southern Peruvian and northern Bolivian sections of these eastern Andean slopes, 3 biomes (Figure 1.3) and 6 terrestrial ecoregions (Figure 1.4) have been recognised by the World Wide Fund for Nature (WWF). These ecological divisions are defined by their geographically distinct assemblages of species and communities, together with present day environmental conditions (Olson et al., 2001). These 6 ecoregions form 3 main groups; the Bolivian and Peruvian Yungas, Bolivian montane dry forests and the Central Andean Puna.

Figure 1.3 South American biomes. As defined by the WWF (Olson et al., 2001).
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Figure 1.4 Ecoregions of the Bolivian and southern Peruvian Andes. As defined by the WWF (Olson et al., 2001).

Biome: Tropical and subtropical moist broadleaf forest

Ecoregions: Bolivian and Peruvian Yungas

The tropical moist cloud forests of the Bolivian and Peruvian Yungas ecoregion occur from 500 m asl and can extend to elevations of 3500 m asl, forming the transition between Amazonia to high elevation habitats (Olson et al., 2000; Stattersfield et al., 1998). The high humidity is an important climatic component of the deciduous and evergreen forests and is a cause of the ecoregion being one of the most diverse in the Neotropics. Many species of plants, birds, mammals, reptiles, amphibians and invertebrates are endemic to the Yungas ecoregions (Young, 2007). Epiphytes such as Bromeliaceae, Orchidaceae and arboreal ferns (e.g. *Cyathea* spp.) are major components of the cloud forest vegetation, which shows greatest diversity at lower elevations (Figure 1.5A; Ferreyra, 1988).

Biome: Tropical and subtropical dry broadleaf forest

Ecoregions: Bolivian montane dry forests

The montane dry forests ecoregion is located within the arid valleys and steep ridges of central and southern Bolivia, within the Eastern Cordillera and Subandean physiographic provinces of the Andes. The ecoregion marks the transition between the Yungas to the east, and the Puna to the west (Olson et al., 2000). The ecoregion vegetation is
characterised by dry, sparsely vegetated slopes with shrubs, dry forest, thornscrub and cactus formation. Important genera include *Acacia* and *Prosopis* (family Fabaceae), *Dodonea* (Sapindaceae) and *Schinopsis* (Anacardiaceae) and *Proustia* (Asteraceae) (Ergueta and de Morales, 1996).

**Biome: Montane grassland and shrubland**

**Ecoregions: Central Andean Puna**

Above the continuous montane forest line (also called timberline), uncultivated sections of the high Andes are principally grassland, commonly referred to as Puna (Figure 1.5B). The area encompasses elevations higher than ~3500 m asl. This includes snow-capped peaks, volcanoes, salt flats, high lakes, plateaus, mountain pastures and several rivers systems (Olson et al., 2000). Puna ecoregion vegetation consists primarily of grasslands made up of different grass (Poaceae) species, primarily the genera *Calamagrostis*, *Agrostis* and *Festuca*. Within the the Central Andean Puna, two ecoregions are identified, the Central Andean wet Puna, and the Central Andean dry Puna. Additional important vegetation of the wet Puna includes the grass genera *Paspalum* and *Stipa*. Plants other than grasses that predominate include 12 genera of Asteraceae, and up to 3 genera of Brassicaceae, Campanulaceae, Caryophyllaceae, Rosaceae, Scrophulariaceae and Rubiaceae (Young et al., 1997). Wetter areas include Cyperaceae, Juncaceae and Plantaginaceae. In some areas of the Central Andean dry Puna ecoregion the vegetation has adapted to high concentrations of salt. Examples of some specialist families forming these halophyte communities are Amaranthaceae, Juncaginaceae and Asteraceae (UNESCO, 1980).

Within the Puna ecoregions matrix, are pockets of woodland dominated by the tree genus *Polylepis* Ruiz & Pav. (Rosaceae, Sanguisorbeae) (Figure 1.6). *Polylepis* woodlands form the treeline (the upper elevation limit of individual tree growth) and are considered fundamental to the biodiversity of the high Andes, supporting endemic and habitat specialist species (e.g. Cahill and Matthysen, 2007). These woodlands and are one of South America’s most endangered ecosystems, with 15 species of *Polylepis* classified as vulnerable by the International Union for Conservation of Nature (IUCN) (Jameson and Ramsay, 2007; Navarro et al., 2005).
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Figure 1.5 Two of the main ecoregions of the Bolivian and Southern Peruvian Tropical Andean hotspot. A) Yungas cloud forest. B) Central Andean Puna. Photograph A is provided by William Gosling.

Taxonomically complex, the earliest estimate of the number of Polylepis species was made using herbarium specimens (Bitter, 1911), and concluded that 33 were known with an additional 9 subspecies and 18 varieties. Since this pioneering work, subsequent taxonomic refinement following field collection by Simpson (1979), led the number of species to initially drop to 15, but subsequently this has steadily risen (Kessler and Schmidt-Lebuhn, 2006). The most recent study recognised 26 species across the continent (Table 1.1), but the authors note that 2 additional Peruvian populations may merit species rank if more supporting evidence (herbarium and field material) is located to adequately confirm their status (Kessler and Schmidt-Lebuhn, 2006). The genus has its centre of diversity and highest endemism in an area ranging from central Peru to southern Bolivia (Navarro et al., 2005: Table 1.1).


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<table>
<thead>
<tr>
<th>Country</th>
<th>Species Richness (Endemism)</th>
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<tbody>
<tr>
<td>Venezuela</td>
<td>1</td>
</tr>
<tr>
<td>Colombia</td>
<td>3 (1)</td>
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<tr>
<td>Ecuador</td>
<td>7 (2)</td>
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<tr>
<td>Peru</td>
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<td>Bolivia</td>
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<td>Chile</td>
<td>2</td>
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<tr>
<td>Argentina</td>
<td>4 (1)</td>
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</tbody>
</table>

Table 1.1 The distribution of Polylepis species across South America (north – south). Data from Kessler and Schmidt-Lebuhn (2006). Total and endemic special numbers shown.

Polylepis is one of only two arborescent genera that grow at elevations of up to almost 5000 m asl. The highest tree species found in the Northern Hemisphere, Juniperus tibetica Kom, has been documented in a stand at 4900 m asl in Tibet (Miehe et al., 2007). In comparison, adaptive radiation of the genus Polylepis, led its colonisation of higher and more arid environments, and today it can surpass 5000 m asl (Kessler, 2002; Navarro et al., 2005). This survival is due to several adaptations of Polylepis: i) increased frost resistance (Graf, 1981), ii) an ability to alter nutrient uptake in cold conditions (Hertel et al., 2008), and iii) to survive the damaging effects of increased UV-radiation at high elevation (González et al., 2007).

Although, the high altitude survival and adaptations of Polylepis still warrant discussion, it is the fragmented network of Polylepis growth above the continuous treeline (Figure 1.7), and the enclaves of high biodiversity they support, that have attracted the attention of conservationists and ecologists (Gosling et al., 2009). The cause of the woodland patches or stands is a question scientists have struggled to interpret and the ongoing discussion of these forest islands in South America led Miehe and Miehe (1994) to name the debate the “Polylepis Problem”, which was further discussed by Kessler (2002a).
Figure 1.6 *Polylepis* woodlands of Cochabamba, Bolivia. **A)** Typical setting of modern *Polylepis* woodland stands within a boulder field. **B)** Dense growth structure and understory vegetation of *Polylepis*. **C)** Distinctive papery bark of *Polylepis* branches, a frost resistant adaption. Photographs A and B provided by William Gosling.
Figure 1.7 Schematic representation of the potential causes of *Polylepis* fragmentation. A) Anthropogenic fragmentation caused by clearance of woodland. B) Natural fragmentation caused by microclimates. In both scenarios, a very similar woodland structure can be created, and unless obvious local forcing factors are apparent, distinguishing the relative impact of drivers can be difficult. Based upon a drawing of Körner and Paulsen (2004) of mountain vegetation types.

Early explanations of the patchy distribution were based upon the idea that naturally occurring features in the landscape created unique microclimates. These allow for locally favourable conditions of air temperature and/or moisture content of the soils, and thus support tree growth above the closed timberline of the montane forests (Figure 1.7B; Fjeldså and Kessler, 1996). Apparent favourable conditions were located amongst boulder fields or rock falls (e.g. Figure 1.6A), and within steep sided valleys or ravines.

A challenge to the original view of natural factors governing the *Polylepis* distribution was put forward by Ellenberg (1958), who argued that the current state of the forests was due primarily to a long history of human activity which removed large areas of the woodland leaving only isolated patches. This hypothesis was later built upon by the work of Kessler (1995) and Wille et al (2002). Fundamentally, Ellenberg argued that *Polylepis* was the natural climax forest of the high Andean regions without human interference. Since this suggestion, climate niche reconstructions based on present-day distribution, has allowed estimations of past *Polylepis* cover. From this, Fjeldså and Kessler (1996) estimate that
human impact is responsible for a 90% reduction in *Polylepis* woodland across the Bolivian Andes.

Short term observations of current human impact qualitatively support Ellenberg’s conclusion, but definitive quantitative study is inconclusive. A study was conducted in the Department of La Paz, Bolivia, in 2003 to resurvey *Polylepis* extent. The findings concluded that in a period of twelve years since the original survey (Fjeldså and Kessler, 1996), an 87% loss in extent had occurred (Purcell and Brelsford, 2004). The authors note that the sites studied were easily accessed by road and thus may have been especially vulnerable to human interference, but following further research they discovered that even remote, inaccessible stands appear to be impacted in some way. In addition, a study of air photographs over a 50-year period showed a “significant” decline in canopy density in 10% of forest patches, from Cordillera de Vilcanota, Peru (Jameson and Ramsay, 2007).

However, despite these survey results, it remains unclear to what degree and extent the Andean *Polylepis* woodlands have been impacted by human activity across the region, and if the woodland patches are also being formed or altered by changing environmental conditions, and/or the creation of unique microclimates. Indeed, Fjeldså (2002) reports two photographic studies from Peru, one over a period of >60 years, that both show minimal or no change in the abundance of *Polylepis* woodlands (Byers, 2000).

Fuelling the “*Polylepis* Problem” debate is the uncertainty that remains regarding the natural extent to which *Polylepis* woodland would cover the land if there was no human interference, and whether or not the current stands are remnants of a formerly much more extensive vegetation zone.
1.1.3) Environmental changes

Worldwide, mountainous regions are considered to be early warning sites for changes in processes related to environmental adjustments (Ørbæk et al., 2004). In the Tropical Andes, the Intergovernmental Panel on Climate Change (IPCC, 2007) predicts warming of 2.5–3.5°C by 2100 under a moderate emissions scenario (A1B) (Gosling and Bunting, 2008). Alarmingly however, modelling studies specific to the Tropical Andes, suggests that warming will be greatest at higher elevations. Predictions propose that under a high emissions scenario (A2), a 4–5°C increase in annual temperature is expected on the eastern slopes above 3500 m asl by 2100 (Urrutia and Vuille, 2009). Globally, climate warming is considered one of the most serious threats to biodiversity. Using predictions of habit distribution and size under a scenario of doubled CO$_2$ levels, 3000 plant and 200 vertebrate species are estimated to become extinct in the Tropical Andes alone as a result of climatic warming (Malcolm et al., 2006).

**Modern climate**

Climate, particularly precipitation, in the Tropical Andes is associated with a number of major atmospheric features (Figure 1.1). Seasonally this area is dominated by the South American Summer Monsoon (SASM; Zhou and Lau, 1998), which is in broad association with movement of the Intertropical Convergence Zone (ITCZ), variability of the South American Low Level Jet (SALLJ; Vera et al., 2006) and the South Atlantic Convergence Zone (SACZ; Sylvestre, 2009). Over inter-annual, decadal and longer timescales, adjustments in the El Niño-Southern Oscillation (ENSO) are considered to be the largest source of climate variation (Chiang, 2009; Philander, 1990).

In the Bolivian Andes the most striking evidence of a changing climate is presented by glacier retreat, and today, the Zongo, Chacaltaya, and Charquini Sur glaciers are shrinking in area and volume (Francou et al., 2005). The Chacaltaya glacier, previously the site of the World’s highest ski field, lost 90% of its area in the 13 years before 2005, with total loss expected soon after 2010 (Berger et al., 2005). As well as changes in precipitation, the cause of this regional retreat is due to a warming troposphere (Francou et al., 2003), which is particularly concerning considering the upper and middle parts of this atmospheric layer are expected to experience the greatest heating in the future (Urrutia and Vuille, 2009). Although detailed, these records rely on direct measurements, and as
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such only extend back c. 70 years. These records include the analysis of historic photographs, exploration notes and cultural references. However, to fully understand how changing climates, both rapid and gradual, have influenced the vulnerable ecosystems of the Tropical Andes, longer-term data sets are required. Knowledge of past ecosystem response to climate change, including information about the rate and duration of changes, enables scientists to predict and understand the possible responses to anticipated warming in the future.

Past climate

Records of past climatic changes driven by orbital cycles have been available for more than 30 years. These include records from ice cores (e.g. Greenland; Camp Century, GRIP, NorthGRIP (Johnsen et al., 2001), Antarctica; Vostok, EPICA (EPICA Community Members, 2004; Jouzel et al., 1987)), and marine sediment records (e.g. the Deep Sea Drilling Project and the Integrated Ocean Drilling Program (Bond et al., 1993; Herbert and D'Hondt, 1990). Today, several long-term records of climatic change are also available from the Andean mountain range from predominantly lake and ice cores (see Section 1.2). Although there is some asynchrony between hemispheres in the timing of both glacial-interglacial transitions and abrupt events (Lynch-Stieglitz, 2004; Vandergoes et al., 2005), in general there is a global pattern of climate change.

In the Central Andes, the climate of the Last Glacial Maximum (LGM; 21 ± 2 ka BP; Mix et al., 2001) has been characterised as being ~7–8°C colder than modern climate (on the Altiplano) with regionally variable changes in moisture availability (Baker et al., 2003; Cook, 2009; Sylvestre, 2009). The subsequent deglaciation and the Holocene (c. 11.7 ka BP–present) is now understood as a time of fluctuating moisture availability, with some small-scale variation in temperature (Bush et al., 2005). Although the timings, impacts and mechanisms driving environmental change during this period are still debated, the response of environmental systems to key global events have now been recognised, including; a Bølling/Allerød type warming (c. 15–14.0 ka BP), a Younger Dryas type cold event (c. 12.9–11.6 ka BP), and the mid-Holocene dry event (MHDE; c. 8–5 ka BP; Rasmussen et al., 2006; Sandweiss et al., 1996; Thompson et al., 1998; Urrego et al., 2009; Zech et al., 2010). In addition, adjustments in climate systems such as the El Niño-Southern Oscillation (ENSO), the South American summer monsoon (SASM), and the
Intertropical Convergence Zone (ITCZ) have also been observed in the palaeorecords (e.g. Bräuning, 2009; Moy et al., 2002; Vuille and Werner, 2005).

With an increase in the number of records available, it has become apparent that the impact, scale and nature of climate events has been spatially non-uniform across the Tropical Andes. Local factors, included human occupation, often disguise regional patterns. In addition, the distribution of study locations is unevenly spread across the Tropical Andes and so many regions that are climatically sensitive today remain unexplored in the palaeoclimate context and thus unrepresented in regional scale studies.

Climate impacts on ecology

Future climate changes are considered a serious threat to biodiversity in the Tropical Andes (Malcolm et al., 2006). Plants may respond to changing environments by adapting, migrating to follow their climatic envelope, or by becoming increasingly threatened and ultimately locally extinct (Bazzaz, 1996; Fossa et al., 2004). Upslope migration of high altitude plants has been recorded in many mountainous regions in response to increasing temperature (Lenoir et al., 2008; Walther et al., 2005). The greatest concern therefore exists for those species that already occupy the highest colonisable sections of mountain peaks, as their upward migration space is already severely limited. As a result, it is likely that high elevation, slow-growing, competition-intolerant species with narrow habitat ranges will subsequently become outcompeted by the predicted expansion of fast-growing lowland species which have broad altitudinal and ecological ranges (Klanderud and Birks, 2003). However, in the Andes, where future precipitation changes are believed to be spatially much less coherent and unpredictable (Urrutia and Vuille, 2009), the likely response of vegetation to these future changes is much less understood. Furthermore, in these Andean environments the usual concepts of upslope vegetation migration in response to temperature increase are complicated by nonlinear changes and complex feedback mechanisms (Bush et al., 2010).

Although future climate changes threaten the biodiversity, the past history of climatic fluctuation is likely to have had a major influence on the development and shaping of the Tropical Andes. Natural changes in climate could cause movement in the position of
ecological limits for species and communities, thus contracting or expanding suitable habitat ranges. Indeed, the natural ecological limits of *Polylepis* woodlands have been investigated and help to explain, in part, the boundaries with the Andean grassland matrix. Modified from the ideas put forward by Fjeldså and Kessler (1996), Gosling et al. (2009) further developed conceptual models of the environmental limitations upon *Polylepis* woodland under a variety of climate conditions (Figure 1.8). These models help the visualisation of the influence of the governing factors of moisture, temperature and insolation and how these are linked to the actual ecological limits of *Polylepis* woodland niche space. Unfortunately however, these ecological limits are frequently obscured during modern field recording studies by the often un-measurable impact of recent human activities.

![Figure 1.8](image)

*Figure 1.8* Natural limits of *Polylepis* in Bolivia under modern conditions. **A** Distribution of woodland amongst other vegetation types. **B** Conceptual model of limiting factors. *Polylepis* niche space = dark green, *Polylepis* potential niche space = light green, Altiplano zone = grey. Redrawn from Gosling et al. (2009) and based on the original schematic of Fjeldså and Kessler (1996).

1.1.4) Human occupation

Although human populations have existed in the South American Andes since the late Pleistocene, debate still continues on whether their arrival was before or after the start of the Holocene (11.7 ka BP) (Coltorti et al., 2010; Dillehay, 1999; 2000; 2008; Lavallée,
2000; Lynch, 1990; Roosevelt et al., 1996). The extent of the environmental impact caused by humans is also unresolved. Some authors consider that fire may have been utilised as a hunting aid from the arrival time of humans (Ellenberg, 1979), while others consider early hunter-gatherer based exploitation to be opportunistic with minimal environmental impact (Mondini, 2002). Evidence that fire has been a natural component of central Andean ecosystems long before the arrival of humans (Gosling et al., 2009), adds complexity to the debate as differentiating a human vs. natural signal is required. What is clear however, is that reliance on local, seasonal (plants) and/or mobile (animal) resources led early human populations to utilise the terrain and the ecological diversity of the Andean mountains and the Amazon basin, and tracked changes in biota driven by the climatic shifts (Dillehay, 2008). Increasingly evident, is that by the early Holocene (c. 9 ka BP), dependence on resources had increased, and people began to alter the natural habitats by persistent hunting, transportation of plants, and the deliberate or accidental burning of the landscape (Dillehay, 2008).

Compared to other areas of the Andes, very little is known about prehistoric populations in Bolivia, and few occupation markers have been discovered (Aldenderfer, 2009). While this is potentially an artefact of archaeology, it is also likely that it reflects reality and is indicative of very low population densities and perhaps an inability to exploit difficult environments (Dillehay, 2008). Kolata (1993), speculated that the first humans reached Lake Titicaca, on the Altiplano border of modern Peru and Bolivia, around 14,000 years ago, although a greater consensus suggests that humans did not reach the region until 1000 years later (Dillehay, 2000; Lavallée, 2000). By 10,000 years ago, seasonally nomadic populations in the inter-Andean valleys interacted with other such groups centred on the Altiplano (around Lake Titicaca) and Pacific coast, and presumably, those of the Amazonian Basin (Kolata, 1993).

Across much of the Andes, including Bolivia, the middle-Holocene period (c. 9–3 ka BP), suffered what has been disputably labelled as times of “archaeological silence” (Grosjean et al., 1997). Although variable in the north-south timings (Sandweiss and Richardson, 2008), it is linked to the mid-Holocene dry event (8–5 ka BP) identified from many Andean locations (e.g. Hillyer et al., 2009; Paduano et al., 2003; Urrego et al., 2010; Valencia et al.,
2010). During this time very little evidence of human population exists for the region, even from Lake Titicaca, one of the heartlands of dominant pre-Columbian populations. However, until about 6000–4000 years ago, populations around the Titicaca Lake basin, remained hunter-gatherers (Kolata, 1993; Young-Sanchez, 2004). By 6000 years ago foraging, hunting, fishing, and birding had all become valuable and well developed subsistence strategies (Hastorf, 2008). This cultural style most likely also represents the general situation across Bolivia at this time. By c. 3500 years ago, farming began in the fields surrounding Lake Titicaca (Kolata, 1996). It is likely this agricultural development was in response to the increasing water levels of Lake Titicaca (Abbott et al., 1997) (see Figure 1.9). The middle stages of the Holocene saw the widespread utilization of fire and, in many locations, expansion of agricultural development.

The first evidence of permanent settlements in the region surrounding the Titicaca Basin starts c. 3500 years ago. This date marks the start of the Formative Period or Initial Period (Figure 1.9) and is described as the time when humans began marking the landscape, creating more permanent settlements and domesticating plants and animals (Hastorf, 2008). Since the start of this period, two major pre-Columbian societies or polities had influence over large areas of the Bolivian Andes: the Tiwanaku (c. 1500–900 yr BP) and the Inca (c. 650–550 yr BP) (Figure 1.10). During these times, it is generally agreed that central Andean civilised cultures first evolved as city-like constructions appear (Isbell, 2008).
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Figure 1.9 Basic cultural chronology and inferred climatic conditions of the Bolivian Altiplano. Dust levels from the Quelccaya ice core record (Thompson et al., 1985). Yellow = dryer, Blue = Wetter. Lake Titicaca water levels (Abbott et al., 1997). Blue shaded area represents range of uncertainty. Cultures based on the chronologies of Bandy (2004), Isbell (2008) and Janusek (2008).

The collapse of the Tiwanaku state, around 900–1000 years before present (yr BP), has been linked to a prolonged drought around Lake Titicaca, as indicated by low lake levels (Abbott et al., 1997; Binford et al., 1997), and an elevated dust signal from the nearby Quelccaya (Peru) ice core record (Figure 1.9 and 1.10; Thompson et al., 1985). The subsequent transitions from Tiwanaku fragmentation and collapse, Inca Empire rule and violent Spanish conquest (c. 550 yr BP) is certain to have had major impacts on both societies and the landscapes they occupied.
Figure 1.10 The territorial spheres of the Inca and Tiwanaku. The locations of important pre-Columbian cities, palaeo records discussed, and the Cochabamba Basin (location of this study) marked. Territorial extents from Silverman and Isbell (2008).

**Human impacts on ecology**

Ancient human impacts on the biodiversity of the Tropical Andes, are often difficult to detect and interpret. Overall, impacts can be linked to five main features: settlement and monument building, agricultural development, irrigation, domestication of animals and the use of fire. Today, much of our information has been gained from macroscopic and microscopic sediment charcoal analysis, but the cause of fire can be both natural and human driven. Besides the use of fire, camelid pastoralism and caravans were also hugely important for pre-Columbian peoples (Lynch, 1983), and there is now good evidence to suggest that raised bed agriculture around Lake Titicaca was occurring before c. 2400 years ago (Kolata, 1996). Later, *Alnus* agroforestry by the Inca has been identified in other
regions in response to its economic and symbolic importance (Chepstow-Lusty and Winfield, 2000). The Inca were also responsible for agricultural transformation, and developed locations in the Bolivian, Peruvian and Ecuadorian Andes for maize production (Fjeldså, 2007).

The direct impacts on Polylepis forests by ancient humans are largely unknown. Potentially strictly protected during Inca (c. 650–550 yr BP) times, due to its symbolic and social meaning (Capriles and Bedregal, 2002), major forest loss may have occurred in the pre-Inca period of agricultural development 3000–5000 years ago (Fjeldså, 2002). However, the detrimental impact of modern humans on the Polylepis woodlands is clear. Used for firewood, construction materials (Macek et al., 2009) and cattle fodder (Fjeldså and Kessler, 1996), the regeneration of the woodlands is also severely impacted by soil degradation (Renison et al. 2005; 2004) and fire (Hensen, 2002; Renison et al., 2006). Grazing has also been shown to be detrimental to forest re-establishment (Cierjacks et al., 2008; Teich et al., 2005), although a more recent study found the complete absence of grazers actually decreases seedling recruitment, due to excessive litter cover build up from herbs and grasses (Zimmermann et al., 2009).

Regardless of the reasons why Polylepis woodlands are at present reduced to enclaves of greater or lesser extent, the biodiversity they support, together with their social and economic importance, marks them as an unique habitat that clearly warrants our attention (Fjeldså and Kessler, 1996). Conservation and securing their survival is especially important when one considers that the much of the unique flora and fauna, including endemic species of birds, mammals and amphibians is perhaps a result of the long-term presence of the woodlands (Fjeldså and Kessler, 1996; Young, 2007). However, to asses and develop an effective policy to conserve and manage any ecosystem, including Polylepis woodlands, a robust understanding of the region’s natural history through periods of varying stress levels is fundamentally required (Godwin, 1956; Willis et al., 2010; Willis and Birks, 2006).
Land managers in the high Bolivian Andes are currently encouraged to emphasize the use of *Polylepis* for the control of erosion and for the provision of firewood (Fjeldså and Kessler, 1996). This is due to its presumed former extent and high elevation ecological tolerance (Gosling et al., 2009) and the ability of *Polylepis* to thrive under a variety of modern climate and soil types (Ellenberg, 1979). One such project, the Asociación Ecosistemas Andinos (ECOAN), initiated the planting of 60,000 *Polylepis racemosa* trees, in a direct attempt to join up fragments of existing woodland (Aucca and Ramsay, 2005).

While this extensive use of native tree species over exotic species holds many advantages, including for biodiversity conservation (Fjeldså and Kessler, 1996), without a record of the natural history of these high Andean ecosystems, we rely on speculative information about the natural woodland/grassland structure in order to guide our conservation approaches. Specifically to the ECOAN planting project, there is at present no consensus on whether the *Polylepis* woodland was continuous laterally in the Andean grasslands, and linking up modern day patches may actually be detrimental to the overall biodiversity of the Andes. Indeed, it has been shown that species endemism is highest at woodland patches and not in the continuous forest (Figure 1.11; Fjeldså and Irestedt, 2009). The type of long-term, baseline status data that is vital to inform conservation policy (Willis and Birks, 2006), can only be provided by palaeoenvironmental studies, and well designed palynology projects are vital in assessing at least some parts of the *Polylepis* problem (Bader, 2007; Kessler, 2002).
Figure 1.11 Bird species richness and endemism along an elevational transect in the Carrasco National Park, Cochabamba, Bolivia. Green shading = zones with patchy arboreal vegetation, Blue line = species richness (number), Red line = mean species endemism (average inverse range size per species). While species richness shows a gradual decline with elevation, endemism peaks in woodland patches. Redrawn from (Fjeldså and Irestedt, 2009) using survey data and interpolations for missing sampling points.

1.2) Palaeoecology: tracing human and climate ecosystem impacts

In response to the demand for a long-term "natural" ecosystem baseline, records of climatic changes and/or holistic ecosystem adjustments have been examined in many parts of the Tropical Andean mountain range. From Bolivia and southern Peru, information has been sourced from ice cores (e.g. Thompson et al., 1998); lake sediments (e.g. Baker et al., 2001); and tree rings (e.g. Argollo et al., 2006). In addition, recent achievements in dating glacial moraines has successfully allowed the timings of ice expansion and retreat to be mapped in a broad range of locations (e.g. Blard et al., 2009; Rabatel et al., 2008; Smith and Rodbell, 2010; Zech et al., 2007; 2009).

Of all record types, lake sediments have been the most successful for Andean palaeoenvironmental reconstruction. From the time of formation, lakes almost always accumulate sediments continually, and are usually only halted during times of aridity when desiccation and sediment loss can occur if the lake dries out completely. Lake sediments comprise a mixture of biological remains and non-biological material which
predominately originates from within the lake and its catchment. Thus, with careful analysis of a selection of (generally) microscopic biological remains and geochemistry, a lake sediment succession is a continuous environmental archive of the history of the lake and its surroundings.

There are of course limitations associated with palaeoecological, including palaeolimnological, investigations. With the increasing number of records, a growing awareness of complexities has become apparent, especially the nonlinear responses of proxies and lakes to climate fluctuations. The nature of the limitations specific to palaeolimnology are discussed in specific context to the methodologies utilised in this thesis (Chapter 3). However, despite these limitations, palaeolimnological investigations across the Bolivian and southern Peruvian Tropical Andes have successfully started to provided the baseline environmental (e.g. Abbott et al., 2003), ecological (e.g. Urrego et al., 2010) and human impact (e.g. Paduano et al., 2003) data required in order to improve understanding of past landscape changes.

To obtain an understanding of past Andean woodland distribution from the fossil pollen record it is necessary to consider pollination mechanism and dispersal. Although anemophilous (wind pollinated), *Polylepis* does not produce much pollen (Chepstow-Lusty et al., 2005; Fjeldså, 2002), and the pollen is not transport far from the parent tree (Salgado-Labouriau et al., 1977) and so its presence in a fossil record indicates a local, site-specific abundance. This, combined with many previous fossil pollen studies being conducted outside *Polylepis* diverse and dominant areas, means that detection in many records is poor. Therefore, any investigation that attempts to examine the natural history of the *Polylepis* woodlands needs to be careful considered and planned for that purpose, not appended to a project designed to investigate another research focus.

Thus far however, palaeo data is inconclusive in addressing the questions surrounding the *Polylepis* problem. Several studies of fossil pollen have highlighted the potential impact of humans on the woodland (Graf, 1979; Hansen et al., 1984). However, newer longer-term fossil pollen data from Lake Titicaca suggest that during previous interglacial periods, prior to human arrival in the catchment, *Polylepis* woodland cover fluctuated in response to climate (Hanselman et al., 2005; 2011). This sedimentary record has also revealed that
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fire, ascertained by charcoal abundance, was a natural part of the environment long before human arrival (Gosling et al., 2009). These findings have highlighted the ambiguity surrounding the nature and degree to which human and climate factors ultimately govern the ecology of the Andes and vulnerability of the woodlands.

1.3) Thesis rationale and objectives

Population growth and predicted global climate change are applying new, and increasing, pressure to Andean environments, but the consequences of these changes upon the biodiverse and vulnerable Tropical Andean ecosystems are poorly understood. Although attempts are being made to protect the current status of these sensitive habitats, the only way to obtain empirical data that demonstrates how these ecosystems are likely to respond to future change, is to look to the past. The sensitivity of the Tropical Andean vegetation allows the evaluation and monitoring of change not only of modern, real-time observed adjustments but, crucially via the use of palaeolimnological investigation, of long-term shifts in species association to environmental changes in the past.

The period c. 21,000 yr BP, when the last major global climatic transition occurred (full glacial to interglacial conditions), and humans spread throughout South America, is a critical phase for understanding human and climate interactions. Within this time frame, the deglaciation period and early Holocene represents the most recent time when the ecosystems of the Tropical Andes were not substantially influenced by human practices, but were exposed to naturally varying ecological stress levels. The subsequent development of human culture through the Holocene lead to changes in resource use and practices, and placed the ecosystems they occupied under a unique set of pressures not previously experienced.

Because of the interrelated nature of human, vegetation, climate and fire (see Chapter 3), a knowledge of climate history is vital before we can fully understand the developments and impacts of early (and later) cultures (Dillehay, 2008; Sandweiss and Richardson, 2008). However, the palaeoenvironmental history of the Tropical Andes, as in much of the Neotropics, is still insufficiently understood and fragmentary due to a paucity and uneven spread of records, together with controversy in the interpretation of them. The
correlation of changing palaeoenvironments and human cultures, together with the scale of human-environment interactions, is an important issue that warrants continued discussion and debate. This is especially true if we are to fully understand the threats upon ecosystems today and how they may respond to changing environments in the future.

To address these knowledge gaps three specific research goals have been established for this thesis:

i. To determine the scale and impact of climatic events, climate system adjustments and ecosystem responses in the Bolivian Andes since deglaciation, and to compare the uniformity and correlation of these changes with other Andean locations.

ii. To determine how pre-Columbian population enclaves, distant from the civilization centres of Cusco and Tiwanaku, impacted the landscape that they occupied via the exploitation of agricultural development, domestication of animals and fire. To examine if these impacts were wholly detrimental to the biodiversity of the Tropical Andean region in which they existed.

iii. To assess the drivers governing the current distribution of Polylepis woodland and Andean grassland, and determine if the historic growth patterns suggest a previous, more widespread dominance. To provide new data useful for conservation policies and management strategies to assist with the re-establishment of the natural ecosystem structure.

To address the research aims identified and the knowledge gaps outlined, there was a careful selection of study areas. Important to aid this selection is locating an area with: i) material suitable for the measurement of a variety of climate records that extend back to the deglacial period, ii) a high level of Tropical Andean biodiversity and vegetation sensitivity (e.g. Polylepis woodland), iii) a sensitivity to climatic change, and iv) a long history of human occupation. It is also important to locate an area understudied in the palaeo context, in order to provide the maximum amount of new information that can be then incorporated into the regional knowledge of environmental and human impacts of
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Tropical Andean ecosystems. With these key requirements, the Cochabamba Basin in the Eastern Bolivian Cordillera was selected for investigation.

1.4) The Cochabamba Basin, Bolivia

1.4.1) Geographical location and setting

The department of Cochabamba covers an area of \( \approx 55,000 \text{ km}^2 \) and is composed of 16 provincial units, with a total population of 1.5 million (Montes de Oca, 2005). The department spans several geographic zones ranging from the high mountains of the Eastern Cordillera and Altiplano (>4000 m asl) through to the lowland regions (<200 m asl). The department capital, Cochabamba city, (17°40, 66°14, 2500 m asl) lies in the Cochabamba Basin which is composed of a series of inter-Andean montane valleys within the Eastern Cordillera. The basin is characterised by the pronounced depression and flat terrain in the central portion of the Eastern Cordillera (Figure 1.2).

Within the Eastern Cordillera (McQuarrie, 2002), the Cochabamba Basin lies in the heart of the Bolivian Orocline and is limited on the northern and western sides by the Tunari mountain range (Figure 1.2 and 1.12). As discussed by Montes de Oca (2002), the Cochabamba valleys are narrow (<10 km wide) and consist of Ordovician (488.3–443.7 Ma), Silurian (443.7–416 Ma) and Cretaceous (145–65.5 Ma) basement rocks (Saavedra, 2005). The area is described by Keenan et al. (1997) as a Plio-Pleistocene Basin (after 5.33 Ma) due to the large volumes of sedimentary material deposited during the Quaternary. These Quaternary deposits consist of lacustrine material which develops into fluvio-lacustrine and fluvial sediments in the upper sections (Saavedra, 2005). The Quaternary successions attest to the existence of large water bodies in the valleys of Cochabamba, a situation recognized in the origins of the city name from the native words “Cocha” and “Phampa”, meaning swampy or waterlogged plains (Montes de Oca, 2005).

Today remnants of this large water body exist within the Cochabamba Basin, and together with smaller lakes created by local glaciation features in the surrounding mountain ranges, the region provides the palaeolimnological records required to address the research aims discussed (Section 1.3). From within and surrounding the Cochabamba
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Basin, 8 lakes from 4 locations were identified from satellite imagery and maps as potential sites for palaeoecological investigation (Figure 1.12 and Table 1.2). Investigation of the sites at Cochabamba city (Laguna Alaylay), Sacaba (Laguna Larati and Caluyu), Vacas (Lakes Parkokocha, Acerokocha, Juntutuyo, Kollpakocha, Challacaba and Yanatama) and Cordillera el Ronco (Lagunas Komer Kocha Upper and Lower) allowed for an informed site selection.

Figure 1.12 The Cochabamba Basin with study locations marked in boxes. Altitudes, historic settlements, strongholds and routes marked. Modified from Sánchez (2008). Inset map locates Cochabamba Basin within Bolivia. Modern Cochabamba city extent not shown.
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**Cercado, Cochabamba City - Laguna Alaylay**

The largest lake within Cochabamba city district, Laguna Alaylay, is consistently being impacted by the city's growing population. The lake was deepened and connected to the Rio Rocha in the 1930's, dredged in the early 1990's, and has since suffered from illegal sewage inputs (Ayala et al., 2007 and personal observations). Laguna Alalay, temporarily dried out during the Autumn of 1990 (Ayala et al., 2007). Restoration work that began in June 1997 has begun to act to upon the significant damage caused by sewage input, but clearly the lake's history renders it unsuitable for any palaeo study.

**Chapare, Sacaba - Laguna Larati and Laguna Caluyu**

Situated 1 km apart and only 15 km northwest of Cochabamba city, near the settlement of Larati, both sites presented potential excellent study locations for investigating the impact of ancient human populations. This was reinforced by the subsequently published investigation into the network of Inca trails in the vicinity (Sánchez, 2008) (see Figure 1.12). However, 5 m high dams had been constructed on both sites and, as it was impossible to attain the status of the lakes prior to construction, no further investigation other than surface sediment extraction was conducted.

**Arani, Vacas Lake District – Lakes Parkokocha, Acerokocha, Juntutuyo, Kollpakocha, Challacaba and Yanatama**

The Vacas Lake District is a system of six lakes situated 60 km east of Cochabamba city and 35 km north of the Mizque valley, and is easily accessible by a paved road from Arani (see Section 2.1, Figure 2.1). Ritter (2000), speculated that it is likely that all six lakes within the Vacas municipality would have, at one time, been one large connected system.

Within the Vacas Lake District, Parkokocha is a shallow (1.6–2 m) lake, and the largest by surface area. Initial investigation estimated ~2 m of sediment could be recoverable although sediments were of hard consistency and showed potential signs of periodic desiccation. The second largest lake, Acerokocha, is a deep U-shaped basin probably formed by glacial scouring. The water depth exceeded 12.7 m and therefore proved too deep to core with the equipment available. Lake Juntutuyo and Kollpakocha appear to be hyper–saline lakes today and were therefore rejected. Previous investigation at Juntutuyo suggests it has a maximum depth in excess of 3.5 m (Ritter, 2000), but in was found to
have dried out for a prolonged period prior to 2300 yr BP (Abbott et al., 2003). Lake Challacaba and Yanatama are the smaller lakes in the Vacas system. Lake Challacaba was selected as the most suitable of the Vacas lakes for coring after the preliminary investigations were conducted. A full site description follows in Section 2.1. Yanatama was not investigated due to logistical difficulties and time constraints.

Chapare, Cordillera el Ronco – Lagunas Khomer Kocha and Khomer Kocha Upper
This area has vehicle access by an unpaved track leading from the settlement of Aguirre towards Villa Tunari, and is 45 km west of Cochabamba city and 35 km north of the Vacas Lake District (see Chapter 2, Figure 2.5). It is a system of two lakes located on the steep, northeast facing slopes several hours hike from the unpaved track. Laguna Khomer Kocha is the larger of the two water bodies. It is glacially formed. The depth is unknown but suspected to be in excess of 10 m (per. coms. D.Hertel). Laguna Khomer Kocha was not investigated due to the poor accessibility of the site because of the steep, unstable nature of the slopes leading down to the lake shore and the additional time needed to transport the coring equipment. The second lake in the area was previously unnamed, but from here on is referred to as Laguna Khomer Kocha Upper, as it is situated <800 m to the west and approximately 250 m above Laguna Khomer Kocha. Following preliminary investigation, Laguna Khomer Kocha Upper was selected for coring. A full site description follows in Section 2.2.
1.4.2) Modern ecology

The topographic and climatic variation place the Cochabamba Basin at the confluence of four of the main Tropical Andean ecoregions (Figure 1.4). The ecoregions are the Bolivian Yungas, the Bolivian montane dry forests, the Central Andean Puna and the Central Andean dry Puna. A summary description has already been provided for each (Section 1.1.2). However, the ecological community composition varies with even small lateral and altitude changes. As a result, the vegetation is extremely varied and cannot be easily summarised for the entire Cochabamba Basin and surrounding mountain ranges. Therefore, a more detailed description of vegetation is reserved for later discussion in relation to each specific study site (Chapters 2, 4 and 5).

One of the key features of the vegetation surrounding the Cochabamba Basin is the relative abundance of *Polylepis* woodland. *Polylepis* woodland patches are found at altitudes ranging from 2900–4100 m asl (Hensen, 2002), and so have the ability to survive in many locations throughout the region. Today, many species of *Polylepis* occur in the area, including: *Polylepis neglecta*, *P. sericea*, *P. racemosa lanata*, *P. besseri subtusalbida*, and *P. tormentella incana, P.t. incanoides and P.t. nana* (Hensen, 2002; Navarro et al.,

<table>
<thead>
<tr>
<th>PROVINCE</th>
<th>Municipality</th>
<th>Locality</th>
<th>Name</th>
<th>Latitude (S)</th>
<th>Longitude (W)</th>
<th>Altitude (m asl)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CERCADO</td>
<td>Cochabamba city</td>
<td>CERCADO</td>
<td>Laguna Alalay</td>
<td>17° 40.027</td>
<td>66° 13.638</td>
<td>~2500</td>
</tr>
<tr>
<td>CHAPARE</td>
<td>Laguana Larati</td>
<td>CHAPARE</td>
<td>Laguana Caluyu</td>
<td>17° 20.889</td>
<td>65° 59.954</td>
<td>3576</td>
</tr>
<tr>
<td>Sacaba</td>
<td>Laguana Caluyu</td>
<td>Sacaba</td>
<td>Laguana Caluyu</td>
<td>17° 20.889</td>
<td>65° 59.954</td>
<td>3586</td>
</tr>
<tr>
<td>ARANI</td>
<td>Parkokocha</td>
<td>ARANI</td>
<td>Parkokocha</td>
<td>17° 32.708</td>
<td>65° 38.548</td>
<td>3425</td>
</tr>
<tr>
<td>Vacas</td>
<td>Acerocha</td>
<td>Vacas</td>
<td>Acerocha</td>
<td>17° 35.375</td>
<td>65° 35.745</td>
<td>3423</td>
</tr>
<tr>
<td>Vacas Lake District</td>
<td>Challacaba</td>
<td>Vacas Lake District</td>
<td>Challacaba</td>
<td>17° 33.257</td>
<td>65° 34.024</td>
<td>3419</td>
</tr>
<tr>
<td>CHAPARE</td>
<td>Komer Kocha</td>
<td>Villa Tunari - Paracti</td>
<td>Komer Kocha</td>
<td>17° 16.514</td>
<td>65° 43.945</td>
<td>4144</td>
</tr>
<tr>
<td>Cordillera el Ronco</td>
<td>Upper</td>
<td>Cordillera el Ronco</td>
<td>Upper</td>
<td>17° 16.514</td>
<td>65° 43.945</td>
<td>4144</td>
</tr>
</tbody>
</table>

Table 1.2 Location details of the lakes visited in this study during May and June 2007.
2005). Of these, Navarro et al. (2005) also report that the eastern Andes of central Bolivia is the location of endemism for the species of *P. neglecta*, *P. besseri subtusalbida*, *P. racemosa lanata*, *P. tomentella nana* and *P. t. incanoides*. If as previously discussed (Section 1.4.1), a large Pleistocene wetland did exist, the stabilising effect of such a large water body could provide the explanation for the Cochabamba Basin being one of five assumed Andean “refuges” during glacial periods (Fjeldså and Kessler, 1996). If this was the situation, then it may help explain the high levels of endemism seen in the area today.

As well as endemic plant species in the Cochabamba Basin and surrounding mountain ranges, several species of birds, mammals and amphibians also exist solely in this area (Young, 2007). In order to secure the future of this unique flora and fauna, conservation is required. At present, two national parks local to the Cochabamba Basin exists: the Tunari, situated to the north and east (~3300 km\(^2\), established 1962), and the Carrasco, located to the northwest (~6200 km\(^2\), established 1991). In addition, the Cochabamba Basin was earmarked by Fjeldså and Kessler (1996) as a first-level conservation priority area. This designation was designed to draw attention to the importance of the *Polylepis* forests and associated habitat, but currently no additional protection of the habitat has been put into place.

Although *Polylepis* sp. are the dominant constituent of the woodland patches, they exist in a variety of complex communities with other plant species. Hensen (2002), reported that in a survey of 23 different woodland patches, in excess of 250 other species were also recorded either within or in the immediate surroundings. The fauna and flora of the Cochabamba Basin creates a high level of Tropical Andean biodiversity in the locality. As well as the influence of the varied and complex topography, the vegetation of the region is highly sensitivity to any environmental changes.

1.4.3) Climate

The climate of the Cochabamba Basin varies considerably due to the pronounced variation in topography. Montes de Oca (2005), reports that Eastern Cordillera regions in general have temperature and precipitation ranges of 16–20°C and 1000–1800 mm/year. In comparison, the Subandean regions at lower elevations experience a more humid climate with temperatures of 20–22°C and precipitation of 1500–2000 mm/year.
However, the climate of the sheltered valleys (e.g. Cochabamba city, ~2500 m asl), is more arid with average annual precipitation of ~480 mm and a temperature range of ~13-19°C (Montes de Oca, 2005). Precipitation shows high seasonal variation, with rainfall greatest during the summer months (December to March) (Figure 1.13).

The Cochabamba Basin and surrounding mountain ranges of the Eastern Cordillera back-arc are highly influenced by changes in inter-annually varying climate systems such as ENSO, and future models predict locally specific adjustments particularly in precipitation amount (Urrutia and Vuille, 2009; Vuille and Werner, 2005).

Figure 1.13 Monthly average climate data for the Cochabamba Basin, 2000-2009 inclusive. Shaded areas represent minimum and maximum values recorded over the 10-year period. Data provided by Tutiempo Network (2010). Weather station number: 852230 (SLCB), 17° 41.8 S, 65° 10.0 W, 2548 m asl.
1.4.4) Human occupation

Cochabamba is, today, the principle agricultural region of Bolivia (Larson, 1998). Grains, tubers and coffee are cultivated in the highlands with sugarcane, cocoa beans, tobacco, semi-tropical fruit and coca grown in the more tropical climates of the Bolivian Yungas (Sage, 1984). Compared to other locations in the highlands, crops, primarily the grains wheat, barley and maize, grow well on the fertile soils of the Quaternary deposits, and in the largely temperate seasonal climate of the Cochabamba Basin (Figure 1.13). Geographically, the area lies on an easily accessible trade route between upland and lowland regions, which, in more recent times (since the 1950’s), has been exploited by the construction of a number of main arterial roads.

Today, the growing centre of the Cochabamba Basin is only a remnant of a much more productive time during pre-Columbian occupation. The agricultural importance of the Cochabamba Basin and surrounding mountain ranges extends back to before the Spanish conquest and, although limited, archaeological evidence from the Cochabamba Basin suggests agricultural activities have occurred for at least 3000 years (Hensen, 2002). By the time of the Tiwanaku state (c. 1500–900 yr BP), which was the first major culture to control a large proportion of the Bolivian Andes (Figure 1.10), the warm fertile main Cochabamba Valley had become a centre for farming, and frontier for trade into the subtropical Mizque Valley and beyond (Higueras, 1996; Janusek, 2008). Archaeological investigations have revealed a number of historic roadways in the regions which connected many of these local and regional settlements, and acted as trade and transport routes (Sánchez, 2008) (Figure 1.12).

During Inca state rule (c. 650–550 yr BP) (Figure 1.9) activity in the Cochabamba Valley escalated and the area became the largest known Inca production enclave. According to Lone and Lone (1987), the Inca recognised the favourable environmental conditions of the valley and the potential for agricultural opportunities, particularly the cultivation of maize, which exceeded those of all other southern highland locations. Conquering and reorganization occurred, and the replacement/supplement of the local population by 14,000 labourers increased production, particularly in the prime maize valley lands in the western section of the Cochabamba Basin. This restructuring effort saw the Cochabamba valleys become known as the “breadbasket” or “granary” of Bolivia and of the whole

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south central Andes, a term that is still used today (Zimmerer, 2000). As well as supplementing the everyday diet of tubers, namely oca (*Oxalis*) and the freeze-dried potato, Chuño (Solanaeae), which were grown successfully on the Alitplano, the production of maize (*Poaceae, Zea mays*), chilli peppers (*Solanaceae, Capsicum*) and squashes (*Cucurbitaceae; Cucurbita*) was also successful in the Cochabamba Basin. The presence of storage structures in the archaeological record suggests that growth of these crops was so successful in the Cochabamba valleys that it allowed provisions to be built up for periods of low productivity (Larson, 1998). However, the importance of the Cochabamba Basin and adjoining valleys to the Inca also had symbolic and ceremonial significance. The abundance of maize led to the production of chica, an alcoholic drink presented as a food to the gods to guard against divine manifested disasters (Larson, 1998). During the Inca period of intense agriculture it is likely that the grazing of livestock was largely reduced in the prime agricultural lands (Wachtel, 1982).

The Cochabamba Basin and surrounding mountain ranges are ideal for addressing the research aims identified (Section 1.3) due to the abundance of obtainable palaeolimnological records, a high biodiversity of vegetation, sensitivity to climatic change and a long history of human occupation. The Cochabamba Basin provides the ideal location in which to disentangle climatic and human signals in order to determine the drivers and rates of ecosystem change in a previously unstudied region of the Tropical Andes. Using a range of palaeoecological indicators (see Chapter 3), climate, vegetation, fire and human impact will be reconstructed (see Chapters 4–6). This new information can then be incorporated into the current understanding and management of environmental and human impacts of Tropical Andean ecosystems (Chapter 7).

1.5) Thesis structure and layout

Following this introductory chapter, this thesis is presented in the form of seven additional chapters that systematically examine the research aims. In Chapter 2 the study sites are described in detail. The geographical setting, modern ecology, climate and human impacts of each location are discussed. Chapter 3 describes the research methods and discusses the rationale and limitations of each technique used in this thesis. This
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chapter examines the uses of each analytical technique and provides a summary of the protocols followed.

Chapters 4 and 5 present the main palynological, geochemical and charcoal results and discussion of the two study sites, Lake Challacaba, and Laguna Khomer Kocha Upper. A discussion of chironomid taxonomy notes and taxa discovered is provided in Chapter 6. This section highlights that the published knowledge of Andean chironomid research is in its infancy and shows how this study compliments and builds upon the knowledge gap. Descriptions of the chironomid types discovered are provided and discussed in reference to the data obtained from the sediment cores.

An overall thesis discussion is drawn together in Chapter 7. This chapter, whilst referring to much of the previously presented data from Chapters 4, 5 and 6, places the findings of this thesis into a conservational perspective, focussing on the biogeography of the landscape during the past and likely changes for the future. This chapter applies this new data in by assessing environment sensitivity and vulnerability and how a palaeoecological perspective can inform conservation managers and policy makers. A short summary of conclusions together with recommended future lines of inquiry is presented in Chapter 8.

Year numbering system

It is commonplace in archaeology to present dates in reference to the start of the Christian era (i.e. BC/AD). While this is appropriate for discussions strictly archaeological in nature, when combined with other disciplines time-scales can become confusing. Therefore, throughout this thesis, and following the majority of palaeoecological and palaeoclimatological studies, dates are given as years before present (BP), with AD/BC dates following in brackets where appropriate.
This chapter provides a description of the specific study sites investigated in this thesis. Two locations from the surrounding mountain ranges of the Cochabamba Basin were investigated, Lake Challacaba and Laguna Khomer Kocha Upper. For each site a description of the geographical and geological setting, modern ecology, climatic conditions and human history is provided.

2.1) The Vacas Lake District - Lake Challacaba

Following preliminary investigation on the 16th June, 2007, Lake Challacaba was selected as the most suitable site for coring within the Vacas Lake District (see Section 1.4). The criteria for coring was based upon its apparent permanence, relative freshwater content, suitable depth and accessibility. Coring was completed on the 23rd June, 2007.

2.1.1) Geographical location and setting

Lake Challacaba is a small, ~1.5 km², freshwater system, situated at 3419 meters above sea level (m asl) within the cold and dry Vacas valley (17°33.257'S, 65°34.024' W; Figure 2.1). At the time of fieldwork, Challacaba had a maximum water depth of 3 m (Figure 2.2 and Figure 2.3). The lake is approximately 1.2 km in length and 1 km in width, with a total perimeter of ~4 km, and it is aligned northwest to southeast. As previously discussed (Section 1.4.1), it is likely that at several times in the history of the Vacas Lake District, Lake Challacaba was connected to other lakes in the valley, forming one large water body (Figure 2.1). Today however, there is no connection present between the lakes. Instead the lake is fed by an ephemeral stream running off the surrounding mountains to the northeast, and is drained via an outflow at the southeast end. This direct lake input and outflow may explain the freshwater status of the lake in contrast to the increased salinity, due to evaporation, of several of the other Vacas lakes investigated (i.e. Acerokocha and Parkokocha). The south and west boundary of the Challacaba lake basin is formed by sparsely vegetated slopes that rise ~70 m and separates Challacaba from Kollpacocha. In contrast the north and east shore is formed by a flatter expanse of land, currently farmed, that would become inundated by water during the wetter months (January–March).
The local geology is not known in detail but the surrounding high ground consists of Ordovician (488.3–443.7 Ma) quartzite and sandstone that is a common feature along the length of the Eastern Cordillera (see Section 1.1.1 and 1.4.1). The Vacas valley is most likely to have been formed within Quaternary sedimentary deposits, similar to the main Cochabamba Basin, but no detailed study is available and the causes of lake formation for Challacaba and all in the Vacas lakes remains unknown. It is likely however, that several lakes, most obviously Acerokochocha, were created during previous glacial events, as attested to by the deep glacial scour nature of the lake basins. If the lakes were once connected, the separation, due to reduced water levels, may have been because of a decrease in hydrological input or the opening up of an outflow channel. However, with erosion a major feature of Andean landscapes, we suggest that deposition of material originating from the surrounding hillsides might also have played a significant role in separating the lakes.
Figure 2.2 Composite photograph of Lake Challacaba, Vacas Lake District. Photograph taken from northeastern shore looking south (far left of image) to west (far right of image). Recently planted fast growing trees (*Eucalyptus*) on far southern shore. Mudbrick (adobe) huts and farmed land at forefront (northwest shore). Location from which the photograph was taken is shown in Figure 2.3.
Figure 2.3 Map of Lake Challacaba and local topographic features. Contour lines at 20 m intervals. Lake depths determined by bathymetric survey (see Section 3.1).

2.1.2) Modern ecology

Lake Challacaba and the other lakes within the Vacas District are positioned within the Central Andean Puna ecoregion (see Chapter 1). Further vegetation classification has been achieved on a regional scale for Bolivia. The Vacas Lake District has been regionally classified as being within the “northern Puna–semi-humid” (Ibisch et al., 2003) and “sub–humid Puna and Punean woodlands of the Tunari” (Navarro and Maldonado, 2002) biogeographic regions. Additionally, Navarro and Ferreira (2007) produced a digitised vegetation map of Bolivia (scale 1:250000), with field verification, that currently offers the most detailed description of vegetation. This database is importable into applications such as ArcGIS and GoogleEarth and so exact locations can be pinpointed. This classification identifies the lake vegetation of great importance for livestock. The vegetation of the surrounding lands can be summarised as sub–humid ranging from grassland, shrubland, saxicolous vegetation to Polylepis forest (Navarro and Ferreira, 2007).
Important botanical families of the Vacas Lake District and surroundings include Asteraceae, Brassicaceae, Bromeliaceae, Caryophyllaceae, Gentianaceae, Poaceae and Rosaceae (Montes de Oca, 2005; Navarro and Ferreira, 2007). While these classifications are a broad-brush approach, they can offer insight into the dominant vegetation types and potential vegetation communities. Although not conducted in the Vacas vicinity, Navarro and Maldonado (2002; pg 248-251) offer a more detailed description of the flora typical of the Vacas biogeographic zone, suggesting the importance of genera including: Poa, Festuca, Deyeuxia, Muhlenbergia, Stipa (all Poaceae), Gomphrena (Amaranthaceae), Baccharis (Asteraceae), Polylepis (Rosaceae), Peperomia (Piperaceae), Astragalus (Fabaceae) and Puya (Bromeliaceae).

There are no terrestrial vegetation surveys available for the Vacas area. However, previous studies on the aquatic vegetation of Acerokocha, Juntutuyo, Kollpakocha and Parkokocha are available (see De la Barra, 2003; Molina et al., 2007). Of note from these studies is the finding that Zannichellia andina and Potamogeton striatus (both Potamogetonaceae) are indicators of saline or hypersaline conditions, and so their relevance to the freshwater system of Challacaba may be limited. From our own observations of aquatic vegetation at Challacaba, it was clear that Myriophyllum spp. was one of the dominant components. Therefore, the lakes organic input is likely to come from the abundance of aquatic plants, together with other terrestrial sources.

As with the main Cochabamba Valley (see Section 1.4.2), the relatively flat lands surrounding the Vacas lakes appeal to human occupation, and today the area is heavily impacted by humans (Navarro and Ferreira, 2007). In 2001, the settlement of Vacas had a population of 650 (Instituto Nacional de Estadística, 2002). The flat Vacas valley floor is dominated by the cultivation of potatoes and other tubers, barley, beans and oats (Gotkowitz, 2007; Montes de Oca, 2005). The remaining land is Andean grassland that has been heavily damaged by grazing of cattle and goats. Some planted Eucalyptus trees are present on the steeper slopes (Figure 2.2), most likely in an attempt to stabilize the soil and provided a source of building material, but the timing of planting is unknown. Planting of this exotic tree is a common practice across Bolivia and Peru (Fjeldså and Kessler, 1996).
Further away from most directly human impacted lands, and more typical of the vegetation of the surrounding mountains ranges of Vacas, the landscape consists of *Polylepis* woodland patches within Andean grassland. Remnants of *Puya raimondii* exist within the *Polylepis* woodlands and grassland matrix (Navarro and Maldonado, 2002). Studies of the *Polylepis besseri* woodlands at Sacha Loma (17°44' S, 65°34' W; ~3800 m asl, 16 km south of Challacaba) have provided a detailed inventory of species found within them (Fernández, 1997; Fernández et al., 2001). The most local *Polylepis* woodland patches are located ~5 km away in the mountains to the northeast, and ~10 km to the southwest (Figure 2.1). Our own observations of a small *Polylepis nana* stand by the side of the Arani to Vacas road (17°33.540' S, 65°42.329' W; 3379 m asl), revealed tree heights of 1–1.5 m growing in patches along the edge of a rocky field boundary.

2.1.3) Climate

The nearest meteorological station to the Vacas Lake District is located at Arani (17°34' S, 65°46' W; 2865 m asl) (see Figure 1.12). This station is situated 22 km west of the study site and at 314 m lower elevation in the Cochabamba Basin proper. Mean temperature and monthly precipitation data for the Arani meteorological station is provided (Figure 2.4).

As no local instrumental metrological data are available for Challacaba, interpolations of observed data (1950-2000) from closest weather stations provides an estimate of the values for sub 1 km grid squares (Hijmans et al., 2005). Analysis of this data set within the GIS package DIVA shows that at Lake Challacaba during the dry season (June–August) precipitation averages 2.6 mm/month and increases to 114 mm/month for the wettest three months (January–March). Annual temperature varies from 7.2°C to 11.3°C for the wet and dry season respectively. Total annual precipitation is estimated from the interpolated data at 537 mm (Figure 2.4).

Comparison between the interpolated data for Challacaba and the metrological data for Arani shows relative agreement in precipitation. Similar trends are also observed in the mean temperatures although the Arani metrological data is offset by an increase of ~5°C. This difference is in part representative of the variation in altitude (314 m).
Figure 2.4 Monthly average climate data for the Vacas Lake District and surrounding area. Interpolated data for Challacaba (dashed lines) from Hijmans et al. (2005). Meteorological data for Arani (17°34' S, 65°46' W, 2865 m asl) (solid lines), from Gareca et al. (2010).

2.1.4) Human occupation

Lake Challacaba is situated 2.5 km south of the settlement of Vacas (Figure 2.1). Like the rest of the Vacas Lake District, flatter workable lands (i.e. for Challacaba those on the northern shore), are worked up to the water's edge (Figure 2.2). The inundation of this land during the wetter months may help to replenish some of the soil nutrients lost through farming processes. The vegetation of the Vacas valley is noted as being dominated by crops in the national vegetation classification (Navarro and Ferreira, 2007). Set back from the road by a distance as little as a 200 m, the lake is easily accessible today and several small farm buildings are positioned between the lake and the road (Figure 2.2).

In addition to the farmed land, the lakes are also used as a source of water and feed for livestock. The importance of the Vacas lakes for the herding of goats and cows was noted...
in the national vegetation classification (Navarro and Ferreira, 2007), and this activity was personally observed at lakes Parkokocha and Acerokocha during the month of June 2007. Ritter (2000) recorded the same activity at Juntutuyo throughout the dry season, specifically noting the preference of cattle for both *Myriophyllum quitense* (Haloragaceae) and *Stuckenia striata* (Potamogetonaceae). There is no reason to indicate that this animal grazing does not also occur at all the lakes in the region.

There is a long history of human activity in this region which certainly predates the local church records, from the village of Vacas, which contain baptisms and marriage information since 1766 (Registros Parroquiales, 1766-1924). Challacaba is situated only ~15 km away from the well-documented Inca ruin site of Inkallajta. Sánchez (2008) has suggested that the Vacas municipality was significant in regional transport routes (Figure 1.12). Sánchez (2008) suggests that the current road passing through the Vacas Lake District, and within 200 m of Challacaba, is based upon an historical “high road”. This road was one of the principle routes that connected the main Cochabamba Valley to the smaller peripheral settlements.

Routes were established between the fuertes (strongholds) of Inca Rakay in the west, to those in the east and southeast such as Inkallajta, Comarapa, Pulquina and Samaipata. The important Tiwanaku archaeological site of Mizque (Figure 1.12; Higueras, 1996) was also connected to the main Cochabamba valley by the establishment of well used routes. Given the importance of camelid pastoralism and caravans for pre-Columbian peoples (Lynch, 1983), and the movement of Tiwanaku traders between the main Cochabamba valley and the Mizque enclave (Janusek, 2008), it seems likely that many pre-Incan groups would also have done so, using the same routes the Inca’s claimed at a later period. As a result many pre-Columbian cultural groups moving or trading between the Cochabamba valley and Mizque or Inkallajta would have been in direct contact with Challacaba and the Vacas lakes. Therefore Challacaba has likely experienced a long history of human impact on varying scales.
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2.2) Laguna Khomer Kocha Upper

Following preliminary investigation on the 17th June, 2007, Laguna Khomer Kocha Upper was selected for coring based upon its apparent permanence, suitable depth, accessibility and minimal amount of human impact (Section 1.4). Coring and additional data collection occurred during a 3-day expedition (25th–27th June, 2007).

2.2.1) Geographical location and setting

Laguna Khomer Kocha Upper is a small, ~0.1 km², glacially formed lake with a maximum depth, at the time of fieldwork, of 3.6 m and a lake perimeter of ~0.3 km (17°16.514’ S, 65°43.945; W). The lake is situated at 4153 m asl on the slopes of the Cordillera el Ronco and its elongated shape is aligned southwest to northeast (Figures 2.5–2.7). Over looking tributaries of Rio San Mateo, the valley descends more than 2000 m elevation in less than 10 km. The southwest end and southeast side of the lake consist of steep, vegetated but stable faces dominated by tussock-forming Andean grasses. The northwest side is created by an apparent glacial deposit (lateral or median moraine) of around 2 m in height running the length of the lake (~120 m). This moraine separates the lake from an area of flat, waterlogged, ground which is likely to represent an infilled lake of similar size to Laguna Khomer Kocha Upper (see Figure 2.6 and 2.7B).

While there are no obvious fluvial inputs, Laguna Khomer Kocha Upper is likely to be fed by runoff from the step situated above the back wall and subterranean seepage from the small catchment area. At the time of coring the lake was a closed basin, however, an outflow channel at the north eastern end (Figure 2.7A), ~0.25 m above the current water level, provides a partial breech of the moraine. Once past this point, water would descend down the steep forested gully towards larger lake of Laguna Khomer Kocha (~3900 m asl; Figure 2.6).
**Figure 2.5** Map of the Khomer Kocha area and local features. Road, watercourses and mountain ranges shown. Contour lines are at 200 m intervals.

**Figure 2.6** Map of the Khomer Kocha Lagunas (upper and lower). Local terrain, investigated *Polylepis* woodlands and lake inputs/outflows shown. Waterlogged ground shown as dashed line area. Contour lines at 20 m intervals. Photograph locations correspond to Figure 2.7.
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The site specific geology is not known in detail, but a study conducted at a lower elevations on the same range, found the bedrock material to consists mainly of sandstones, lutites and quarzitic rocks of Ordovician (488.3–443.7 Ma) and Devonian (416.0–359.2 Ma) age with areas of granite intrusions. Calcareous rocks were found between 2000–2200 m elevation (Kessler, 2002b). There are mountain peaks in the local area that reach heights in excess of 4500 m elevation but no permanent snow patches were evident. Above ~4300 m elevation, large proportions of the landscape were dominated by rock exposures together with large stone blocks scattered throughout the vicinity.

Figure 2.7 Laguna Khomer Kocha Upper. A) The lake looking from above toward the northeast. B) The lake looking from above towards the east. The area of waterlogged ground is clearly evident. Cloud formation in the valley moving moisture upwards. C) Composite photograph of the lake looking southeast and clearly showing the steep back walls. The locations from which the photographs were taken is shown in Figure 2.6. Photographs A and C provided by William Gosling.


2.2.2) Modern ecology
Positioned within the Bolivia Yungas ecoregion (see Chapter 1), the lagunas of Khomer Kocha lie in a region of rapid changes in ecology in association with elevation. The Bolivian specific classifications of Ibisch et al.’s (2003) and Navarro and Ferreira (2007) position the lakes between the biogeographic regions of the Bolivian Yungas, and the Northern semi–humid Puna. Navarro and Maldonado (2002) offer a more detailed description of the biogeography, and suggest that the site lies in the “transitional humid to sub–humid Punean woodlands”.

The transitional humid to sub–humid Punean woodlands, is a biogeographic zone that splits the Puna and Yungas zones along the Cochabamba section of the Eastern Cordillera (Navarro and Maldonado, 2002). Although, the upper elevation limit of this zone is below the Khomer Kocha lakes, the zonal description otherwise fits well, and the offset in the elevation may be due to Khomer Kocha receiving sufficiently more rainfall than sites on the southwest side of mountain ranges where the description is primarily acquired from. This biogeographic zone is characterised by genera including: Polylepis and Hesperomeles (both Rosaceae), Berberis (Berberidaceae), Ribes (Grossulariaceae), Schinus (Anacardiaceae), Baccharis and Mutisia (Asteraceae) and Escallonia (Escalloniaceae). Navarro and Maldonado (2002), note that this assemblage of vegetation can connect to a riparian meso–tropical forest habitat, where Vallea (Verbenaceae) and Alnus (Betulaceae) become important floristic components.

On a local scale, the flatter lands immediately surrounding Laguna Khomer Kocha Upper, in particular the adjacent area of water logging (see Figure 2.6 and 2.7), can be most suitably characterised as a hygrophilous Puna meadow. Genera common of these areas include: Festuca, Deyeuxia and Poa (Poaceae), Eleocharis (Cyperaceae) Juncus (Juncaceae), Ranunculus (Ranunculaceae) Hypocoeris, Werneria and Perezia (Asteraceae), and Trifolium (Fabaceae) (Navarro and Maldonado, 2002).

Below the lagunas of Khomer Kocha the upper limits of the Yungas montane forest extend up the valley of Rio San Mateo. The upper Yungas vegetation has an elevational limit of 3700–4200 m asl, dependant on local microclimatic conditions. The local vegetation classification is “upper Yungas of the Chapare” which is characterised by the
genera: Polylepis pepei (Rosaceae), Gynoxis (Asteraceae), Pentacalia (Asteraceae), Ribes (Grossulariaceae), Berberis (Berberidaceae), Bomarea (Alstroemeriaceae), Salpichroa (Solanaceae) and Fuchsia (Onagraceae). Companion genera include: Oxalis (Oxalidaceae), Luzula (Juncaceae), Cajophora (Loasaceae), Solanum (Solanaceae), Perizia (Asteraceae) and Festuca (Poaceae), together with species of bryophytes and ferns (Navarro and Maldonado, 2002).

At lower elevations (3100–3700 m), the lower Yungas of the Chapare, is characterized by the tree genera of including: Polylepis racemosa lanata (Rosaceae), Clethra (Clethraceae), Escallonia (Escalloniaceae), Ilex (Aquifoliaceae), Myrsine (Myrsinaceae), Oreopanax (Araliaceae), Podocarpus (Podocarpaceae), Weinmannia (Cunoniaceae). The understory is complex and diverse including many species in addition to those listed for the upper Yungas. See Navarro and Maldonado (2002; pp. 332-334), and Montes de Oca (2005; pp. 209-210) for a species inventory.

A feature that can be quickly determined from the above biogeography and vegetation discussion is the complexity of the Khomer Kocha ecology. The correct definition for the study location probably lies within a combination of the Puna and transition woodlands. However, with such a steep elevation gradient present in the valley of San Mateo, it is likely several Yungas floral components also exist close to the study site.

A study by Hertel and Wesche (2008) in September 2003 represents the only known study specific to Khomer Kocha lake area. Here, the authors reported a Polylepis lanata stand (3650 m asl) with a secondary tree layer dominated by Oreopanax macrocephalus (Araliaceae) and Baccharis pentlandi (Asteraceae), together with Fuchsia and ferns. At higher elevations (3800 and 4050 m asl), Polylepis pepei stands were identified with the genera Gynoxis (Asteraceae) and Ribes (Grossulariaceae), together with moss species and the herbaceous genera Luzula (Juncaceae) and Bomarea (Alstroemeriaceae).
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The only other information from the vicinity is reported by Navarro and Maldonado (2002; p. 333), from observations during field study that:

"...on the laguna of Khamer Kocha; dense forest, little intervention (human impact), with 6–8 m canopy, covered with epiphytic bryophytes on trunks and branches" (Translation from Spanish).

Navarro and Maldonado (2002), also note large extensive mats of *Isoëtes lechleri* (Isoetaceae) that form in shallow, cold waters of Laguna Khamer Kocha. In addition, the authors record the presence of the peaty grassland genera of *Deyeuxia* (Poaceae) and *Senecio* (Asteraceae), and the wetland species of *Plantago tubulosa* (Plantaginaceae).

Our observations of the study location found two *Polylepis* woodland patches in close proximity to Laguna Khamer Kocha Upper (Figure 2.6). One patch, 300 m to the north, was located at the base of an exposed rock face within a screefield with large stone blocks present (Figure 2.8A). The ground is steeply sloped and unstable which made access difficult. The ground appeared well drained and the vegetation, where not *Polylepis*, was limited to tussock forming grasses.

The second woodland patch was found in the gully below Laguna Khamer Kocha Upper and ~400 m northwest (Figure 2.8B). Although the gully was positioned at the base of a scree slope, the woodland here was located on flatter ground that had a small stream flowing through. Large blocks of stone were also scattered amongst the trees and high growing varieties of grasses and rushes were abundant in areas of waterlogged ground near to the stream (Figure 2.8B). The *Polylepis* woodland was dense and tangled which made access difficult (see Figure 1.6B). Individual trees were covered in mosses, a phenomenon not observed at the first site, indicating increased moisture. As reported by Hertel and Wesche (2008), several tree and scrub species were also present, although in sporadic and lower abundances.
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Figure 2.8 The *Polylepis* woodlands around Laguna Khomer Kocha Upper. A) Above the lake looking north. Scree slopes are clearly evident. B) Below the lake looking west, amongst large boulders and high growing grasses in the waterlogged ground.

2.2.3) Climate

The nearest meteorological stations to Khomer Kocha are located at Cochabamba City (17° 41’ S, 65°10’ W; 2548 m asl, 50 km southwest, Figure 1.13) and Arani (17°34’ S, 65°46’ W; 2865 m asl, 35 km south, Figure 2.3). However the difference in altitude between the study site and the meteorological stations (>1300 m), and their position on opposing sides of the mountain ranges (important for precipitation control), renders the data unrepresentative for the Khomer Kocha lakes.

With no local instrumental metrological data available for Laguna Khomer Kocha Upper, interpolations of observed data (AD 1950–2000) from closest weather stations was used to provide estimate values for sub 1 km grid squares (Hijmans et al., 2005). Analysis concluded that during the dry season (June–August) precipitation averages 13 mm/month and increases to 138 mm/month for the wettest three months (January–March). Mean temperature varies from 4.5°C to 7.6°C for the wet and dry season respectively. Total annual precipitation is estimated at 772 mm (Figure 2.9).
Kessler (2002b) reported that condensation of dew and fog also contributed to the humidity, especially between 1600–3400 m asl. Our own observations at Laguna Khomer Kocha Upper (June 2007) show that cloud gradually ascends from the low valleys to the northwest. As a result, large quantities of moisture are deposited on the vegetated slopes, as high as ~4100 m asl, even during the dry season.

Short-term climatic conditions at Khomer Kocha were investigated during the month of September 2003. Daily temperature ranges were recorded at altitudes of 3850 and 4050 m asl and yielded values of -0.6°C to 11.5°C (mean of 3.4°C), and -2.3°C to 9.5°C (mean of 1.7°C) respectively (Hertel and Wesche, 2008). These results indicate a lapse rate of ~0.5°C per 100 m elevation gain.

Figure 2.9 Monthly average climate data for the Laguna Khomer Kocha. Interpolated data from Hijmans et al. (2005).
2.2.4) Human occupation

Today there is minimal sign of human impact at Laguna Khomer Kocha Upper. Investigation of the study site surroundings revealed one small rock shelter near to the track that would be sufficient for 1–2 people, and a small herd of 7 semi-wild horses. Examination of the Polylepis woodland patches surrounding the lake revealed no indications of exploitation (i.e. cutting for fuelwood, burning or excessive browsing). At lower elevations (<4000 m asl) minimal human impact was also observed, although the grassland around the lower lake showed evidence of recent burning in August 2003 (Hertel et al., 2008; D. Hertel, 2010 pers.coms).

The lagunas of Khomer Kocha are situated on the boundary of Carrasco National Park and although not included within the parks management, information regarding modern human practices are likely to relate. Today the current population for the whole ~6200 km² of Carrasco National Park is estimated to be around 100 families who reside in the low elevation Yungas environments and use the land for farming, cattle herding and agroforestry. Potential crops in the Puna environment include tubers, oats, wheat, barley and quinoa, with coca, corn, maize and yucca among those produced in the lowlands of the Yungas (ParksWatch, 1996). The nearest agricultural fields were ~15 km away by road.

Although there are the remains of a small Inca sites (Inkachaca; 15 km west; >2000 m lower elevation; Figure 1.12), there is no direct route available from the lake site due to the steep topography. The ancient road network (Sánchez, 2008; Figure 1.12) that passed through the Vacas Lake District and connected much of the Cochabamba Basin area (see Section 2.1.4), also connected to Inkachaca. However, there is no indication of an ancient roadway near Khomer Kocha and the lake is difficult to access due to site remoteness, altitude and unstable terrain. The track used to access the study area today passes within 1 km of Laguna Khomer Kocha Upper, but is 200 m above the site (see Figure 2.5). It is the old, now unused track that leads from Cochabamba city to Villa Tunari, via ‘Cuevas del Repetición’ and passing along the western limits of Carrasco National Park (Kessler, 2002b). Often described by the name “camino a las nubes” (“road to the clouds”), it is today impassable and closed in the lower elevations of the Yungas due to vegetation regrowth since the opening of a new road that runs farther to the west. While we cannot
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rule out previous higher levels of human impact from just visual examination of the lakes and surrounding, there is no evidence to suggest a greater extent occurred in the past.

2.3) Conclusions

The two study locations provide an ideal situation in which to address the aims set out in Section 1.3. Lake Challacaba's location upon an ancient road network provides the long-term historical information of human occupation of the region. This information is needed to be able to disentangle natural environmental changes from those initiated by human activity. In contrast, the relative natural state of the landscape surrounding Laguna Khomer Kocha Upper allows the assessment of the vegetation dynamics, including the Polylepis woodlands, without the impacts of extensive human occupation. The different climatic conditions and biogeographies at Lake Challacaba and Laguna Khomer Kocha Upper will allow and examination of relative sensitivities and vulnerabilities of the local environment at each location to changes in the climate system. As both lakes are similar sizes, the accumulation of ecological deposits into the sediments should be from comparable spatial scales.
This chapter presents the research methodologies and discusses limitations of the laboratory and statistical techniques employed during this doctoral research. All fieldwork was completed during the months of May and June 2007 in Bolivia. Laboratory preparation and analysis was conducted from 2007–2010 at The Open University. In addition to the methodologies discussed here, detailed analytical protocols and examples of preparation and recording sheets are provided in Appendix A2.

3.1) Lake observations and data recording

Conductivity, pH, depth and turbidity were recorded for each study site to provide a direct indication of conditions represented in the most recently deposited sediments (i.e. top 0–1 cm) (Table 3.1). A basic bathymetric survey of each lake site was completed using a handheld sonar to establish maximum lake depth. Depths were recorded along a transect line passing from the shore to the centre of the lake until the deepest section was located. The position of each depth measurement was marked via the use of a handheld GPS. Next a 2.5 cm diameter core of the top 0.5–1 m of sediment was extracted and examined. This test core provided an indication of the substrate type and allowed an initial assessment of the suitability of the site before the full coring rig was deployed. Measurements of conductivity, pH and turbidity were recorded using handheld devices, as described in Table 3.1.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Method</th>
<th>Instrumentation used</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water conductivity</td>
<td>μS/cm (microSiemens per cm)</td>
<td>Hanna 991300 handheld probe</td>
</tr>
<tr>
<td>Water acidity</td>
<td>pH</td>
<td>Hanna 991300 handheld probe</td>
</tr>
<tr>
<td>Water depth</td>
<td>Bathymetric survey</td>
<td>HawkEye Digital Sonar DF2200PX</td>
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<tr>
<td>Water turbidity</td>
<td>Secchi depth</td>
<td>White anchor bag</td>
</tr>
</tbody>
</table>

Table 3.1 Methods and instrumentation used to measure Bolivian lake variables during the 2007 field season. A detailed protocol for use of the Hanna probe and for water sampling is provided in Appendix A2.
3.2) Lake sediment coring procedures

3.2.1 Long core

All long sediment cores were extracted using a cam-modified Livingstone piston corer (Livingstone, 1955; Wright et al., 1984), belonging to the Open University’s Palaeoenvironmental Change Research Group (OU-PCRG). The coring platform consisted of two Avon inflatable tender boats with a lightweight wooden platform secured across them (Figure 3.1). The platform was secured in position at three points to anchor bags. An extra inflatable was used where possible for storage of additional casings, rods and tools. The coring procedure, together with example designs for platform construction is fully described by Colinvaux et al. (1999).

The deepest part within each lake was located by initial bathymetric survey as previously described in Section 3.1. Coring at the deepest part increased the chances of obtaining the longest available sediment core, and reduces the probability of encountering a phase in the sediments when the lake dried out. Following deployment of the full coring rig, two overlapping sediment cores, positioned 1–2 m apart, were obtained. The overlap was used to ensure that any material that may have been lost from the bottom of one core is safely encased in the middle part of the overlap core. It also allows subsampling of core ends, where contamination may be higher, to be avoided. During the fieldwork for this project the team of three was able to raise two (~5 m) cores from 3 m of water in one full day. Sediments are encased within aluminium core tubes of either 50 or 38 mm diameter, and raised in 1 m long sections (drives) where they are then sealed using caps and tape, and carefully labelled. They were then kept horizontal and flown back to The Open University’s cold storage facility (4°C).

The Livingstone coring procedure chosen prevents a preliminary examination of the sediment in the field. This can be considered a disadvantage when the nature of the sediment, or success of the coring drive is unsure. However, coring systems that keep samples encased until such time when contamination risk is reduced (i.e. in the laboratory), is a significant advantage. This not only reduces potential errors in the ecological proxies to be examined, but also limits the exposure of material that is later...

3.2.2 Short core (sediment/water interface)
Short cores were obtained where possible to ensure the sampling of the sediment/water interface (top ~50 cm), as this material is not easily captured by the long core procedure due to its high content of water. The short cores were extracted using a clear 1.2 m long, 50 mm diameter, Perspex surface sample tube taped securely to a length of the piston rods. The surface sampler was driven into the lake sediment until the bottom is plugged and the whole unit was brought up together and kept upright (Figure 3.1). Once on shore, the sediment was extruded in the field, using a bung (piston) and pusher rod, and continuous subsamples of 1 cm thickness were transferred into labelled plastic sample bags.
Figure 3.1 Diagrams and photographs of coring setup. A) long core. B) short core. C) and D) platform for long core. Labelled parts in A and B are:

a) Wooden platform bridging the boats – circular hole in platform allows for the casing to pass through and be clamped in place.
b) Coring rods and T-bar – used for pushing the core tube into sediment and to extract the unit.
c) Cable clamp – allows the exact depth when sediment capture begins to be determined by the operator.
d) Casing – remains clamped to coring platform throughout and penetrates into the sediment thus allowing coring tubes to relocate the initial core hole created during the previous drives.
e) Cable – to determine the drive depths. Remains attached to piston mechanism for emergency retrieval.
f) Piston mechanism – this is positioned at the bottom of core tube until the desired depth for sediment to be contained, thus preventing erroneous material from entering the tube.
g) Aluminium core tube barrel – are exchanged after each 1 m drive. Diagram A shows the full core tube during extraction, leaving empty the core hole for subsequent drives to pass freely down.
h) Perspex surface core tube barrel secured with the use of tape to the coring rods – only driven part way into sediment thus preserving the sediment/water interface within the core tube. The unit is then transported vertically back to the shore for sampling.
3.3) Sample logging, documentation and subsample extraction

3.3.1 Core splitting
The sediment cores were split using a router with a titanium drill bit, on a specifically designed bench mounted tube holder. Using interchangeable parts, the holder is capable of clamping both the 38 and 50 mm diameter, 120 mm long aluminium core tubes. Cutting of both sides was completed in several sweeps by gradual lowering of the drill bit until a thin layer, a little thicker than 0.1 mm, remains. Once grooves on both sides of the tubing had been reduced to this thickness the final cut through the tubing was made using the clean blade of a retractable knife. The sediments encased within the cut tubing were then split using clean wire held at tension and, where necessary, parted using a clean pallet knife. When not being examined, the cores were wrapped in two layers of plastic wrap and kept horizontal in cold storage at 4°C. See Appendix A2.2 for the full protocol.

3.3.2 Description and cataloguing
Once split, all the cores were immediately photographed and described. This took place before processes which may affect the appearance of the core surface can occur; e.g. iron oxidisation, cracking due to drying, mould growth. The sediments were described using the Troels-Smith system (Birks and Birks, 1980). Colour was recorded using the Munsell Soil Colour Chart (2000). Any macrofossils suitable for radiometric dating were noted and extracted (see Section 3.5 for details).

In the absence of a core scanner facility, overlapping photographs of each core section were taken and processed to provide one image per core drive. To ensure maximum clarity and detail of the core photographs, several methodologies of photography were tested (see Appendix A2.3). Two methods, numbers 5 and 6, were subsequently utilised and the method for composite photographs is described below. Details of the other methodologies tested are given in Appendix A2. The system developed aimed to maximise colour details recorded, improve consistency between photographs and minimise any limitations of the camera.
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Photographic set up and capture

A Kodax V610 Dual Lens digital camera was held 90 cm above the core surface on a tripod that allowed for downward facing photography (Figure 3.2). The camera was set to 6.1 megapixel resolution, a lens zoom of ×3 and the exposure adjusted to 3 seconds. Black sheet paper was positioned underneath the length of the core to provide a uniform background colour and an example card of the Munsell Soil Color Chart (2000) positioned in shot to allow for later calibration if required. Photographs of ~10–20 cm overlapping sections were taken using a 3 second timer to minimise movement of the camera.

Lighting settings created the greatest challenge in the procedure. To produce a homogenous illumination as possible, room lighting (two sets of fluorescent strip lights) was used with the core positioned between the two light sources. It was found that these produced a more uniform illumination than spotlights, which had a tendency to increase shadowing where the core surface was uneven, and rapidly begin to dry out the core. However, fluorescent rooms lights are not suitable for all situations, especially when precise image analysis is to take place, as they rapidly cycle through a range of colour temperatures (Nederbragt et al., 2006). While they therefore do not provide a perfect solution, for this study it was found that once the lighting increased in stability, after ~20–30 minutes, it provided the most suitable and uniform option available.

The photography of a wet core also created additional problems. Dependant on sediment type, several cores allowed water to collect on the surface more readily. While McMillian (2008) reports that wet cores often produces the clearest images of sedimentary structure, the non-uniform reflection created, particularly towards the image edges, often rendered the photographs unusable. To mitigate this problem, the number of photographs taken was increased, thus only making the most central portions of each photograph used in the composite. Another option to alleviate this problem is the use of a polarising filter (Lamoureux and Bollmann, 2005; Nederbragt et al., 2006), but one was not available for use with this camera.
Creating a composite image

Photographs were stitched together using Corel Photo-Paint 13 with 'Blend Value' set to '0'. Blending cannot be used as it alters the individual pixels thus preventing any future image analysis. The software utilised allows an image to be made temporarily transparent so that it can be superimposed onto the existing image and aligned correctly. Once in place both images are combined and the next image in the sequence superimposed as before. While the process is time consuming and requires a high level of user interface, the result allows for easier future presentation and analysis. The writing of algorithms that recognise and position overlapping images would be beneficial in increasing time effectiveness, although thorough checks would still need to be made.

Since the cores used in this study were documented, McMillian (2008) published a guide to producing a simple, low cost core-imaging system, utilising a regularly available handheld digital camera. Another process discussed by McMillian (2008) worth implementation, is the automated batch cropping of photographs to specified dimensions. This process is performed by several image programs which automatically remove any unwanted backgrounds in the photographs and reduces the image file sizes considerably. Additional information on image analysis is provided by Saarinen and Petterson (2001), and Francus (2005).
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3.3.3 Sub-sampling methodology and interval
The cores were subsampled using cleaned metal spatulas with sharp ends to enable precise sampling of sediment boundaries. Before sampling, a thin film (0.1 mm) of sediment was removed from the surface and discarded. This protocol minimises any airborne contamination since the core was split, and also any contamination due to movement of material/ fluid around the edge of the core. Dependant of the analytical procedure, see Sections 3.4 and 3.6, subsamples sizes ranging from 0.5–1 cm$^3$ and 0.5–1.5 g, were extracted at sampling intervals of 5–20 cm. All subsamples were sealed within labelled 15 or 50 ml disposable centrifuge tubes that would be used in the chemical preparation. Where subsamples were taken in advance of chemical preparation, centrifuge tubes were kept sealed in the cold storage facility (4°C) until required. The sampling procedure for chronological determination differs to that described above (see Section 3.5).

3.4) Analysis of ecological proxies
3.4.1 Fossil pollen and spores
Rationale for use
Fossil pollen and spore (Figure 3.3.) analysis has provided a principle method for understanding the Earth’s ecological and climatic history since its initiation by von Post (1929; 1946). The importance of palynology, the study of fossil pollen and spores, lies in the reconstruction of vegetation in response to natural and anthropogenic forced environmental changes (Figure 3.4). Palynology can provide valuable insight into these vegetation responses by analysis of the microscopic fossil specimens contained within of range of deposits of varying duration and resolution. Examples include, but are not limited to; annual lake varve records of the Holocene (e.g. Wick et al., 2003), silica sinter deposits from geothermal field fluctuations (Martin et al., 2000) and time snapshots within carbonaceous shales of the Early Cretaceous (e.g. Brenner, 1996).

Palynological studies provide the majority of our past knowledge about the central Andes. This is primarily due to the abundance and well preserved nature of pollen and spores, found in lake, marine sediments, ice cores, cave deposits and exposed sections.
The resistance properties of sporopollenin, which makes up pollen grains walls, allows harsh laboratory chemical treatment to remove unwanted material, and enables preservation of grains in any environments free from oxidation processes (Bennett and Willis, 2001). Pollen and spores are identified by a variety of features including size, shape, aperture number and surface pattern (Figure 3.3).

Figure 3.3 Morphology of pollen grains and spores. Key structures and sculpture that are commonly used to identify types. Images are of specimens identified in this study. A) *Polylepis/Acaena* type. B) *Podocarpus*. C) Trilete spore. D) Poaceae.

Simple reconstruction of environmental conditions dominated early palynological investigation. However, in more recent years, and in response to questions focussing around mans' influence on the global and local environment, and the potential global changes we have to adjust to, the focus of research has shifted. As a result, detailed, high resolution research into environmental thresholds (Willis et al., 2010), invasive species management (MacDonald, 1993), abrupt climate changes (e.g. 8200 yr BP event; Alley and Ágústsdóttir, 2005), and the protection of threatened ecosystems (Burney and Burney, 2007) are just a few examples of the type of research questions being addressed.
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Figure: 3.4 Conceptual model of the complex multidirectional interactions between climate, vegetation, fire and human occupation. Ideally, a record of all factors needs to be understood in order to interpret the interactions. Modified from the drawing of Brenner et al. (2002). Examples of interactions include:

a) Fire – Climate (aerosols, gas release - wind, lightning, moisture)
b) Fire – Human (hazards - clearance, regime control, ignition)
c) Human – Climate (emissions - lifestyle, resource availability, location choice)
d) Vegetation – Fire (fuel – growth patterns)
e) Human – Vegetation (clearance, selectivity, growth patterns – location choice, resource supply)
f) Climate – Vegetation (temperature, moisture – gas exchange, albedo)

Methodology
From both the Challacaba and Khomer Kocha Upper cores, a subsample of 0.5–1 cm$^3$ was extracted from the core on average every 10 cm for pollen and fungal spore analysis. Pollen concentration was determined by the use of a spike prior to chemical preparation. Due to the natural occurrence of many of the typically used exotic pollen/spore spikes (Lycopodium, Eucalyptus and Alnus), synthetic 16 μm diameter microspheres were added at a 1:2 ratio of the subsample (i.e. 0.25–0.5 cm$^3$). Microspheres were provided by the LacCore facility (Batch 2, lot number 150907). Subsequent chemical preparation followed standard palynological protocol (Faegri and Iversen, 1989). A full detailed protocol and example tick sheet is provided (Appendix A2.4; Figure A2.1).
Samples were mounted on microscope slides in glycerol which allows easy rotation of grains. Pollen and spores were identified using a Nikon Eclipse 50i microscope at \( \times 400 \) and \( \times 1000 \) magnification. For a discussion on identification techniques see Bennett and Willis (2001). In all cases a minimum of 300 fossil terrestrial pollen grains were analyzed in each sample or, where pollen concentrations were exceptionally low, counting was continued until 3000 microspheres of the added spike were counted (regularly requiring the identification of 3–4 slides). Slides were counted by traversing horizontally and the singular identification of pollen and spores was achieved by use of The Open University's pollen reference collection, the Neotropical Pollen Database (Bush and Weng, 2006) and other pollen manuals (Hooghiemstra, 1984; Moore et al., 1991; Roubik and Moreno, 1991). In addition, constructive discussion with members of the OU-PCRG (Dr Will Gosling, Macarena Cardenas and Charlotte Miller) assisted in refining identifications.

Counts were recorded on a pre-designed tally sheet (see Figure A2.2) with regularly occurring types (Poaceae, Isoëtes, Myriophyllum and microspheres) counted on a 5-unit manual cell counter. All unique types were digitally photographed for reference purposes using a Lumenera Infinity 1 digital camera and the image capture software ImageJ (Rasband, 1997-2009). A digital copy all photographs is provided in Enclosure CD1 and full taxa list is given in Appendix A4.1 (Tables A4.1 and A4.2).

Limitations

Like the majority of lake-based palaeoecological studies, palynology began as fundamentally a qualitative discipline. However, its application remains highly appropriate in answering many modern ecological questions from a range of temporal and spatial scales (Willis and Birks, 2006). In addition, the rapidly expanding range of numerical modelling that can now be utilised with palaeoecological data is improving the application of results, and ensures the perception of the discipline now centres as a quantitative analytical science (Birks, 1985; Birks, 1998; Birks and Gordon, 1985). At the heart of this development is growing computing literacy and available software, some of which is open source and/or specific to palaeoecological data (e.g. PaleoMAS). See Bennett and Willis (2001) for a general overview and Correa-Metrio et al. (2010) for a recent Andean application.
Nonetheless, as detailed by Lowe and Walker (1997), several important assumptions about palynology remain. These must be understood and, where possible, accounted for during data interpretation. These can be summarized into two main themes. First, that present-day environmental factors governing species' distribution have not changed and that these present/past distributions represent populations that are/were in equilibrium with the present/past governing environmental factors. In addition, there is a requirement that former plant and animal distributions have modern analogues today that represent their ecological traits. And second, that there is no bias from the processes of preservation and analysis. Therefore, the fossil assemblage extracted is an accurate representation of the assemblage originally deposited and that no differential destruction or contamination occurs, including during laboratory preparation. Also, the identity of remains must be established to a sufficient taxonomic precision and consistency.

Light microscopy allows the identification of pollen types frequently only to family level, using variations observed in structure and sculpture (i.e. size, shape and pattern) (see Figure 3.3). Increased taxonomic precision to genus or species is highly dependant on regional diversity and the availability of a reference collection and/or specific keys. Although, as with fossil chironomid analysis (Section 3.4.3), there may also be offset between the apparent and actual information gained with increasing taxonomic resolution (Figure 3.8). As a result analysts must be cautious when assigning identification to pollen types and in response a range of conventions are now used to indicate certainty in identifications. For example, the suffix “type” is used to acknowledge there is at least one other alternative (Bennett and Willis, 2001).

Of specific relevance to this study, the identification of Polylepis pollen from the genus Acaena (both Rosaceae) poses a difficulty due to morphological similarities. However, previous studies argue that a confident separation of two genera is achievable due to geographical and habitat restrictions (Chepstow-Lusty et al., 2005; Gosling et al., 2009; Weng et al., 2006). Another example of complication in Andean taxa identification is the split of Chenopodioideae (previously Chenopodiaceae) from Amaranthaceae. In the literature, many studies group the types as Chenopodiaceae/Amaranthaceae...
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(Cheno/Ams) due to similarities in the periporate morphology. However, the discussion receives continued attention due to importance of crop pollen (quinoa) from the genus Chenopodium, which is considered an indicator of pre-Columbian human occupation (Bush et al., 2005; Chepstow-Lusty et al., 2003; Valencia et al., 2010). Throughout this study the nomenclatures “Polylepis/Acaena Type” and “Cheno/Ams” are used, as ultimately identification can only be certain with scanning electron microscopy (see Smit, 1978). These and other taxonomic precision complications are discussed (Chapters 4 and 5). Additional discussion on the principles, techniques, advancements, applications and limitations of palynology are readily available (Bennett and Willis, 2001; Faegri and Iversen, 1989; Moore et al., 1991; Traverse, 1988).

3.4.2 Charcoal

Rationale for use

Since the development of charcoal abundance studies, predominantly but not exclusively by Clark and colleagues (Burney, 1987; Clark, 1988a; Clark, 1988b; Clark, 1988c; Clark et al., 1998; Clark and Patterson, 1997; Clark and Royall, 1995; Cwynar, 1978), fire regime calculations are regularly conducted alongside palynological research (Ali et al., 2009; Whitlock and Larsen, 2001). With fire considered as a fundamental ecosystem process, many independent palaeoecological charcoal records have now been used to examine the interactions between fire regimes, climate, vegetation and anthropogenic activity (Figure 3.4). This is particularly true of records derived from lake sediments, which have undergone more testing and today represent the majority of charcoal studies conducted, thus allowing lake sediment charcoal records to be considered as a good proxy for palaeofires (Clark, 1988a; Power et al., 2008).

As well as understanding the processes by which charcoal becomes incorporated into lake basins, research has been conducted into the relationship between particle size and atmospheric residence time (Clark and Royall, 1995). Particles of different size classes will travel different distances in the air column (Figure 3.5), with larger particles travelling much less distances before they are deposited (Whitlock and Larsen, 2001 and references within). With this in mind, and with the scope of this study to examine the local ecosystem changes, with particular focus on the impacts to high Andean woodland,
charcoal analysis was only conducted on macroscopic particles >100 μm. Particles of this size are not deposited far from the fire source by aeolian transportation; <7 km (Whitlock and Millspaugh, 1996), <50 m in alpine environments (Tinner et al., 2006). However, distances are dependant on a variety of factors including fire intensity, size and severity (Whitlock and Larsen, 2001), and debate remains regarding the actual distances over which fall-out occurs (Higuera et al., 2007). Care must also be taken when interpreting fluvial deposits, especially of large river systems as transportation distance can be much greater. Larger macroscopic particles have been shown to detect changes in fire regimes that are often unnoticed in microscopic (pollen slide count) analysis (Clark, 1988c). It is understood that pollen processing methods (e.g. acetolysis), can darken non-charcoal plant remains, increasing uncertainty of counts (Blackford, 2000). While microscopic particles can be a useful record of regional burning signals (up to hundreds of km’s from source) (Ali et al., 2009), they were not analysed in this research due to the scope of the study focussing on impacts on the local spatial scale.

Figure: 3.5 Models displaying the relationship between charcoal particle size and distance before deposition. A) Purely conceptual graph modified from Patterson et al. (1987). Fire source at marked by an asterisk. B) Percent of charcoal deposited at distance from fire source. Based upon a wind speed of 3 m·s⁻¹ and a convection column height of 10 m. Modified from Clark (1988b).
Several different methods now exist for the enumeration of macroscopic charcoal within a sample; number (number of particles/cm³), area (mm²/cm³) and volume (mm³/cm³), which can be achieved through a variety of procedures including counting, weighing or digital image analysis. Whitlock and Larsen (2001) suggested that despite the differences in the methodologies, they tend to produce similar results, a conclusion further supported by a recent comparative study of lake sediment records (Ali et al., 2009). These findings add confidence to our interpretations when comparing charcoal abundance records calculated via different methods, and for this study all charcoal analysis was accomplished via the manual counting of individual charcoal particles.

Methodology
Where possible (but dependant on sediment availability), charcoal analysis was conducted at the same sampling resolution as pollen and spores. Subsamples of 1 cm³ (0.5 cm³ in one sample) were deflocculated with 10% potassium hydroxide (KOH) for 24 hours before being sieved and separated into two size fractions (>180 µm and 100–179 µm). Samples were then suspended in water on a gridded Petri dish and counted using a binocular dissecting microscope (Olympus SZX12) at typically ×12.5 up to ×25 magnifications. Abundances were recorded onto a pre-designed tally sheet prior to digital data entry (Appendix A2.5).

Charcoal particles are readily identified by the angular structure, opacity, the reflective black surfaces (Clark and Royall, 1995) and by obvious fragmentation when pressed. In this study, a distinction was also made between two particle morphotypes. Elongate particles, often flatter or maintaining a semi-circle shape (which can be seen easiest at ends), with smoother edges were classified here as type 1 (herbaceous/grass type). Type 2 (wood) is characterised by particles with angular and irregular shape, that are often denser in appearance and display cell structure especially after breakage (see Figure 3.6).
Figure: 3.6 Sketch drawings of the two charcoal particle morphotype groups defined in this study. A) Type 1: Elongate particles, often flatter or maintaining a semi-circle shape with smoother edges were (herbaceous/grass type). B) Type 2: Angular and irregular shaped particles, often denser in appearance and may display cell structure especially after breakage (wood type).

Limitations

Although non-charred material resembling charcoal particles is often encountered during macroscopic analysis, the combination of defining factors, as listed previously, enables particles to be readily identified with time and practice. Identification is also aided by the manual counting method as each particle can be individually checked by the analyst if unsure (i.e. breaking, light adjusting, etc...). With identification and analytical methodological problems aside, the major limitations of charcoal analysis focus on sampling resolution, the separation of fire events from a background noise signal, and the defining the locality of events. Each of these is discussed in reference to the study presented here (Chapters 4 and 5).

The separation of charcoal particle morphotypes executed during this study does have additional limitations. An insufficient number of publications exist that display images of spilt charcoal types (Enache and Cumming, 2006; Jensen et al., 2007; Walsh et al., 2008) and those that do, demonstrate a need for a reference collection of site specific, experimentally charred specimens before material type can be defined. Therefore, while in this research charcoal particles are separated into types, the source material of each type, whilst insightful, remains unconfirmed.
Several fuller discussions regarding the analysis, limitations and interpretations of charcoal particulates as an indicator of past fire regimes are provided by Whitlock and Larsen (2001) and by Clark and Patterson (1997). Critical for interpretation however, is the understanding that as well as recording a signal of short term fire events, charcoal records also contain a background signal of longer-term burning regimes (Higuera et al., 2007) with separation of the two signals often proving difficult.

3.4.3 Chironomidae

Rationale for use

The Chironomidae are a family of true flies, Diptera, suborder Nematocera, that are commonly referred to as “non-biting midges” during the adult stage and “bloodworms” as larvae (Epler, 2001; Walker, 1987). They regularly represent the most abundant group of macroinvertebrates found in fresh and saltwater habitats and have a worldwide distribution, exploiting vast elevation and temperature ranges (Armitage et al., 1995; Ashe et al., 1987; Ferrington, 2008; Pinder, 1986). The life cycle of chironomids (Figure 3.7A) involves four stages (instars) as larvae with each stage culminating in moulting and the shedding of an exoskeletal cuticle (Walker, 1987). Of the integuments shed, the heavily sclerotised chitinous head capsule (Figure 3.7B and 3.8) becomes well persevered within lake sediments, particularly those of the 3rd and 4th instars (Velle et al., 2010; Walker, 2001).

The suitability of chironomids for palaeoecological studies is due to several characteristics in addition to their good preservation and abundance in lake sediments as previously discussed. With the majority of species stenotopic, chironomids are highly sensitive to changes in environmental conditions. Together with many genera exhibiting short life cycles (quick generation time) and being mobile as adults (carried on winds), chironomids are able to rapidly track environmental changes (Brooks, 2005; Walker, 2001).
Although minimal in comparison to work from other regions, investigation of modern Neotropical distribution has progressed. Notably, the early contributions of Edwards (1931) from research in Patagonia, and the transantarctic relationships shown by Brundin (1966) were significant. The later inventories of Neotropical (Spies and Reiss, 1996) and, specifically, Andean Chironomidae (Roback and Coffman, 1983) have also been important steps in the developing the regional understanding. Examining the global distribution of chironomids, Ashe et al. (1987) reported 109 genera and 369 species from the Neotropics and twenty-one years later, Ferrington (2008) concluded taxon richness had increased to 154 genera and 618 species. This increase of described species and genera represents the greatest increase of any region. Although due to improved taxonomic classification and research, the impact of increased exploration and research of South American freshwater habitats may also be a cause of the described richness.
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The palaeoenvironmental analysis of chironomid remains began with research by Gams (1927). The relevance of subfossil chironomid studies now extends into a broad range of applications, utilising transfer functions or assessment of chironomid assemblage change (Table 3.2). Despite significant advancements in Europe and North America, the discipline remained mainly unexplored in the southern hemisphere, due to the lack of ecological data, poor taxonomic resolution and sampling logistics. Indeed, the first study from South American sediment samples did not occur until 1982 (as reviewed by Verschuren and Eggermont, 2006). The current status of subfossil chironomid research in the Andes is discussed in Chapter 6.

<table>
<thead>
<tr>
<th>Application</th>
<th>Sources</th>
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<tr>
<td>Anthropogenic land disturbance and pollution</td>
<td>(Kansanen, 1985; Woodward and Shulmeister, 2005)</td>
</tr>
<tr>
<td>Geological activity</td>
<td>(Araneda et al., 2007)</td>
</tr>
<tr>
<td>Hydrology (water depth)</td>
<td>(Hofmann, 1998)</td>
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<tr>
<td>Isotopic composition related applications</td>
<td>(van Hardenbroek et al., 2010; Verbruggen et al., 2010)</td>
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<tr>
<td>Lake pH levels</td>
<td>(Brodin and Gransberg, 1993; Johnson et al., 1990)</td>
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<tr>
<td>Lake trophic status</td>
<td>(Brooks et al., 2001; Gathorne-Hardy et al., 2007)</td>
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<tr>
<td>Oxygen regime</td>
<td>(Quinlan and Smol, 2001)</td>
</tr>
<tr>
<td>Salinity</td>
<td>(Chen et al., 2009; Walker et al., 1995)</td>
</tr>
<tr>
<td>Substrate / sedimentation type and input rate</td>
<td>(Schakau, 1991; Verschuren et al., 2000)</td>
</tr>
<tr>
<td>Temperatures (water and air)</td>
<td>(Brooks and Birks, 2001; Lang et al., 2010; Porinchu et al., 2003; Walker et al., 1991)</td>
</tr>
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Table 3.2 Example applications of palaeo chironomid studies together with select, non-exhaustive, reference list. List compiled, in part, with examples referenced by Brooks (2000), Nyman (2007), Verschuren and Eggermont (2006) and Walker (2001). Note: several of these applications are interlinked (water depth – salinity – temperature, sedimentation – human influence, etc...) and so some studies referenced encompass a range of applications.
**Methodology**

Subfossil chironomid analysis was conducted on subsamples of 1 cm³ at an original resolution of 20 cm that coincided, where possible, with pollen and charcoal analysis samples. Sampling resolution was then refined by sampling specific depths where initial results indicated important shifts. Following an adapted version of the procedure described by Brooks, Langdon and Heiri (2007), samples were deflocculated in 10% (KOH), heated in water and sieved and separated into two size fractions of 90–212 μm and >212 μm. Head capsules were picked by hand from a sorting tray under a binocular microscope (Olympus SZX12) at ×12.5 to ×25 magnifications and progressively dehydrated. Depending on size and fragmentation of head capsules, between 1–5 were mounted ventral side up in Euparal mountant under 6 mm diameter coverslips onto a microscope slide. Identification was subsequently achieved using a Nikon Eclipse 50i microscope at ×400 magnification with reference to relevant keys (Brooks et al., 2007; Dieffenbacher-Krall et al., 2008; Epler, 1995; Epler, 2001; Rieradevall and Brooks, 2001; Wiederholm, 1983). Results were recorded on pre-designed recording sheets prior to digital data entry (Figure A2.3). The full preparation protocol is provided in Appendix A2.6.
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Limitations
As with palynology, there are various assumptions for subfossil chironomid analysis. These focus around the stability of environmental – ecological interactions through time, differential rates of preservation and contamination, and taxonomic resolution (see Section 3.4.1). Of all, the biggest prerequisite for meaningful palaeoenvironmental interpretation is consistent and proficient identification (Brodersen, 2008). Although new and well constructed taxonomic keys (e.g. Brooks et al., 2007; Dieffenbacher-Krall et al., 2008), together with advancements in microscope image capturing and comparison continue to help reduce this problematic issue, the damaging effects of misidentification remain high. Researchers are therefore still wary of over-confident nomenclature and are encouraged to adopt conventions to indicate certainty in identifications, as with pollen analysis (Walker, 2001). However, reluctance in refining identification to higher resolution may actually assist with the palaeoenvironmental information gained due to increased resolution often leading to increased errors (misidentification), an idea conceptualized by Walker (2001) (Figure 3.9), and later, in reference to specific outcome of correct and incorrect type separation, by Brodersen (2008) (Figure 3.10).

Recent statistical analysis supports a conclusion that transfer functions based upon the highest level of taxonomic (fine) resolution provide inference models with greater agreement to the modern measurements than those with low (coarse) resolution (Heiri and Lotter, 2010). However, this work also showed that intermediate taxonomic resolution produced very similar results to models based on the finest taxonomic data. In conclusion, it is apparent that the effect of increasing taxonomic resolution is dependent upon the analyst’s expertise. As a result, an experienced analyst is less likely to suffer from the problems identified by Brodersen (2008), and obtain more palaeoenvironmental information when refining the taxonomic resolution (Figure 3.9, dashed line). For a less experienced analyst, attempts to refine the taxonomy are more likely to result in increased misidentifications (see Heiri and Lotter, 2010). Overall, the effect of different taxonomic resolution on environmental reconstructions does warrant continued investigation.
Figure 3.9 Conceptual model representing the correlation between taxonomic resolution and palaeoenvironmental information gained during a study. An offset exists between the apparent (dashed line) and actual (solid line) information gained with perceived increasing taxonomic resolution. The ideal (optimum) situation is achieved just before misidentifications occur. Modified from Walker (2001) and with the later additions of Velle et al. (2010).

Other questions surrounding subfossil chironomid analysis that have attracted discussion include; i) the number (of head capsules) needed to be identified before a representative sample is recorded (Heiri and Lotter, 2001; Larocque, 2001), an issue encountered across palaeolimnology (e.g. Lytle and Wahl, 2005; Payne and Mitchell, 2009), and ii) with chironomid head capsules prone to splitting in some taxa more than others (i.e. Orthocladiinae), how should counts of different head capsule fragments be handled (see Walker, 1987)? These topics are discussed with reference to this study in Chapter 6, with the results of half vs. whole counts of split head capsules shown in Figures 6.4A and 6.5A.

The immaturity of both modern and subfossil chironomid analysis in South America, as previously highlighted, leads to an additional set of problems. There are currently no taxonomic keys to South American larvae and the underdeveloped knowledge of chironomids in all life stages throughout the continent generally inhibits high taxonomic resolution. The most significant progress in palaeoenvironmental reconstruction has been made in southern Chile and Argentina (Verschuren and Eggermont, 2006). Recent studies have highlighted improvements possible in resolving taxonomic difficulties when a research focus exists (Donato et al., 2008; Massaferro et al., 2005; Massaferro and Brooks, 2002; Massaferro et al., 2009). However, this situation is a rarity and the high Andes (Bolivia/Peru) remains deficient in studies.
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**Figure 3.10** Consequences of two types of taxonomic error in association to taxa that a) occupy similar environmental ranges, and b) occupy different environmental ranges. Separation of taxa incorrectly always results in problems while reluctance to define identifications to higher resolution produces fewer problems. Modified from Brodersen (2008). While during analysis it may be advised to split rather than lump, it is crucial that prior to any interpretation or numerical analysis that any splitting is reassessed.

A phenomenon that may assist with the identification of taxa from within high Andean sediments is the apparent hump-shaped relationship with taxon richness and elevation, with low richness at the extremes (Bigler et al., 2006; Nyman et al., 2005). While Andean high elevation lake environments do pose a significant challenge to living organisms, active chironomids have already been observed on glacial ice, -16°C at 5600 m above sea level in the Himalayas (Kohshima, 1984). Therefore the presence of chironomids in Andean sediments is expected.

At present, no data training set exists for the central/high Andean region. As a result, analysis of chironomids from lake sediments can only yield qualitative results, focusing on shifts with reference to current knowledge about the ecology of the taxa involved. However, any shifts fine or large scale, are still valuable indicators of lake or
environmental changes especially when in conjunction with either shifts or stability in other proxy signals.

Despite the obvious limitations of conducting chironomid research in the Bolivian Andes, the current substantial knowledge gap ensures that any study into modern and/or subfossil assemblages represents significant progress in the discipline. Even though quantitative values in changes cannot be assigned in this study, information gathered can still provide valuable insight regarding several, if not all, of the variables listed in Table 3.2. This study represents the first account of subfossil chironomid remains from any location in Bolivia.

A discussion of chironomid biology and ecology is provided by Armitage et al. (1995), Pinder (1986), and uses in palaeoecology by Hofmann (1988), Walker (1987; 2001), Il’yashuk and Il’yashuk (2004), Brooks et al. (2007) and Velle et al. (2010). In addition, a review of southern hemisphere Quaternary reconstructions is also available (Verschuren and Eggermont, 2006).

3.5) Chronological framework

With no other records from the region to compare the Challacaba and Khomer Kocha Upper core stratigraphy to, the extraction of material for radiometric dating presented the most suitable methodology from which to obtain an age control. As there was good indication that neither site would pre-date the last glacial maximum (LGM, c. 21,000 cal y BP) due to lake size and elevation, radiocarbon dating ($^{14}$C) was selected. All dates were obtained via the Radiocarbon Facility (Environment) administered by the Natural Environment Research Council (NERC). All chemical pre-treatment was conducted at the facility prior to conversion to carbon dioxide and a graphite target, followed by accelerator mass spectrometer (AMS) analysis (http://www.gla.ac.uk/nercrl/). Two rounds of funding were awarded by NERC after peer-reviewed consideration by the NERC Radiocarbon Facility-Steering Committee (RCF-SC), one rangefinder (1287.0408/2008) and one standard 1463.0410/2010) application. Calibrated dates are given in Chapters 4
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and 5 with full radiocarbon analysis results and preparation protocol reported in Appendix A3.1. The extraction methods for each sample type is described below.

Macrofossil plant remains
Following core splitting, any macrofossils visible on the split surface were immediately extracted using forceps and wrapped in foil packages. Samples were then dried at 40°C, weighed and the foil packages were placed within cleaned centrifuge tubes. Samples were sent to the NERC Radiocarbon Facility via overnight courier to keep the length of time and less ideal temperatures to a minimum. The laboratory set up and methods used for radiocarbon sample extraction and storage follows protocols established by the Quaternary Palaeoenvironments Group (QPG) at the University of Cambridge (http://www.qpg.geog.cam.ac.uk/resources/14cprotocol/) and guidance received from the NERC Radiocarbon Facility (pers. coms. P. Gulliver).

Lake sediments (gyttja)
Where no obvious macrofossils were available bulk sediment samples were taken for analysis. These were extracted using cleaned metal spatulas and placed within foil packages and centrifuge tubes as above. No drying of bulk sediments was conducted as per the guidelines of the analysing laboratory.

Macroscopic charcoal and seed cases
Following the calibration of the rangefinder dates achieved by extraction of the above two sample types, an offset between macrofossil and lake sediment samples became apparent (see Chapter 4 for discussion). With a lack of further macrofossil plant remains to date, refinement of the chronological control was established by the separation of macroscopic charcoal particles (and additionally discovered seed cases) from the lake sediment samples. Large particles of charcoal were extracted due to their relative ease of picking, and that they are considered to become trapped within lake sediments with a few years of the fire event (Whitlock and Larsen, 2001). Sampling depths were chosen based upon the requirement to pinpoint the timings of key environmental changes already highlighted by multi-proxy analysis, but also upon the available abundances of charcoal particles at those depths. Core subsamples (6–10 cm³) were heated in distilled
water for 10 minutes at 50°C, sieved into two size fractions to aid picking (100–179 and >180 μm), and material transferred to a Petri dish. Fine forceps were used to selectively pick particles of charcoal, seed cases and other plant material which were separated into vials and dried at 40°C overnight to establish dry weights. Samples were then transferred to the NERC Radiocarbon Facility as previously described.

3.6) Analysis of geochemical and physical properties

For all elemental, magnetic susceptibility and spectral analysis, subsamples of the sediment cores were taken every 5 cm, dried at 30°C and ground to a fine-grained powder with an agate mortar and pestle.

3.6.1 Magnetic susceptibility

Rationale for use

The content and composition of magnetic minerals in lake sediments varies in association with the processes of weathering and erosion (Nowaczyk, 2001). These processes fluctuate in response to changes in climatic variability and human activity. As a result, determination of the mineral type and concentration offers a potential valuable source of information (Sandgren and Snowball, 2001).

All objects are magnetic and are affected by a magnetic field. Magnetism is based upon the relative mineral composition of the matter, and therefore can be described by magnetic properties (Dearing, 1994). The type of magnetic behaviour of a mineral is defined by the configuration and interactions of electrons, which orbit around the nucleus of an atom whilst individually spinning about their own axes of rotation (Dearing, 1994; Sandgren and Snowball, 2001). Several types of magnetic behaviour exist including ferromagnetism, ferrimagnetism, anti-ferromagnetism, canted anti-ferromagnets, paramagnetism and diamagnetism. The overall magnetic susceptibility of a material is therefore determined by the sum of all these types. Figure 3.11 summarises the distribution of magnetic vectors within some of the types, and a detailed description of each can be found in Sandgren and Snowball (2001), and Dearing (1994).
Magnetic susceptibility is a measure of how readily a material can be magnetised (Thompson and Oldfield, 1986). It is a simple and common method by which the relative changes in the mineral composition of a sediment can be assessed. For instance, clay minerals are paramagnetic and will give higher magnetic susceptibility values than sediments composed of carbonates. The measuring process involves subjecting the sample to a low magnetic field, which in turn induces magnetisation of the sample material. The initial magnetic susceptibility recorded is a factor of the magnetic field externally applied ($H$) and the magnetisation induced in the sample ($M$). It is defined per unit volume of material and is therefore called magnetic volume susceptibility ($\kappa$).

$$\kappa = \frac{M}{H}$$ (3.1)

Logging of magnetic susceptibility offers a valuable source of information that can be applied to almost any environmental research, acting as proxy indicator for changes in palaeoenvironmentally controlled depositional processes (Blum, 1997; Dearing, 1994). It is a non-destructive and fast process that is applied routinely to the majority of marine and lacustrine sediment cores, often at sufficiently high resolution to enable core-to-core correlation. Modern magnetic susceptibility measuring systems are capable of analysing sediment via a variety of different methods and can be performed on sealed cores, split
core sections or on discrete subsamples using the sensor designed for each purpose. Interchangeable sensors are available and should be selected based upon the material to be examined and the limitations of each sensor. One such popular system is the Bartington MS2 (Figure 3.12).

![Sketch of the Bartington MS2 Susceptibility System](image)

**Figure 3.12** Sketch of the Bartington MS2 Susceptibility System showing several of the interchangeable sensors available, including the MS2B used in this study. It should be noted than only one sensor can be attached at any one time. Diagram redrawn and modified from Nowaczyk (2001). For a full list of sensor types and uses see Dearing (1994).

**Methodology**

All magnetic susceptibility readings were established using a Bartington MS2 Susceptibility System (Figure 3.12). Due to the sediment cores being contained within aluminium tubes, which upon investigation proved to be non-uniform in magnetic mineral composition, magnetic susceptibility measurements were performed on discrete subsamples of each core using the Dual Frequency Sensor (MS2B). The discrete subsampling method is the only methodology that allows for samples near the sediment/water interface to be measured. These samples have very high water contents and so typically do not remain contained during the long core procedure. Instead samples of this nature are obtained separately using a short core and are extruded into samples bags in the field (Sections 3.2.3 and Figure 3.1).
Analysis was conducted on a working surface made from stacked plastic crates positioned in the centre of large laboratory away from metallic objects. The laboratory’s relatively cool and constant temperature also made it a preferred location. Before measurements began, the Bartington sensor system was switched on to equilibrate and all samples were allowed to adjust to room temperature (~30 minutes). Height adjustment of the platform within the MS2B sensor, as detailed by Dearing (1994), was made using a homogenous mixture of sand to locate the point where the highest reading was obtained.

Following the protocol established by Dearing (1994), measurement was conducted continuously on all samples in one session. On continuous sampling mode, readings are displayed every ~10 seconds. For each sample two measurements were taken, between background (air) measurements, with missed/void readings occurring with sample insertion and removal (Figure 3.13). Readings were obtained from the MS2 control unit display set to standard international (SI) with a scale of $10^{-5}$. A range multiplier of 0.1 was determined with the MS2B sensor set to the high frequency (HF) range.

![Figure 3.13](image-url) Simplified measurement procedure using the Bartington MS2 Susceptibility System with the Dual Frequency Sensor (MS2B).
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Initial magnetic susceptibility is defined per unit material and is called volume susceptibility ($\kappa$). Readings were then corrected first for drift in the background (air) reading (Equation 3.2), and then for variation in mass differences and a mass specific susceptibility value ($\chi$) determined (Equation 3.3). No correction for water content was required as the samples were dried prior to analysis.

\[
\kappa_{\text{corrected}} = \text{sample } \kappa - [(\text{first air } \kappa + \text{second air } \kappa)/2] \tag{3.2}
\]

\[
\chi = \kappa_{\text{corrected}} / \text{dry sample weight} \tag{3.3}
\]

Limitations

The majority of limitations associated with recording magnetic susceptibility are connected with the sensor type and measurement protocol used. Nowaczyk (2001) demonstrated the physical limitation of several of the Bartington MS2 sensors and concluded that while the highest sampling resolution can be attained by the logging of a split core, measurements of discrete samples provide the greatest amplitude resolution. Many issues can also be minimised if well tested protocols are followed. Of particular importance is temperature stability during measurement and the need for standard sampling procedure/size. When attempts are made to quantify the results in terms of mineral composition determination, calibration issues increase substantially. In this study magnetic susceptibility is only used on a lake basin specific basis to examine changes identified within each core and measurements are only used in a qualitative sense.

Magnetic susceptibility remains a quick, inexpensive and non-destructive method by which to compliment the multi-proxy study of lake sediments. As a result it often provides the first data obtained from a new sediment core and can inform the researcher on overlapping core correlation, atypical depositional rates and gaps in accumulation (Thompson et al., 1975). However, there are situations where variations in magnetism of sediments may be influenced by diagenetic effects which need to be considered during any interpretation (Oldfield, 1991).
3.6.2 Spectral / Colour

Rationale for use

Colour logging is considered a useful and descriptive tool for assessing soil and sediment core composition (Rogerson et al., 2006). Today, it is routinely applied during the initial stage of core cataloguing using systems such as the Munsell Soil Color Chart, as demonstrated by this study (Section 3.3). However, this methodology of colour description still remains to some degree subjective and only produces descriptive results of the sedimentology. Digital spectral analysis provides a technique for the quantification of colour variations observed. Like magnetic susceptibility, it offers a rapid, inexpensive and non-destructive approach for logging many types of stratigraphic successions, including geologic strata and lake or marine sediments (Nederbragt and Thurow, 2005; Rogerson et al., 2006). Once complete, results can then often be associated with a range of controls including regularly occurring phenomena (e.g. ENSO), longer-term cyclic events (e.g. Milankovich orbital cycles) or just gradual changes in sediment composition (e.g. deglaciation). In sediment cores, total organic carbon, carbonate, iron and clay content have been found to be some of the possible controls of sediment colour (Nederbragt et al., 2006; Rogerson et al., 2006).

The predominant numerical system used to describe colour is defined by the Comission International de l’Eclairage (CIE) by the L* a* b* system which allows lightness (L*) and chroma (a*, b*) to be quantified. However, the common method by which colour data is collected digitally is by measuring the intensities of the red (R), green (G) and blue (B) colour channels. In the RGB system, values range from 0–255 in each channel with pure white defined as 255,255,255 and black as 0,0,0. The RGB recording method is the most common in digital cameras/scanners and is now one of the primary outputs of image analysis software. From the examination of lake sediment cores, it has also been found that some colour channels exhibit significantly higher variance than the others due to site specific conditions (e.g. Moy et al., 2002). As a result colour channel data can be analysed individually to obtain the maximum amount of information possible.

The most essential part to any image analysis, including colour, is the primary step of image acquisition (Nederbragt and Thurow, 2005; Saarinen and Petterson, 2001). For lake
and marine sediments this is commonly achieved using a multifunction instrument such as Itrax Corescanner system which produces detailed colour images as well as performing simultaneous elemental x-ray fluorescence analysis and magnetic susceptibility. However, as described previously (Section 3.3.2), other methods of obtaining images of a sediment core surfaces exist. Due to the limitations of the core photographing procedure undertaken during this study, and the observation that only small sections of the cores obtained show lamination, image analysis for this study was conducted upon discrete, dried samples of sediment already extracted from the core for the purpose of elemental analysis. This avoided the effects of darkening or glare caused by wet sediments, but at the expense of a higher resolution.

Methodology

Colour properties of discrete samples were analyzed using a Canon LiDE30 flatbed scanner, which uses LED (light emitting diode) illumination. The uniformity of illumination was tested by scanning a sheet of pure white paper and no deviation in colour was found across the scanning surface. Clear sample vials were positioned directly onto the scanning surface and ambient light excluded using a blacked-out box which covered the scanning unit. Each sample was scanned in two different locations on the scanning surface 10 spaces apart (Figure 3.14A and B). Prior to scanning, each sample vial and the glass of scanning surface was cleaned thoroughly to remove any fingerprints, dust or other marks. The sediment in each vial was agitated until the whole of the vial base was uniformly covered in sediment.

Scanning was performed at the highest resolution possible (611 dpi) and imported into Corel Draw Graphic Suite. Files were then saved as a windows bitmap image (.bmp) file to maintain as high resolution as possible (~100 mb per file) and imported into ImageJ. Using the standard tools available in ImageJ, a standard elliptical section from the central portion of each scanned vial was individually selected for analysis, being careful to avoid blemishes on the sample vials or voids were the sediment quantity was low (Figure 3.14C). The area selected on each vial image corresponded to a circular area of ~15 mm in diameter. This resulted in the RGB colour channels recorded being an average of >145,000 individual pixels values. Averaging pixel values from across an area of this size
minimises the effects of any non-uniform colour distribution across the sample. Data was copied into an Excel spreadsheet files for future handling alongside other proxy data.

Figure 3.14 A and B) Scanning procedure layout. C) Screenshot of colour analysis using ImageJ. For each sample, only the central section (as identified by dashed line) is selected for colour analysis.

**Limitations**

As already discussed, the critical requirement, and therefore major limitation, of colour analysis is image acquisition. As a result of the protocol undertaken for this study, the sampling resolution was not high enough to detect any laminations in the core, which requires detailed continuous core photographs. While the photographic procedure outline in Section 3.3, produced results that upon visual inspection appear to accurately represent the core surface, there are several issues with the cores that would severely
impact on the production of a high resolution colour image. Firstly, pooling of water on the surface of the core introduces glare which, while can be reduced by increasing the number of photographs taken, cannot be eliminated completely. Secondly, the smoothness of the surface of the core, due to the sediment composition, was not completely uniform and a greater shadowing effect occurs where the surface is rougher. Also, several sections of the cores display cracking while other sections suffered degrees of sediment slumping. General image analysis techniques and methods of colour quantification are discussed by Saarinen and Petterson (2001) and Francus (2005).

3.6.3 Elemental: carbon, sulphur and nitrogen

Rationale for use

Geochemical analysis is a common procedure performed on many sediment cores, and dependant on the required information, the procedure length and complexity varies. It is a key variable by which lake sediment composition can be defined, and for most studies organic and inorganic carbon abundance determination is sufficient to provide complimentary data for many palaeoecological investigations. The data obtained can provide information on the dominance of different processes; for example, lake productivity, mineral inwash, local vegetation dynamics, glacial re-advances, preservation rates, and temperature and precipitation changes (see Birks and Birks, 2006). However, these interpretations are only readily achieved when the geochemical data are analysed alongside other multi-proxy findings. In most instances, the primary source of lake sediment organic matter is from plants situated in, or in close proximity to, the lake site (Meyers and Teranes, 2001). This understanding has important implications for the interpretation of the spatial scales represented in a sediment core.

Baker et al. (2001) identified calcium carbonate (CaCO₃) as a potential indicator of low lake level as it is affected by both water depth and salinity. Precipitation of CaCO₃ occurs because of decreased solubility with the decreased pressure, decreased partial pressure of CO² (pCO2) and increased temperature, together with an associated salinity increase due low water level. CaCO₃ concentrations have already been used in several Andean environments to indicate periods of reduced lake level (Cross et al., 2000; Hillyer et al., 2009).
The amount or organic and carbonate contents in sediments can be measured via the sequential loss on ignition (LOI), or by the use of geochemical instruments. Heiri et al. (2001) discussed some of the limitations that surround LOI, which predominantly are due to non-standardised laboratory protocols. The main advantages of elemental determinator instruments are that the combustion and measurement of all carbon is ensured due to temperatures in excess of 1350°C, that the protocol is standardised and comparable results between labs, and that the time taken to run samples is minimal due to autoloading devices (Schumacher, 2002). Another advantage of using an elemental analyser to determine sediment carbon content is that the abundances of nitrogen and sulphur can be measured simultaneously. Previously studies have shown that these can be potential palaeoenvironment indicators (e.g. increased evaporation and lake low stand linked to sulphur (Brenner et al., 2002; Fritz and Saros, 2006), and so represent additional information gained at no extra time expense.

Methodology

The abundance (wt%) of total carbon (TC), total inorganic carbon (TIC), sulphur (S) and nitrogen (N) was determined using the in-house LECO CNS-2000 elemental analyzer. Sample runs were achieved using weights of 0.2 g for TC, S and N measurements. For TIC, values 0.15 g were first “ashed” at 450°C to remove all organic carbon and then run as per the TC measurement. Samples are measured only after stability is achieved and the instrument is calibrated using known standards. Intermittent standards measured every 10 samples allows for any long-term drift to be assessed and 80 samples can routinely be measured in one day (Figure 3.15). See Appendix A2.7 for a detailed analytical protocol. Total organic carbon (TOC) and calcium carbonate (CaCO₃), are calculated by the following (Equation 3.4 and 3.5):

\[ \text{TOC} = \text{TC} - \text{TIC} \]  \hspace{1cm} (3.4)

\[ \text{CaCO₃} = \text{TIC} \times 8.33 \]  \hspace{1cm} (3.5)
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Limitations

Ultimately, determination of sediment elemental composition is a productive, yet easily achieved analytical technique. However, as noted by Shuman (2003), despite this simplicity, interpretation can be remarkably complex due to in-lake processes (Birks and Birks, 2006). As previously discussed, the advantages of analysis using instrumentation, such as the LECO determinator, over sequential LOI are significant. However, limitations associated to all sensitive instrumentation are cost (initial set up and ongoing consumables), and that stability must first be achieved prior to analysis. In particular to the LECO analyser, a leak free gas flow must be established otherwise atmospheric gases will increase the values obtained.

2.7) Statistical functions and software packages

A range of software and statistical methods were utilised throughout the course of this study (Table 3.3). Where necessary (i.e. radiocarbon calibration, zonation and ordination), a rational for the choice of method used is provided in the relevant data chapter. In many cases, the choice of software was limited to that currently available at The Open University, and it should be noted that other software packages will provide the necessary functions to the required standard. Discussion of the application of software to data sets and output in this research occurs in Chapters 4–6.
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Table 3.3 Software packages and functions applied in this study.
Chapter 4) Four thousand years of environmental change and human activity in the Cochabamba Basin, Bolivia

In this chapter, all fossil pollen, spore, charcoal, geochemical and geophysical data from the Lake Challacaba study site are presented and discussed. This chapter has been published separately:

Williams, J.J., Gosling, W.D., Coe, A.L., Brooks, S.J. and Gulliver, P. Four thousand years of environmental change and human activity in the Cochabamba Basin, Bolivia. Quaternary Research (Online) DOI: 10.1016/j.yqres.2011.03.004

4.1) Abstract

The Cochabamba Basin (Bolivia) is on the ancient road network connecting Andean and lowland areas. Little is known about the longevity of this trade route or how people responded to past environmental changes. The eastern end of the Cochabamba valley system constricts at the Vacas Lake District, constraining the road network and providing an ideal location in which to examine past human–environmental interactions. Multi-proxy analysis of sediment from Lake Challacaba has allowed a c. 4000 year environmental history to be reconstructed. Fluctuations in drought tolerant pollen taxa and calcium carbonate indicate two periods of reduced moisture availability (c. 4000–3370 and c. 2190–1020 cal yr BP) compared to adjacent wetter episodes (c. 3370–2190 and c. 1020 cal yr BP-present). The moisture fluctuations broadly correlate to El Niño/Southern Oscillation variations reported elsewhere. High charcoal abundance from c. 4000 to 2000 years ago indicates continuous use of the ancient road network. A decline in charcoal and an increase in dung fungus (Sporormiella) c. 1340–1210 cal yr BP, suggests that cultural changes were a major factor in shaping the modern landscape. Despite undisputable impacts of human populations on the Polylepis woodlands today, we see no evidence of woodland clearance in the Challacaba record.
Chapter 4) Four thousand years of environmental change and human activity

4.2) Introduction

The highly diverse ecosystems of the elevated tropical Andes are vulnerable to change from increasing human occupation of the area and predicted future climate change (Cincotta et al., 2000; Malcolm et al., 2006; Myers et al., 2000). To develop an effective policy to conserve and manage this ecosystem, a robust understanding of the region’s natural history is required (Godwin, 1956; Willis and Birks, 2006). Today, uncultivated sections of the high Central Andes are principally grassland within which are pockets of woodland dominated by the tree genus *Polylepis* (Rosaceae). Kessler (2002) has implied that the relationship between grassland and woodland ecosystems is influenced strongly by human practices and an intensive landuse at high elevations has limited severely *Polylepis* woodland distribution today (Ellenberg, 1958; Fjeldså and Kessler, 1996). However, the nature and degree to which human factors ultimately govern the ecology of this region remains unclear and recent research has highlighted the vulnerability of these Andean woodlands solely to climatic lead changes (Gosling et al., 2009).

The main Cochabamba Basin (eastern Andes, Bolivia; Figure 4.1A) is, today, a major region for food production. The topography favors agriculture because it is: i) on an easily accessible trade route between upland and lowland areas and, ii) provides a flat area of land upon fertile Quaternary deposits, that largely experience a temperate seasonal climate. Limited archaeological evidence from the region suggests a long human history around Cochabamba with agricultural practices from at least 3000 years before the present (cal yr BP) (Hensen, 2002). By the time of the Tiwanaku state (c. 1500–900 cal yr BP), the warm fertile main Cochabamba Valley had become a center for farming, and frontier for trade into the subtropical Mizque Valley (Higueras, 1996; Janusek, 2008).

The collapse of the Tiwanaku state, around 1000–900 cal yr BP, has been linked to a prolonged drought on the Altiplano as indicated by the low water levels of Lake Titicaca (Abbott et al., 1997; Binford et al., 1997) and an elevated dust signal from the nearby Quelccaya (Peru) ice core record (Thompson et al., 1985). Elsewhere in the eastern Central Andes (*i.e.* Marcacocha), the impacts of human occupation on the landscape, identified from lake sediment records, are correlated to changes in agricultural practices, herbivore domestication and cultural adjustments over the last 4000 years (Chepstow-
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Lusty et al., 1998; 2007). Regardless of whether climatic events were coupled with a social transformation (Janusek, 2008), the transition from Tiwanaku fragmentation and collapse (1000–900 cal yr BP), towards rule by the Inca Empire (c. 650–550 cal yr BP, 1400–1533 AD), is certain to have had major impacts on both societies and the landscapes of the Cochabamba valleys.

In this study, we present a continuous 4000 yr paleolimnological record from the Vacas Lake District in the Cochabamba Basin, using a multi-proxy approach to provide the first submillennial-scale reconstruction of vegetation, fire and cultural change from the Eastern Cordillera of the Bolivian Andes. These data provide new insights into the interaction between climate change, pre-Columbian societies and the environment.

4.2.1) Regional setting
The Vacas Lake District is a system of six lakes located within a cold (7.2–11.3°C), seasonally dry (2.6mm/month June–August, 114mm/month January–March), high elevation valley (Hijmans et al., 2005; Ritter, 2000). The district is situated east of the main Cochabamba Basin and north of the Mizque valley (Figure 4.1). Located within the Inter Andean/Eastern Cordillera forethrust zone (McQuarrie, 2002), the local geology is not known in detail, but the surrounding high ground consists of Ordovician quartzite and sandstone, with the Vacas valley, as with the main Cochabamba Basin, sitting on Quaternary sedimentary deposits (Cassard, 1999). Ritter (2000), has speculated that all six lakes within the Vacas municipality were once a single connected system.

Regional climate, predominantly precipitation, is controlled by a variety of systems including the movement of the Intertropical Convergence Zone (ITCZ) (Leduc et al., 2009), and the variability of the South American summer monsoon (SASM; Zhou and Lau, 1998). However, it is the El Niño-Southern Oscillation (ENSO) that is considered to be the largest source of inter-annual variation (Chiang, 2009; Philander, 1990).

The Vacas Lake District is positioned within the Central Andean Puna ecoregion (Olson et al., 2001), and specifically, within the “northern Puna-semi-humid” and “sub-humid Puna and Punean woodlands of the Tunari” biogeographic regions (Ibisch et al., 2003; Navarro...
and Maldonado, 2002). Vegetation types range from grassland, shrubland and woodland (Navarro and Ferreira, 2007). Important genera of these biogeographic regions, include: *Poa, Festuca, Deyeuxia, Muhlenbergia, Stipa* (Poaceae), *Gomphrena* (Amaranthaceae), *Baccharis* (Asteraceae), *Polylepis* (Rosaceae), *Peperomia* (Piperaceae), *Astragalus* (Fabaceae) and *Puya* (Bromeliaceae) (Navarro and Maldonado, 2002).

Today, the flatter land surrounding the Vacas lakes is dominated by the cultivation of potatoes and other tubers, and has also been heavily impacted by grazing (Gotkowitz, 2007). Further away from most harshly effected lands, and more typical of the Cordillera of Tiraque-Vacas, the landscape consists of *Polylepis* woodland patches within Andean grassland. Studies of *Polylepis besseri* woodlands at Sacha Loma (17°44' S, 65°34' W; 3800m elevation) have provided a detailed inventory of associated species (Fernández, 1997; Fernández, et al., 2001). The most local *Polylepis* woodland patches are located ~5 km away in the mountains to the northeast, and ~10 km to the southwest (Figure 4.1B). Our own observations of a *Polylepis nana* stand by the side of the Arani-Vacas road (17°33.540' S, 65°42.329' W; 3379 m asl), revealed tree heights of 1–1.5 m growing in patches along the edge of a rocky field boundary.

Surveys of the aquatic vegetation at Acerokocha, Juntutuyo, Kollpakocha and Parkokocha lakes (Figure 4.1B), highlighted the presence of *Lemna* (Lemnaceae), *Schoenoplectus* (Cyperaceae), *Myriophyllum* (Haloragaceae) and, *Zannichellia* and *Potamogeton* (Potamogetonaceae) (De la Barra, 2003; Molina et al., 2007). The Vacas lakes are regarded as an important source of water and feed (*Myriophyllum quitense*) for cattle which are driven into the lake during the dry season (Ritter, 2000).

Vacas is only ~15 km away from the well-documented Inca site of Inkallajta. Sánchez (2008) has suggested that the Vacas municipality was significant in regional transport routes (Figure 4.1A). Based upon the historical “high road”, the current road passing through the Vacas lakes was once a principle route linking the main Cochabamba Valley and the fuertes (strongholds) of Inca Rakay in the west, to those in the southeast such as Inkallajta and the Tiwanaku archaeological site of Mizque (Higuera, 1996) (Figure 4.1A). Given the importance of camelid pastoralism and caravans for pre-Columbian peoples
(Lynch, 1983) and the movement of Tiwanaku traders between the main valley and the Mizque enclave (Janusek, 2008), it seems likely that many groups of people would have had direct contact with the Vacas lakes.

Following preliminary investigation, Lake Challacaba was selected as the most suitable of the Vacas lakes for coring based upon its apparent permanence, relative freshwater content, suitable depth and accessibility. Our investigation into Parkokocha concluded that only 2 m of sediment would be recoverable from beneath 1.6–2 m of water, while Acerokocha proved too deep to core with the equipment available. The only previously published investigation recorded that Juntutuyo dried out for prolonged periods prior to 2300 yr BP (Abbott et al., 2003), despite at present having a maximum depth in excess of 3.5 m (Ritter, 2000).
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4.2.2) Study site

Today, Lake Challacaba is a small, \( \sim 1.5 \text{ km}^2 \), freshwater system, 2.5 km from the settlement of Vacas (17°33.257' S, 65°34.024' W; 3400m elevation; Figure 4.1C). Land is worked up to the water's edge with associated small buildings nearer the road (Figure 4.1D). Many of the areas of worked land, especially those on the flatter northern shore, are inundated by water during the wetter months. *Myriophyllum* spp. was the dominant component of the aquatic vegetation.

At the time of coring (June 2007) Challacaba had a maximum water depth of 3 m. It is fed at its northernmost point by a stream from the surrounding mountains and drained via an outflow at the southeast end. Water turbidity was defined by measurement of a secci depth of 0.58 m. A conductivity reading of 332 \( \mu \text{S/cm} \) (microSiemens per cm) and a pH reading of 9.45 were recorded using a Hanna 991300 handheld probe. These reading are the average of three taken on 24th June 2007; no longer term data sets are available.

4.3) Methods

A sediment core of 2.97 m was extracted from the deepest point in Challacaba during the 2007 dry season using a cam-modified Livingstone piston corer (Figure 4.1C; Appendix A1; Plate A1.1). The deepest point was chosen to maximize sediment recovery and reduce the chances of encountering a sediment gap caused by any periods of reduced areal extent of the lake.

Two sediments cores (Challacaba-B and Challacaba-C) were recovered with staggered, overlapping, starting depths below the sediment–water interface (46 cm and 27 cm). The overlap ensured that a continuous record was recovered despite potential loss from some tube ends. Sediment cores were recovered in aluminum tubes (50 mm diameter, 1 m long) and sealed on site. The sediment–water interface and top 60 cm of sediment were recovered using a Perspex surface sample. The surface sampler was extruded in the field and continuous subsamples of 1 cm thickness bagged. All sediment recovered was transferred to The Open University cold store (4°C). The sediment cores were split and then sediment divided using a fine strand of wire held at tension. Once split, sediments
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were immediately digitally photographed and described following the Troels-Smith system (Birks and Birks, 1980) and Munsell Soil Color Charts (2000). See Appendix A1.1 and Table A1.1 and A1.2 for description methodology and key.

A radiocarbon chronological framework was established for Challacaba-B. Three bulk gytta, two macrofossil plant remains, and one set of picked charcoal/seed case fragments were submitted to the NERC Radiocarbon Facility (Environment) where they were processed to graphite. Samples were digested using an acid–alkali–acid pre-treatment (2M HCl, 80°C, 2 hrs; 1M KOH 80°C, 2 hrs; 1M HCl 80°C, 2 hrs) then rinsed free of acid, dried and homogenised. The total carbon in a known weight of the pre-treated sample was recovered as CO$_2$ by heating with CuO in a sealed quartz tube. The gas was converted to graphite by Fe/Zn reduction. Sample graphite’s were analysed using Accelerator Mass Spectrometry (AMS) at the SUERCAMS Facility, East Kilbride. All samples were pre-treated and prepared to CO$_2$ in the same way but SUERC-32100 contained <500 µgC and required AMS analysis at low current (Appendix A3.1).

All radiocarbon dates were calibrated using CALIB 6.0.1 and the SHCal04 Southern Hemisphere data set (McCormac et al., 2004; Stuiver and Reimer, 1993; 2010). Top sediments were assumed to be of modern age (0 yr before present). Radiocarbon samples SUERC-22351, 21929 and 21930 were used to create the age model using the mean value of the largest probability at 2 sigma. Linear interpolations were used between dates and to extrapolate for the basal sediments. The chronology for Challacaba-C core was established by matching sediment units to Challacaba-B.

For physical and chemical analysis, samples were taken every 5 cm, dried for 7 days at 30°C and ground with an agate mortar and pestle. The magnetic susceptibility of each sample was measured using a Bartington Dual Frequency Sensor (MS2B), corrected for mass differences (Section 3.6.1). Color properties were analyzed using a Canon LiDe flatbed scanner and the software ImageJ (Rasband, 1997–2009). Separate readings for red (R), green (G) and blue (B) color intensities were recorded but after analysis, all three showed similar variance so a mean red, green and blue (RGB) value is used in this work (Section 3.6.2). The abundance of total organic carbon (TOC) and calcium carbonate...
(CaCO₃) was determined using a LECO CNS-2000 elemental analyzer (Section 3.6.3; Appendix A2.7).

Cores were subsampled (1 cm³) for pollen and fungal spore analysis and, after spiking with microspheres to allow for concentration calculation, chemical preparation followed standard palynological protocol (Faegri and Iversen, 1989; Appendix A2.4). Samples were mounted in glycerol and pollen was identified using a Nikon Eclipse 50i microscope at ×400 and ×1000 magnification. A minimum of 300 fossil terrestrial pollen grains were analyzed in each sample or, where concentration was extremely low, counting was continued until 3000 microspheres had been recorded. Percentage values for aquatic taxa (Lemnaceae cf. Lemna, Cyperaceae, Isoëtes, Myriophyllum, Typha), the spore group and the green algal genus Pediastrum were calculated relative to the pollen sum and their own abundance. Pollen grains and spores were identified using The Open University pollen reference collection, the Neotropical Pollen Database (Bush and Weng, 2006) and other pollen keys (Hooghiemstra, 1984; Roubik and Moreno, 1991). All pollen and spore types recorded were described and digitally photographed for reference purposes (Appendix A4: Enclosure CD1).

Charcoal analysis was conducted at the same sampling resolution as pollen. Subsamples of 1 cm³ were deflocculated with 10% KOH for 24 hours before being sieved and separated into two size fractions; >180 μm and 100–179 μm (Appendix A2.5). Samples were then suspended in water on a gridded petri dish and counted using a binocular microscope (Olympus SZX12) at ×12.5 to 25 magnifications. A distinction was made between wood and herbaceous fragments based upon appearance. Charcoal is shown as particulates per cm³ (counts/cm³).

All data sets were entered as EXCEL spreadsheet files with necessary conversions accomplished using WinTran V1.4 and diagrams plotted using the program C2 (Juggins, 2002; Juggins, 2003). Pollen zones were determined by optimal sum of squares partitioning (Birks and Gordon, 1985) performed using the software ZONE v. 1.2 (Lotter and Juggins, 1991). Assessment of zonal significance was subsequently completed using the broken-stick model (Bennett, 1996; Birks, 1998) in the software BSTICK v. 1.0 (Line
and Birks, 1996). Non-metric multidimensional scaling (NMDS) was performed in PC-ORD v5.0 (McCune and Mefford, 2006). See Appendix A3.3.4 for the full list of ordination data.

4.4) Results

4.4.1) Chronology

The age–depth model is based on three radiocarbon dates of plant macrofossils or bulk sediment samples (Table 4.1, Figure 4.2). Two bulk sediment and one charcoal/seed case date were not incorporated into the age–depth model based upon the preference for macrofossil dates (leaf/stem) located at the same, or similar, depths. It is likely that a hard-water error and/or mineral carbon error is the cause of the consistently older bulk sediment dates. Mineral carbon error may be further increased due to in-wash of soils from either anthropogenically induced soil erosion or increased precipitation (Grimm et al., 2009; Oldfield, 1978). In addition, the alkalinity of water samples from Challacaba suggests it is rich in bicarbonate ions (Björck and Wohlfarth, 2001). Despite neither macrofossil being formally identified, the leaf remains were almost certainly of a non-submerged origin. Stem remains are likely to be from an emergent or submerged aquatic plant. The most modern bulk gyttia date (770–925 cal yr BP), whilst also possibly older than indicated by the bulk data, is accepted here as no other material for dating was available. It is also likely that any difference between a bulk and macrofossil date at this age would be insignificant and probably within the age uncertainty already established. The large age range of the charcoal/seed cases date, due to the small sample size, allows the date to potentially fit a spectrum of age–depth curves. The age range for the calibrated date does not overlap with our age/depth model. We hypothesize that this offset could be caused by the age of the original wood material prior to burning, at Sacha Loma Polylepis individuals live in excess of 60 years (Gareca, et al., 2010), and/or the retention of the charcoal in the catchment prior to incorporation into the lake sediments.
Figure 4.2 Age-depth curve of sediment cores raised from Challacaba. Rejected $^{14}$C dates shown by open circles. Details of $^{14}$C dates given in Table 4.1.

<table>
<thead>
<tr>
<th>Laboratory code</th>
<th>Depth (cm)</th>
<th>Description</th>
<th>$^{14}$C Age (yr BP ± 1σ)</th>
<th>Cal. Range (cal yr BP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SUERC-22351</td>
<td>91</td>
<td>Bulk sediment</td>
<td>982 ± 37</td>
<td>770–925</td>
</tr>
<tr>
<td>SUERC-21929</td>
<td>197</td>
<td>Leaf macrofossil</td>
<td>2333 ± 37</td>
<td>2155–2270</td>
</tr>
<tr>
<td>SUERC-22352</td>
<td>197</td>
<td>Bulk sediment</td>
<td>2612 ± 35</td>
<td>2490–2643 *</td>
</tr>
<tr>
<td>SUERC-32100</td>
<td>265</td>
<td>Micro-charcoal and seed cases</td>
<td>3640 ± 92</td>
<td>3639–4102 *</td>
</tr>
<tr>
<td>SUERC-21930</td>
<td>284</td>
<td>Stem macrofossil</td>
<td>3611 ± 36</td>
<td>3716–3933</td>
</tr>
<tr>
<td>SUERC-22355</td>
<td>284</td>
<td>Bulk sediment</td>
<td>4471 ± 36</td>
<td>4864–5071 *</td>
</tr>
</tbody>
</table>

Table 4.1 Radiocarbon dates and calibrated ages for Challacaba-B core. Calibration determined using CALIB 5.1 and SHCal04 data set (McCormac et al., 2004; Stuiver and Reimer, 1993; 2010). * = Rejected ages.
4.4.2) Sediments

The 2.97 m core was divided into five sedimentary units (Figure 4.3). The lowest, unit 1, comprises greenish-gray sandy clay (297–290 cm, c. 4070–3940 cal yr BP). This is overlain by, unit 2, (290–230 cm, c. 3940–2800 cal yr BP), which comprises darker-colored gyttjas, with a lower sand content than unit 1 and irregular brownish bands, 1–3 cm thick, with gradational boundaries. The 3rd unit (230–210 cm, c. 2800–2420 cal yr BP) comprises alternating dark and pale colored bands and it has a sharp base and top. Unit 4 comprises mottled sediments progressing from black to gray in color and ending in a moderately sharp boundary at 197 cm (c. 2190 cal yr BP). From 197 cm, up to and including the bagged surface–water interface, the 5th unit comprises sediments which gradually become paler to a medium-gray and contain progressively higher quantities of clays. At 83 to 81 cm (c. 750–770 cal yr BP) there is a horizon comprising mainly microscopic organic fragments.

Inspection of the sediments indicates no significant breaks in deposition since the inception of the lake, c. 4000 cal yr BP. Assuming there are no hiatuses, sediment accumulation rates gradually increase (Figure 4.2) from ~0.05 cm/yr (c. 4070–2210 cal yr BP), to ~0.07 cm/yr (c. 2210–850 cal yr BP) to ~0.11 cm/yr (c. 850 cal yr BP–present). Physical and chemical analysis is sub 100 year and pollen and charcoal sub 200 year resolution.

4.4.3) Physical and chemical properties

Magnetic susceptibility (MS) and RGB color values (Figure 4.3) show similar overall trends. The RGB values shows an overall decrease from the base of the core to 225 cm (c. 2700 cal yr BP). Superimposed on this are small scale variations, with one that is particularly well marked in both the MS and RGB values between 248 and 230 cm (c. 3140–2800 cal yr BP). From 225 to 190 cm (c. 2700–2100 cal yr BP), both data sets show a higher frequency fluctuation and a generally increasing, trend. There is a sharp increase in MS values between 193 and 190 cm (c. 2140–2100 cal yr BP). After reaching their highest values in this interval, both MS and RGB show generally decreasing trends up to 135 cm (c. 1400 cal yr BP) where values are similar to those recorded at 225 cm. From 125 cm (c. 1280 cal yr BP) there is an overall increase to the highest MS values (41 SI units) seen in
the entire core and the highest RGB values (148) since the base of the core. Both MS and RGB value show high frequency and high amplitude variation in parts of this interval. There is a slight decline occurring from 22 cm (c. 200 cal yr BP) into the modern day sediment readings.

Figure 4.3 Physical, chemical properties and lithology of Challacaba sediment cores. White lines represent sample points. $^{14}$C ages shown (●). (Wt% = weight percent. RGB = mean value of red, green and blue color intensities).
Two intervals of high CaCO₃ values are evident (Figure 4.3). These span 290–248 cm (c. 3940–3140 cal yr BP) and 185–125 cm (c. 2040–1280 cal yr BP), and have maximum values of 17.2 and 11.6 wt% respectively. The remaining sediments have fairly constant low values (0.1–0.5 wt%) with the exception of a single reading of 1.4 wt% at 213 cm (c. 2480 cal yr BP). TOC values increase from the base of the core to 278 cm (c. 3710 cal yr BP) where relatively high values (>5 wt%) persist until 103 cm (c. 1000 cal yr BP). This interval of high TOC values is marked with three maxima at 248, 230 and 135 cm (22, 27 and 21 wt% respectively). From 103 cm to the core top, lower values of <5 wt%, are recorded (Figure 4.3).

4.4.4) Pollen, spore and charcoal zone description

Pollen assemblage zonation was completed using the pollen taxa included in the pollen sum, i.e. all terrestrial pollen and excluding aquatics, spores and charcoal values. The genus *Ludwigia* (Onagraceae) was included in the pollen sum and other statistical analysis because it: i) comprises both terrestrial as well as aquatic species (Wagner, 2007), ii) is associated with lake margin habitats (Marchant et al., 2002), and iii) can be a weed in cultivated fields (Wagner, 2007). Broken stick modeling assessment concluded that four Vacas Challacaba pollen (VCC-P) zones were significant; VCC-P1, VCC-P2, VCC-P3 and VCC-P4 (Figure 4.4). In total, 88 different pollen types where identified from 38 families. 37 unknown spore/pollen types were also recorded.

**VCC-P1, 297–260 cm (c. 4070–3370 cal yr BP). 4 samples**

Except for the basal sample (295 cm), which contained only a few spores and damaged grains, fossil pollen concentration is high (c. 370,000–480,000 pollen grains/cm³) (Figure 4.4A). The major constituents of the pollen assemblage throughout this zone are Poaceae (20–30%), Caryophyllaceae (5–10%) and, except for one sample, Chenopodiaceae/Amaranthaceae (Cheno/Ams) (20–30%). Asteraceae, Moraceae/Urticaceae, Bromeliaceae and *Acalypha* increase towards the upper part of this zone. *Polylepis/Acaena* pollen is recorded in this zone and throughout the sedimentary succession at low levels (<7%). *Myriophyllum* (30–60%) and Cyperaceae (<2%) are the only recorded aquatics. There is also one occurrence of the green algal
genus *Pediastrum* (Figure 4.4B). Large (>180 μm) herbaceous charcoal is absent while the other fractions all show increasing trends (Figure 4.4B).

**VCC-P2. 260–197.5 cm (c. 3370–2190 cal yr BP). 8 samples**

This interval is characterized by substantially reduced fossil pollen concentrations (~8000–180,000 pollen grains/cm³) and higher percentage values of Poaceae (40–50%), Moraceae/Urticaceae and *Acalypha* (both 5–15%), although their concentration values remain constant or decrease. There are first occurrences of Piperaceae and Papaveraceae, and values of Cheno/Ams and Caryophyllaceae decreases to <9%. The aquatics *Isoëtes*, Lemnaceae and *Typha* are recorded for the first time, and both the percentage composition and concentration of *Myriophyllum* decreases. Large (>180 μm) herbaceous charcoal is recorded, and whilst rapid fluctuations are shown in the smaller wood fraction (100–180 μm), counts per cm³ remain relatively high (>40) (Figure 4.4B).

**VCC-P3. 197.5–105 cm (c. 2190–1020 cal yr BP). 9 samples**

This zone has high pollen concentrations (~62,000–530,000 pollen grains/cm³) and the percentages of the majority of taxa are similar to zone VCC-P1. The most striking exception to this is the continued presence of Piperaceae, Papaveraceae and *cf. Pfaffia*, which were absent in zone VCC-P1. In addition *Polylepis/Acaena* is present and Juglandaceae pollen is first recorded. From c. 1470 cal yr BP a slight decline in Caryophyllaceae and an increase in *Acalypha* are shown. *Myriophyllum* and Cyperaceae again dominate the aquatic assemblage and from c. 1210 cal yr BP a maxima (80%) in *Pediastrum* occurs. This is accompanied by the first significant amount of spores of the dung fungus *Sporormiella* (Figure 4.4B). Charcoal particles levels are similar to the two previous zones but all size fractions show a well defined and large magnitude decrease trend by c. 1340 cal yr BP.
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### Figure 4.4A

Percentage diagram of pollen sum taxa and total pollen concentration for Challacaba. White lines represent sample points. $^{14}$C ages shown (※).

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Cal yr BP</th>
</tr>
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<tbody>
<tr>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>40</td>
<td>200</td>
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<tr>
<td>80</td>
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<tr>
<td>360</td>
<td>1800</td>
</tr>
<tr>
<td>400</td>
<td>2000</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Pollen Taxa</th>
<th>Depth (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Poaceae</td>
<td>40</td>
</tr>
<tr>
<td>Chenopodiaceae/Amaranthaceae</td>
<td>80</td>
</tr>
<tr>
<td>Canophyllaceae</td>
<td>120</td>
</tr>
<tr>
<td>Asteraceae</td>
<td>160</td>
</tr>
<tr>
<td>Brassicaceae</td>
<td>200</td>
</tr>
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<td>Asteraceae</td>
<td>240</td>
</tr>
<tr>
<td>Apiaceae</td>
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</tr>
<tr>
<td>Fabaceae</td>
<td>320</td>
</tr>
<tr>
<td>Urticaceae</td>
<td>360</td>
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<td>400</td>
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<tr>
<td>Sedumaceae</td>
<td>440</td>
</tr>
<tr>
<td>Compositae</td>
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</tr>
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<td>Cyperaceae</td>
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</tr>
<tr>
<td>Juncaceae</td>
<td>560</td>
</tr>
<tr>
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<td>600</td>
</tr>
<tr>
<td>Juncaceae</td>
<td>640</td>
</tr>
<tr>
<td>Cyperaceae</td>
<td>680</td>
</tr>
<tr>
<td>Juncaceae</td>
<td>720</td>
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</table>

<table>
<thead>
<tr>
<th>Pollen Concentration</th>
<th>Depth (cm)</th>
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<tbody>
<tr>
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</tr>
<tr>
<td>40</td>
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<td>360</td>
<td>1800</td>
</tr>
<tr>
<td>400</td>
<td>2000</td>
</tr>
</tbody>
</table>

(note different scales)
Figure 4.4B) Percentage diagram of aquatic taxa, spores and algae for Challacaba. Carbon particulates shown in counts per cm$^3$. White lines represent sample points. $^{14}$C ages shown (\*).
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**VCC-P4. 105–0 cm (c. 1020–0 cal yr BP). 12 samples**

Characterized by the appearance and significant percentage of the wetland associated genus *Ludwigia*, this zone represents the period of lowest fossil pollen concentration (~4000–90,000 pollen grains/cm$^3$). Caryophyllaceae percentages are substantially reduced (<3%), and *Alnus, Hedyosmum, cf. Pfaffia, Brassicaceae* and *Asteraceae* reach previously unattained high levels. Whilst Cheno/Ams percentages are reduced a slight increase (3–6%) is recorded between 77 and 50 cm. *Polylepis/Acaena* reaches its highest percentage in this zone, up to 3–6%, but show large fluctuations. As in zone VCC-P3, *Myriophyllum* percentage is generally low until 20 cm (c. 190 cal yr BP). Lemnaceae (0–2%) and *Typha* (0–40%) abundances fluctuate throughout VCC-P4, while *Cyperaceae* maintains the high levels from the previous zone (VCC-P3) before showing a decreasing trend from c. 560 cal yr BP till the modern day. *Sporormiella* is present throughout this zone but does show a decreasing trend from c. 190 cal yr BP. *Pediastrum* is present at mid to low values in 5 sample depths. A large scale reduction of all charcoal fractions is evidenced throughout this zone (Figure 4.4B).

**Ordination**

NMDS ordination was run to explore trends within the variability of the pollen sum data. NMDS was preferred as it makes no assumption as to the distribution of the variables (McCune and Mefford, 2006). The ordination was run using the pollen sum taxa with rare types (<3% abundance) removed. A 3-dimensional solution was then chosen with distance relationships established using Sorensen’s index (Bray–Curtis). Final stress levels stabilized at 9.06% after 109 iterations. After examination of the output data, axis 1 and 2 scores are plotted against time (Figure 4.5B). The biggest changes occur during the transitions from VCC-P2 to P1 and VCC-P4 to P3. The ordination plot (Figure 4.5A) demonstrates how samples from different zones plot in distinctly different spaces. The most spatially separate sample relates to the very base of the core (295 cm) which has high values in both axis one and two. The rate of change (Figure 4.5B) is calculated as the Euclidean distance between two adjacent samples, divided by the time between them (see Urrego et al., 2009). While this ordination can provide us with a rudimentary rate of change (RoC), a more robust chronology would be required to refine this sufficiently and make it comparable to other studies.
Figure 4.5 Results of NMDS of pollen sum taxa for Lake Challacaba. A) Ordination plot of sample scores for Axis 1 and 2. Point symbols refer to relevant attributed zone. B) Axis 1 (solid line) and Axis 2 (dashed line) scores (left graph), and rate of change (right graph) both plotted against time.

4.5) Environmental reconstruction and discussion
4.5.1) Late Holocene climatic changes: moisture balance fluctuations

The Challacaba lake formed at c. 4070 cal yr BP as shown by the deposition of lake sediments on top of what is interpreted to have been windblown deposits. The very basal sample (295 cm) attests to this period of lake formation as pollen grain concentration is low and preservation poor. Spores, which are more robust to the affects of oxidation, dominate (Figure 4.4B). The basal sample at 295 cm, plots in a unique space on the NMDS ordination (Figure 4.5A), indicating its general dissimilarity to all other samples.

The relatively higher quantity of sand present in the sediment from 297 to 290 cm (c. 4070–3940 cal yr BP) (Figure 4.3), supports the pollen and spore data and suggests a shallow, ephemeral lake. The transition from sandy silt to gyttja deposits, sometime before 3820 cal yr BP, indicates the point at which the basin center became more or less continually inundated. The presence of a permanent water body resulted in improved microfossil preservation and deposition of a local to regional scale pollen assemblage. The multi-proxy analysis of the sediment cores, indicates two periods of reduced moisture
availability (pollen zones VCC-P1 and VCC-P3) and two adjacent wetter episodes (VCC-P2 and VCC-P4).

After the (c. 250 yr) period of lake stabilization, high abundances of drought-tolerant vegetation (Caryophyllaceae, Chenopodiacae and Bromeliaceae) (VCC-P1; Figure 4.4A), are evident. CaCO$_3$ has been shown in other Andean records to be an indicator of dry events and lowered lake levels (Baker et al., 2001; Hillyer et al., 2009). High CaCO$_3$ values (up to 17.2 wt%) (Figure 4.3) at Challacaba during VCC-P1 are therefore interpreted here to indicate that the lake was not overflowing and that water level was lower than today. Although zone VCC-P1 is considered a period of reduced moisture availability compared to other periods of the Challacaba record, the zone does represent a reduction in drought events which dominated the mid-Holocene dry phase between c. 8000 and 5000 years ago.

The VCC-P1 period reconstructed from Challacaba supports the water level history reported from Lake Titicaca (~370 km north-east). Abbott et al. (1997), indicate a regional climate influence and suggest lake levels were at their lowest prior to 3500 cal yr BP, and that the mid-Holocene dry phase ended abruptly between 3500 and 3350 cal yr BP. Challacaba seems to have undergone a more gradual transition out of the mid-Holocene dry phase, but it is considered likely that Challacaba lake formation is linked to this wide, regionally recognized, moisture signal. In the Eastern Andes, other sediment records also attest to the presence of the mid-Holocene dry phase, either by lowered lake levels (e.g. Lake Consuelo; Urrego et al., 2010) or post event lake formation (e.g. Marcacocha; Chepstow-Lusty et al., 1998).

The increase in regional moisture, which led to the inundation of the Challacaba lake basin could have been caused by a resumption of more “normal” (less declined) ENSO activity following the “weak” El Niño regime that it has been suggested dominated during the mid-Holocene period, 8–5.6 ka (Rein et al., 2005). The timing of formation of Challacaba does not concur with that of nearby Juntutuyo (Abbott et al., 2003), which shows lake development some c. 1500 years later. This may be a result of Challacaba being fed, in part, from the surrounding hills to the east and/or that the Juntutuyo core
record of CaCO₃ was not taken from the deepest part of the lake (Abbott, M., personal communication, 2010). There is no evidence to suggest that a local tectonic change created a depression in which Challacaba formed.

The initial phase at Challacaba (VCC-P1) persisted until a change some time between 3460 and 3270 cal yr BP where arid and salt tolerant vegetation, particularly Cheno/Ams, begin to decline, CaCO₃ wt% decreases and TOC begins to increase. The ordination of samples from the first wetter phase, VCC-P2, shows a distinct clustering with negative scores in both axis 1 and 2 (Figure 4.5A). A marked decrease in fossil pollen concentration throughout VCC-P2 is here interpreted to show an increased areal extent and deepening of the lake and thus a dilution of the pollen input. This conclusion is supported by the decreased percentage of *Myriophyllum*, a genus which has been observed to predominate in shallow waters, 0.4–4 m (Ybert, 1992), as it becomes further removed from the core location at the lake depth maxima. The shift towards a wetter interval again correlates well to an increase in ENSO variability recorded at Laguna Pallcacocha in southern Ecuador sometime from 3500 to 3400 cal yr BP (Moy et al., 2002).

From c. 2190 to 1020 cal yr BP (VCC-P3) a shift in the NMDS ordination (Figure 4.5A) highlights a change in the pollen data which, in our interpretation, suggests a return to conditions of reduced moisture; this is particularly well demonstrated by an increase in Caryophyllaceae (10–19%), which favors dry conditions. In addition Cheno/Ams and Bromeliaceae percentages increase as does the total pollen concentration (Figure 4.4A). While the vegetation does share many similarities with that immediately after lake formation (VCC-P1), important differences exist, the most noticeable being the continued presence of Piperaceae and the gradual continued increase of Cyperaceae. This second interval of drier conditions, is supported further by significantly higher CaCO₃ concentrations between c. 1970 and 1340 cal yr BP, suggesting a lowered lake level.

From c. 1020 cal yr BP (VCC-P4) a reduction in the abundance of arid and salt tolerant vegetation, together with the much lower concentrations of CaCO₃, we interpret to indicate a return to conditions that, on average, were locally wetter than the previous period (VCC-P3). As in the previously recorded wet period, VCC-P2, *Myriophyllum*
percentage is generally reduced. The very low pollen concentration values are, at least in part, a result of the dilution effect of a larger lake, but it is also possible that this reflects a less productive landscape (i.e. less vegetation cover). We recognize however that short phases of increased aridity, particularly regional scale ones, may have occurred within this period that are not represented in the limnological record either due to their duration or a buffering effect of the locality. Nonetheless, the apparent shift to on average wetter conditions at Challacaba could be related to a more widespread Andean trend of ENSO events as evidenced in the Laguna Pallcacocha record. At Pallcacocha a frequency maximum has been identified at c. 1200 cal yr BP and a general increased number of ENSO events between c. 900 and 300 cal yr BP, albeit punctuated with shorter term reductions and a steadily declining frequency trend. (Moy et al., 2002).

Intriguingly, the pollen spectra recovered from VCC-P4 is markedly different to that of the previous wet interval (VCC-P2). The NMDS ordination (Figure 4.5A), whilst supporting the general conclusion that samples aging from c. 1020 to 0 cal yr BP display a wetter environment signal (more negative values on axis 2), also highlights that from 1030 cal yr BP, the pollen assemblage is distinctive from that of VCC-P2 (less negative values on axis 1). In addition, the maxima in the RoC score that centered around the VCC-P2 to VCC-P1 boundary (c. 1020 cal yr BP) (Figure 4.5B) indicates a major vegetation change in the Challacaba record that we associate here with an adjustment in human activity.

While the Challacaba record supports the conclusion that a period of increased moisture availability existed during the zone VCC-P4, adjusting human impact on the local landscape undoubtedly complicates the signal of moisture fluctuation. With this mind, we interpret the period after c. 1020 cal yr BP, to primarily represent a time of changing, possibly increasing, human impact levels. The site of Marcacocha also points to increasing human activity around this time as indicated by both archaeological and sedimentary records (Chepstow-Lusty et al., 2009). However, the Marcacocha record has been interpreted to indicate a temperature increase from around c. 900 cal yr BP which led to warm and relatively stable conditions, but crucially, without any associated increase in precipitation (Chepstow-Lusty et al., 2009). While we are unable to speculate if warmer conditions might also have begun at Challacaba around this time, due to the lack of an
independent temperature proxy, we interpret the combined data sets here to indicate a general increase in the moisture availability, which could be linked to either changes in temperature, precipitation or both.

4.5.2) Changing human activity

The high level of charcoal from the start of the Challacaba record (> 50 particulates / cm³) probably indicates that people have utilized this area continually from at least c. 4000 cal yr BP (Figure 4.4B). The high abundance of large woody charcoal fragments and low levels of woodland pollen taxa between c. 4030 and 1090 cal yr BP suggests that people were possibly transporting fuel wood collected elsewhere to burn close to the lake. The earliest indicator of trading and pastoralism is recorded by a marked rise in fungal dung spores, and tentatively algal remains c. 1280 cal yr BP (Figure 4.4B). As neither of these biological groups were included within the pollen sum, they have no influence upon the statistical zonation or the NDMS ordination.

The first significant occurrence (>2%) of Sporormiella fungal spores in the core occurs at c. 1340-1210 cal yr BP (Figure 4.4B). Sporormiella is a coprophilous ascomycete fungus common on the dung of herbivores (Ahmed and Cain, 1972). Recent work on modern lakes acknowledged Sporormiella as a useful proxy to indicate herbivore presence, but highlighted a strong positive relationship between proximity to shoreline and Sporormiella abundance (Raper and Bush, 2009). However, in the case of Challacaba, the Sporormiella increase coincides with a transition from drier to wetter conditions as attested to by both the terrestrial palynological and the geochemical data indicating that the lake shoreline became further away from the coring site. We can therefore be confident in the assessment that herbivore presence around Challacaba substantially increased between c. 1340 and 1210 cal yr BP. The increase in Sporormiella is concurrent with the oribatid mite record from Marcacocha, which shows a progressive increase in livestock number, from c. 1200 cal yr BP (Chepstow-Lusty et al., 2007).

Challacaba is the freshest lake in the Vacas Lake District and is located close to a narrowing of the valley which constrains the historic road running east to Inkallajta (Figure 4.1A). It therefore seems likely that any pre-Columbian increase in dung
deposition surrounding the lake would have been due to an increase in domesticated camelids (alpaca and llama herds) being watered at the lake whilst being driven along the road. The tendency of camelids to defecate in restricted communal piles, often close to a water source (Sillar, 2000) adds weight to this interpretation. While the primary rise in camelid numbers, inferred from the increased abundance of *Sporormiella*, coincides with archaeological evidence indicating Tiwanaku cultivation expansion between 1200 and 1000 years ago, it is possible that a second increase in *Sporormiella* seen in the Challacaba record (c. 920 cal yr BP) is related to Tiwanaku fragmentation. The abandonment of urban centres around Lake Titicaca is evidenced by a silence in monument construction between c. 800 and 500 years ago, which may represent a dispersal of people into new, more rural, lands (Albarracin-Jordan, 1992; Binford et al., 1997; Kolata, 1993).

Two multi-centennial dry events (c. 1410–1190 and 850–550 years ago) that have been associated with the collapse of Tiwanaku (Binford et al., 1997) do not appear to have had as much a dramatic impact on the terrestrial vegetation or the human impact levels around Challacaba (Figure 4.4A). Given the current chronology available it is difficult to tie the Challacaba record to these rapid fluctuations; however the Challacaba record does hint at responses that are roughly concurrent with this dry-wet-dry oscillation noted around Lake Titicaca: i) the decrease in CaCO₃ in Challacaba at c. 1270 cal yr BP coincides with the end of the first of these dry episodes (Figure 4.3), ii) the peak in *Pediastrum* (c. 1210–920 cal yr BP) straddles the intervening wet period (Figure 4.4B), iii) the peak in *Typha* (c. 850 cal yr BP) coincides with the onset of the second dry period (Figure 4.4B), and iv) drought tolerant Cheno/Ams values are slightly elevated (c. 720–470 cal yr BP) through the second dry episode (Figure 4.4A). The absence of elevated CaCO₃ during the second dry phase may be due to camelid dung acidifying the lake. The persistence of high *Sporormiella* values through these postulated short-term lake level fluctuations supports the interpretation that the rise in *Sporormiella* is due to a higher numbers of camelids visiting the lake.

Simultaneous with the initial herding increase (c. 1270 cal yr BP) a maximum in the algal genus *Pediastrum* is also detected. This algal peak is interpreted to reflect an adjustment in lake nutrient status. Whilst other studies have interpreted lake eutrophication to be a
result of increased nutrient in-wash after deforestation (Paduano et al., 2003; Woodward and Shulmeister, 2005), we here suggest that a direct input of nutrients from a local increase of animal activity is responsible. The *Pediastrum* maxima of 88% are simultaneous with the arrival of substantial quantities of camelids for the first time, as indicated by the abundance of *Sporormiella* spores. Two later increases in *Sporormiella* (c. 920 and 560 cal yr BP) also correlate to *Pediastrum* blooms, albeit ones of lower magnitude.

The large increase in *Ludwigia* marks the transition from zone VCC-P3 to VCC-P4. *Ludwigia*, as discussed previously, is a genus generally associated with wetland habitats (Marchant et al., 2002). The increased abundance of *Ludwigia* is contemporaneous with the reduction in arid and salt tolerant taxa and we interpret the pollen record from c. 1020 cal yr BP to represent vegetation composition typical of an increased marshy habitat, created as the lake level rose and water inundated the flat expanse of the north and east shores.

The sudden increase of *Ludwigia* at this time and lack of a similar abundance during the early wetter phase (VCC-P2) may be linked to human influence. The arrival of increased camelid numbers and thus nutrient input, together with increased grazing on existing moist vegetation (aquatics), may have led to the creation of a niche space suitable for *Ludwigia* to exploit. *Ludwigia* is an invasive species and it is plausible that its arrival in the Challacaba region is related to the transport of *Ludwigia* seeds by camelids from wetlands they have previously visited. The sporadic increase in *Typha*, that is seen through zone VCC-P4, could also indicates a response to changing nutrient status through this time (Marchant et al., 2002).

4.5.3) Fire history

There appears to be no connection between the fire history and the wider vegetation signal at Challacaba and we attribute the majority of carbon particulates throughout the last 4000 cal yr BP to be from local anthropogenic sources (fuelwood for cooking, heating and possibly some clearance burning). The main shift occurs from c. 1340 cal yr BP when all size fractions show a dramatic decreasing trend and by c. 1020 cal yr BP, the start of
VCC-P4, particulate counts are consistently under 20 per cm$^3$ (Figure 4.4B). A similar scale decrease was found in the Titicaca record (Lago Grande), as particulates declined and ultimately disappear after 2 ka (Paduano et al., 2003). Paduano et al. associated the decline in charcoal at Titicaca with a reduced availability of fuelwood, as supported by a concomitant woodland pollen decrease. At Challacaba there is no palynological evidence for decreased woodland cover instead the decline in charcoal abundance is coincident with the rise in camelid dung fungus.

In many rural Andean regions today dried cattle dung acts as a main energy source and in Bolivia it accounts for 19% of total biofuel (Winterhalder et al., 1974; World Bank, 1994; Yevich and Logan, 2003). Since wood has been a scarce resource in these environments for a considerable time, including Tiwanaku times, camelid dung has long provided an alternative fuel for fires (Janusek, 2008). While traditionally the importance of dung burning may have its origins in pottery firing, its long term historical use suggests that during times of increase camelid numbers, dung supply would have been greatly increased and so would its utilization in a much wider context (Sillar, 2000). It therefore seems plausible that between c. 1340 and 1020 cal yr BP the people travelling through the Vacas region switched from collecting, or possibly travelling with or trading fuelwood, to the utilization of dried dung.

4.5.4) The *Polylepis* woodland / grassland matrix

Through the duration of Challacaba record, except for two samples (basal and 2190 cal yr BP), *Polylepis/Acaena* pollen has low abundances (0.2–6.6%). It is assumed that the pollen recorded here is predominantly from the tree genus *Polylepis* rather than *Acaena*; the latter is a herb genus associated closely to moist valleys, typically within cloud forests (Chepstow-Lusty et al., 2005; Weng et al., 2006).

As discussed in Section 1.1.2, some modern ecological data suggest that today the high Andean *Polylepis* woodland only covers around 10% of its potential distribution (Fjeldså and Kessler, 1996). However, the fossil pollen record from Challacaba shows no evidence for a reduction in *Polylepis* woodland cover around Vacas during the last 4000 yr. The continually low abundance at Challacaba is contrary to the decline in *Polylepis* pollen at c.
3100 cal yr BP evident from Lake Titicaca (Paduano et al., 2003) but parallels the c. 4000 yr record from Marcacocha (Peru) (Chepstow-Lusty et al., 1998).

The regionally variable pattern of the past *Polylepis* woodland extent emphasizes uncertainty in the assumption that the natural state of the Andes is a continuous belt of a permanent *Polylepis* woodland (*sensu* Ellenberg, 1958), and supports the case for persistent regional variability defined by microclimate conditions (Gosling et al., 2009). Given the long history of human occupation of the Andes it is possible that woodland clearance was completed prior to the formation of the Challacaba record (pre c. 4000 cal yr BP), or that the *Polylepis* forests never recovered after the mid-Holocene dry period, as around this time major human impact (agriculture) in the Andes began. However, the vegetation reconstruction presented here shows only minor fluctuation in the grass to *Polylepis* woodland matrix through the period of major regional pre-Columbian cultural expansion and contraction.

The conclusion of late Holocene *Polylepis* woodland stability is supported by Lake Pacucha pollen record in the central Peruvian Andes, which represents a site for continuous human occupation for at least the last 4000 years (Valencia et al., 2010). At Pacucha there is no evidence for *Polylepis* woodland reduction in response to human activity. The *Polylepis* woodland was most abundant during deglaciation (c. 16000–14000 cal yr BP), which parallels new findings from the pollen record of Laguna Khomer Kocha Upper (17°16' S, 65°43' W; 4153m elevation), situated 40 km north-west of Challacaba (Chapter 5).

### 4.6) Conclusions

The complete paleolimnological history of Lake Challacaba reveals that vegetation change in the Cochabamba Basin, Bolivia, has been driven by both human and climatic factors during the last 4000 years. Two distinct drier than modern stages; before c. 3370 and 2190–1020 cal yr BP are recorded. The older dry event can be linked to the latter stages of lower regional moisture availability caused by the "weak" El Niño system that dominated during the mid-Holocene (Rein et al., 2005). The second drier interval, whilst
likely to be again related to a regional ENSO signal, is less clearly correlated with other records. Between the Challacaba dry phases there was an interval of increased moisture availability (c. 3370–2190 cal yr BP).

Although the pollen data from Challacaba may suggest a shift to generally wetter conditions from c. 1020 cal yr BP, it is likely that shorter term reductions in the moisture balance occurred throughout. Ultimately however, there is strong evidence to show that a change in human activity at some point between c. 1340 and 1210 cal yr BP was a major factor in shaping the modern regional landscape. The pollen assemblage from the last 1000 years is very different to that from any other time during the preceding 3000 years. The charcoal record indicates that the local ecosystem has been under anthropogenic influence for the duration of the time spanned by the Challacaba core (c. 4000 yrs). As such we are unable obtain a baseline record for what is the natural state of the ecosystem without human influence, but, it is evident that overall the Polylepis woodland maintained a relatively stable presence and abundance even during the height of human pressure.

This research supports the interpretation that the Vacas Lake District was an important point on the ancient roadway network during pre-Columbian times. Further work is required to clarify the extent to which the observed changes in human activity are a product of unconnected wider social changes or a smaller scale local impacts. In particular, refining the chronology of the sequence will help to better constrain the timings of significant environmental changes observed within the record and this will be critical if they are to be linked to any known cultural events.

4.7) Acknowledgements

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Chapter 5) The sensitivity of eastern Andean vegetation to climate and fire

In this chapter, all fossil pollen, spore, charcoal, geochemical and geophysical data from the Laguna Khomer Kotcha Upper study site are presented and discussed. This chapter has been submitted for publication separately:


5.1) Abstract

A c. 18 ka cal BP long sediment record from Laguna Khomer Kocha Upper (4153 m asl), Bolivia, shows that fire regime, governed by climatic variation, has long been a transformative agent in the eastern Andes. Before c. 14.5 ka cal BP, warming and relatively moist conditions free from fire, facilitated the expansion of high Andean *Polylepis* woodland. Fire onset at c. 14.5 ka cal BP, quickly transformed the local vegetation and the woodlands became restricted to areas protected from fire. A major increase in burning at c. 10.1–6.4 ka cal BP removed *Polylepis* woodland locally and this is correlated with a region-wide Holocene dry event (HDE) which caused falling lake levels and allowed fire intensification. A decline in burning at c. 6.4 ka cal BP and an increase in marsh-woodland (*Alnus*) marks the termination of the HDE and the return to wetter conditions. As well as recording the environmental history of local vegetation dynamics, long-distance pollen transport provides evidence of changes in the montane forests, highlighting their sensitivity to climate and burning regimes. Simultaneous adjustments in both Andean and lowland taxa suggests that vegetation dynamics in the two environments are linked to a common climatic driver. There is no evidence to indicate that human activity had any impact on the local landscape.
5.2) Introduction

Worldwide, mountainous regions provide early warning for changes in environmental processes and climate change (Ørbæk et al., 2004; Tiberti et al., 2010). In the Tropical Andes, one of the richest and most biologically diverse regions on Earth (Myers et al., 2000), future climate changes are considered a serious threat to biodiversity (Malcolm et al., 2006). High biodiversity levels are partly attributable to the complex topography and large elevational range (2500-4500 metres above sea level [m asl]) which supports many microclimates. The extreme altitudinal variation means that continuous montane forests can be found within just a few tens of kilometres of grassland and bare rocky peaks (Bush et al., 2007; Young et al., 2002). The narrow vertical species ranges mean that even small variations in temperature or precipitation can result in considerable changes in species distribution. This sensitivity allows the evaluation and monitoring of change, not only of modern floras (e.g. Feeley et al., 2011; Sarmiento et al., 2003) but crucially, via the use of palaeolimnological investigation, of long-term shifts in response to climatic changes in the past (e.g. Bush et al., 2004; Cárdenas et al., 2011).

In the Andes, the climate of the Last Glacial Maximum (LGM; 21 ± 2 thousand years before present [ka cal BP]; Mix et al., 2001) was 7–8°C cooler than today (on the Altiplano) and moisture availability varied regionally (Baker et al., 2003; Cook, 2009; Sylvestre, 2009). Moisture balance fluctuated throughout the deglaciation period and the Holocene (11.7 ka cal BP to present) and there was small-scale variation in temperature (Bush et al., 2005). Although the timings, impacts and mechanisms driving environmental change in the Andes during this period are still debated, the response of the environment to key global events have been determined and include warming during the Bølling-Allerød chronozone (c. 15–14.0 ka cal BP), a cold event during the Younger Dryas chronozone (c. 12.9–11.6 ka cal BP) and a mid-Holocene dry event (MHDE) (c. 8–5 ka cal BP; Rasmussen et al., 2006; Sandweiss et al., 1996; Thompson et al., 1998; Urrego et al., 2009; Zech et al., 2010). Adjustments in climate systems such as the El Niño-Southern Oscillation (ENSO; e.g. Moy et al., 2002), the South American Summer Monsoon (SASM; e.g. Vuille and Werner, 2005), and the Intertropical Convergence Zone (ITCZ; e.g. Leduc et al., 2009) have also been highlighted as important drivers of climatic signatures observed within palaeorecords.
As more records become available, it is apparent that the impact, scale and nature of climate events have been spatially non-uniform across the Tropical Andes (Bush and Gosling, 2011). Local factors, including human occupation, often disguise regional patterns. In addition, the distribution of study locations is unevenly spread and many regions, which are climatically sensitive today, remain unexplored palaeoclimatologically and are unrepresented in regional-scale studies.

The biodiversity of the Tropical Andes is also vulnerable to increasing human occupation (Cincotta et al., 2000). Although human populations have existed in South America since the late Pleistocene (pre 11.7 ka cal BP) (Coltorti et al., 2010; Lynch, 1990; Roosevelt et al., 1996), the extent of human environmental impact is inconclusive and variable (Bush et al., 2008). The early use of fire by humans in the Andes (Ellenberg, 1979) can potentially be traced in palaeoenvironmental record through the examination of fossil charcoal (Whitlock and Larsen, 2001). However, evidence that fire has been a natural component of central Andean ecosystems long before the arrival of humans (Gosling et al., 2009; Hanselman et al., 2011; Paduano et al., 2003), adds complexity in distinguishing a human or natural signal. In addition, the subsequent development of human cultures (e.g. Wari, Tiwanku, Inca) led to changes in resource-use and land-use, and a variation in the human impact on the landscape through time (Chapter 4; Williams et al., 2011).

The period since the LGM is critical for understanding human-climate-ecosystem interactions in the central Tropical Andes because it is: i) when the last major global climatic transition occurred (full glacial to interglacial conditions), and ii) when humans spread throughout South America. As a result, the deglaciation and early Holocene period is the most recent time in which central Tropical Andean ecosystems were not substantially influenced by human practices, but were exposed to natural stress. Understanding long-term ecological shifts in response to past environmental change is fundamental to the development of effective conservation and management policies (Godwin, 1956; Willis and Birks, 2006).
In this study, we present the findings of a new palaeolimnological record from the moist mountain ranges northeast of the Cochabamba Basin, Bolivia (Figure 5.1A). These eastern slopes, where moist air from the Amazon collides with the Andean mountain chain, is one of the most biologically rich areas on Earth (Killeen et al., 2007). However, it is on these flanks above 3500 m asl that climatic models predict some of the greatest environmental changes will occur (4–5°C rise by 2100; Urrutia and Vuille, 2009). The sediment record of Laguna Khomer Kocha Upper, situated 4153 m asl, is ideally placed to provide insights into past environmental change in the complex and sensitive landscapes linking Western Amazonia to the Andean mountain ranges. Multi-proxy analysis (geochemical and physical properties, fossil pollen, spores and charcoal) of lake sediments, at sub-millennial resolution, has allowed the detailed reconstruction of the environment (vegetation, precipitation, temperature and fire) of the eastern Bolivian Andes for the first time.

5.3) Study location

Laguna Khomer Kocha Upper is a small, ~0.007 km$^2$, glacially formed lake with a maximum depth in June 2007 of 3.6 m (17°16.514’ S, 65°43.945’ W; 4153 m asl). Previously unnamed, we refer to the lake as Laguna Khomer Kocha Upper (LKKU), as it is situated <800 m to the west and ~250 m above Laguna Khomer Kocha (~3900 m asl). On the slopes of the Cordillera el Ronco, the lake overlooks the tributaries of the Rio San Mateo, a valley which descends more than 2000 m elevation in less than 10 km (Figure 5.1B). The site is accessed by a track leading from Aguirre to Villa Tunari, which passes along the western limits of Carrasco National Park.

The southwest and southeast sides of LKKU consist of steep, but seemingly stable, slopes dominated by tussock-forming Andean grasses (Figure 5.2A and B). The northwest side is created by a glacial deposit, ~2 m in height, running the length of the lake (~110 m). This moraine separates the lake from an area of flat, waterlogged ground, which probably represents an in-filled lake of similar size to LKKU (Figure 5.1C and 5.2A). The lake is fed by runoff from the surrounding slopes. While LKKU was not overflowing during our visit, an outflow channel to the northeast cuts through a small moraine before descending into a steep, wooded (Polylepis sp.) gully towards Laguna Khomer Kocha (Figure 5.2B). The following lake-water variables were measured in June 2007: turbidity (secci depth) 3.2 m;
Chapter 5) The sensitivity of eastern Andean vegetation to climate and fire

conductivity 28 μS (microSiemens) per cm⁻¹; pH 7.38. All values are means of three readings and no long-term data are available.

The local geology is not known in detail. However, regionally the bedrock consists mainly of sandstones, lutites and quartzitic rocks of Ordovician age (488.3–443.7 Ma), with areas of granite intrusions (Cassard, 1999; Kessler, 2002b). Calcareous rocks have been found between 2000–2200 m asl (Kessler, 2002b). Peaks in the Cordillera el Ronco reach elevations above 4500 m asl but no permanent snow-line was observed in June 2007. Above ~4300 m asl, large proportions of the landscape are dominated by rock exposures and scattered large stone blocks.

As no local meteorological data are available, interpolations of observed data (AD 1950–2000) from closest weather stations provides estimates at sub 1 km resolution (Hijmans et al., 2005). Analysis of the meteorological dataset reveals dry season (June–August) precipitation averages 13 mm month⁻¹ which increases to 138 mm month⁻¹ during the wet season (January–March). Mean temperature varies from 4.5°C to 7.6°C for the wet and dry season respectively. Total annual precipitation was estimated at 772 mm. Kessler (2002b) reports that additional humidity is contributed by the condensation of dew and fog, especially between 1600–3400 m asl. Our own observations at LKKU show that even during the dry season, cloud gradually ascends from the valleys to the northwest, depositing moisture on the sparsely vegetated slopes up to 4200 m asl (Figure 5.2A). Temperature ranges recorded at 3850 and 4050 m asl during September 2003, yielded values of -1.7 to 6.1°C (mean 1.8°C), and -2.3 to 9.5°C (mean 1.7°C) respectively (Hertel et al., 2008). These results indicate a lapse rate of ~4.5°C 1000 m⁻¹, a value similar to those previously calculated elsewhere in the Andes (~6°C 1000 m⁻¹; Baker et al., 2003).
Figure 5.1 Map of the study site, Laguna Khomer Kocha Upper, Bolivia. A) Cochabamba Basin with elevations and study area marked. Modified from (Sánchez C., 2008). Inset map locates Cochabamba Basin within Bolivia and marks location of other records discussed in the text. B) Local features of the Laguna Khomer Kocha area including roads, watercourses and mountain ranges shown. Contour lines at 200 m intervals. C) Khomer Kocha Lagunas (upper and lower). Local terrain, investigated Polylepis woodlands and lake inputs/outflows shown. Contour lines at 20 m intervals.
The lagunas of Khomer Kocha lie in a region of rapid ecosystem changes in association with elevation. With such steep elevation gradients present in the San Mateo Valley, biogeography and vegetation is complex. Based on Bolivian classification, the lakes lie within in the sub-humid Puna and transitional Punean woodlands that split the Puna and Yungas zones along the Cochabamba section of the Eastern Cordillera (Ibisch et al., 2003; Navarro and Ferreira, 2007; Navarro and Maldonado, 2002).

Today the landscape immediately surrounding LKKU is dominated by Andean grassland (Figure 5.2A and B), within which are pockets of woodland dominated by the tree Polylepis (Rosaceae). Kessler (2002a) implied that the relationship between grassland and woodland ecosystems is strongly influenced by human practices and that intensive land-use has severely limited Polylepis woodland distribution today (Ellenberg, 1958; Fjeldså and Kessler, 1996). However, the nature and degree to which humans ultimately govern the ecology of this region remains unclear and recent research has highlighted the vulnerability of these Andean woodlands solely to climatic changes (Gosling et al., 2009).
Today, two *Polylepis* woodland patches are in close proximity to LKKU (Figure 5.1C). One stand, 300 m to the north, was located at the base of an exposed rock face amongst a scree and boulder field. The second was found in the gully below LKKU. Further *Polylepis* woodland patches are also located at 3650 (P. lanata), 3800 and 4050 (P. pepei) m asl (Hertel et al., 2008).

Today there is minimal sign of human impact at LKKU. Examination of the *Polylepis* woodland patches surrounding the lake revealed no indications of exploitation. At lower elevations (<4000 m asl) minimal human impact was also observed, although in August 2003 the grassland around the lower lake showed evidence of recent burning (Hertel et al., 2008; D. Hertel, 2010, pers.coms.). One small rock shelter and seven semi-wild horses were found near the track. The nearest agricultural fields were ~15 km away by road. Although there are remain of Inca sites regionally (e.g. Inkachaca 15 km west, >2000 m lower elevation), there is no direct route to the lake because of the steep topography.

**5.4) Material and methods**

A sedimentary succession 413 cm long was extracted from the deepest point in LKKU during the 2007 dry season using a cam-modified Livingstone piston corer (Colinvaux et al., 1999; Appendix A1; Plate A1.2). The deepest point was chosen to maximize sediment recovery and reduce the chances of encountering a sediment gap caused by any periods of reduced lake area. Two sediment cores (KKU–A and KKU–B) were recovered with staggered, overlapping, starting depths below the sediment-water interface (8 cm and 40 cm). The overlap ensured that a continuous record was recovered despite potential loss from core tube ends. Sediments cores were recovered in aluminium tubes (50 or 38 mm diameter, 1 m long) and sealed on site. Due to the fluid nature of the uppermost sediments, the sediment-water interface could not be recovered. The sediments were flown to the UK and stored at 4°C in The Open University cold store. The cores were split, digitally photographed and described following the Troels-Smith system (Birks and Birks, 1980) and Munsell Soil Colour Charts (2000). See Appendix A1.1 and Table A1.1 and A1.2 for description methodology and key.
The sediment chronology was based on $^{14}$C accelerator mass spectrometry (AMS) dating of three bulk sediment samples and five samples of charcoal fragments. All samples were submitted to NERC Radiocarbon (Environment) and analysed at the SUERC AMS Facility, East Kilbride (see Freeman et al., 2007). Samples were digested using an acid–alkali–acid pre-treatment ($2 \text{ M } \text{HCl}, 80^\circ\text{C}, 2 \text{ h}; 1 \text{ M } \text{KOH} 80^\circ\text{C}, 2 \text{ h}; 1 \text{ M } \text{HCl} 80^\circ\text{C}, 2 \text{ h}$) then rinsed free of acid, dried and homogenised. The total carbon in a known weight of the pre-treated sample was recovered as $\text{CO}_2$ by heating with CuO in a sealed quartz tube. The gas was converted to graphite by Fe/Zn reduction. All samples were pre-treated and prepared to $\text{CO}_2$ in the same way but SUERC-32101 and 32102 contained <500 µgC and required AMS analysis at low current. Radiocarbon dates <11 ka were calibrated using CALIB 6.01 and the SHCal04 Southern Hemisphere data set (McCormac et al., 2004; Stuiver and Reimer, 1993; 2010). Dates >11 ka were calibrated using the Fairbanks Calibration Curve (Fairbanks et al., 2005). Mean age values of the largest probability at 2 sigma were used to create the age model, with linear interpolation between dates and for the top and basal sediments. Cores KKU–A and KKU–B were matched using changes in the sediment units and banding patterns.

For physical and chemical analysis, samples were taken every 5 cm, dried for 7 days at 30°C and ground with an agate mortar and pestle. Colour properties were analyzed using a Canon LiDe flatbed scanner and the software ImageJ (Rasband, 1997-2009). Separate readings for red (R), green (G) and blue (B) colour intensities were recorded but after analysis, all three showed similar variance so a mean red, green and blue (RGB) value was used (Section 3.6.2). Total organic carbon (TOC), calcium carbonate (CaCO$_3$), nitrogen (N) and sulphur (S) were determined using a LECO CNS-2000 elemental analyzer (Section 3.6.3; Appendix A2.7). The magnetic susceptibility (MS) of each sample was measured using a Bartington Dual Frequency Sensor (MS2B), corrected for mass differences (Section 3.6.1).

Cores were subsampled at 1 cm$^3$ for charcoal, pollen and fungal spore analysis at, where possible, identical sampling depths and resolution. For charcoal analysis, samples were deflocculated using 10% potassium hydroxide (KOH) for 24 hours before being sieved and separated into two size fractions >180 µm and 100–179 µm (Appendix A2.5). Samples
were then suspended in water on a gridded petri dish and were counted using a binocular microscope (Olympus SZX12) at ×12.5–25 magnification. Charcoal abundance is represented as particulates cm⁻³.

For pollen and spore analysis, samples were first spiked with microspheres, for concentration calculation, and then prepared using standard methods (Faegri and Iversen, 1989; Appendix A2.4). Samples were mounted in glycerol and pollen was identified using a Nikon Eclipse 50i microscope at ×400–1000 magnification. A minimum of 300 fossil terrestrial pollen grains were analyzed in each sample or, where concentration was extremely low, counting was continued until 3000 microspheres had been recorded i.e. sample concentrations were confirmed to be below 5500 terrestrial pollen grains/cm³ (barren). Percentage values for aquatic taxa, the spores and algae were calculated relative to the pollen sum and their own abundance. Pollen grains and spores were identified using The Open University pollen reference collection, the Neotropical Pollen Database (Bush and Weng, 2006) and pollen keys (Hooghiemstra, 1984; Roubik and Moreno, 1991). All pollen and spore types recorded were described and digitally photographed for reference purposes (Appendix A4: Enclosure CD1). All data sets were entered as EXCEL spreadsheet files and converted using WinTran V1.4. Diagrams were plotted using C2 (Juggins, 2002; Juggins, 2003). Ordination analysis was run in PC-ORD v5.0 (McCune and Mefford, 2006). See Appendix A3.3.4 for the full list of ordination data.

5.5) Results

5.5.1) Chronology and sediment description

Eight ¹⁴C AMS dates have been used to establish the LKKU chronology (Table 5.1). Radiocarbon ages and inspection of the sediments revealed that there were no significant breaks in deposition since the inception of the lake at c. 18 ka cal BP, and that the last c. 950 years (top 47 cm) of sediment had not been recovered. Assuming no hiatuses, the age-depth model (Figure 5.3) suggests accelerated sediment accumulation rates during the early to middle Holocene (c. 10–6.5 ka cal BP).
Table 5.1 Radiocarbon dates and calibrated ages for Laguna Khomer Kocha Upper cores. Calibration determined using CALIB 6.01 and the SHCal04 dataset for dates <11 ka (McCormac et al., 2004; Stuiver and Reimer, 1993; 2010). Dates >11 ka were calibrated using the Fairbanks Calibration Curve (Fairbanks et al., 2005).

<table>
<thead>
<tr>
<th>Laboratory code</th>
<th>Depth (cm)</th>
<th>Description</th>
<th>$^{14}$C Age (yr BP ± 1σ)</th>
<th>Cal. Range (cal yr BP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SUERC-22356</td>
<td>61.5</td>
<td>Bulk sediment</td>
<td>1359 ± 37</td>
<td>1148 - 1300</td>
</tr>
<tr>
<td>SUERC-32101</td>
<td>123</td>
<td>Charcoal fragments</td>
<td>3123 ± 89</td>
<td>2998 - 3461</td>
</tr>
<tr>
<td>SUERC-31725</td>
<td>210</td>
<td>Charcoal fragments</td>
<td>5910 ± 38</td>
<td>6545 - 6783</td>
</tr>
<tr>
<td>SUERC-31726</td>
<td>263</td>
<td>Charcoal fragments</td>
<td>6190 ± 38</td>
<td>6906 - 7162</td>
</tr>
<tr>
<td>SUERC-22357</td>
<td>321</td>
<td>Bulk sediment</td>
<td>8086 ± 41</td>
<td>8661 - 9029</td>
</tr>
<tr>
<td>SUERC-31727</td>
<td>358</td>
<td>Charcoal fragments</td>
<td>8400 ± 40</td>
<td>9149 - 9479</td>
</tr>
<tr>
<td>SUERC-32102</td>
<td>385</td>
<td>Charcoal fragments</td>
<td>8727 ± 125</td>
<td>9472 - 10153</td>
</tr>
<tr>
<td>SUERC-22358</td>
<td>445.5</td>
<td>Bulk sediment</td>
<td>14112 ± 61</td>
<td>16363 - 16645</td>
</tr>
</tbody>
</table>

The 413 cm core was divided into seven basic sedimentary units (Figure 5.3). Unit 1 comprises greenish-gray clays (460–455.5 cm, c. 18.1–17.6 ka cal BP). Unit 2, (455.5–449.5 cm, c. 17.6–16.9 ka cal BP) consists of light brown very coarse sandy sediment. Unit 3 (449.5–360 cm, c. 16.9–9.4 ka cal BP) comprises pale strongly banded sandy deposits between gyttjas. The bands are up to 1 cm with gradual to sharp boundaries. Banding becomes less prominent and gyttjas darker brown in colour towards the upper boundary of this zone as the quantities of sandy material reduces. Unit 4 (360–219 cm, c. 9.4–6.7 ka cal BP) comprises dark brown gyttjas with a jelly-like consistency. Unit 5 (219–133 cm, c. 6.7–3.6 ka cal BP), contains dark grey gyttjas with some frequent, broad (1–2 cm) bands of darker gyttjas with gradational boundaries. In unit 6, 133–77 cm, (c. 3.6–1.7 ka cal BP) banding is reduced and the sediments return to dark brown gyttjas similar to that of unit 4. The uppermost unit, 7, begins at 77 cm (c. 1.7 ka cal BP) and consists of very dark brown gyttjas, but with some strong banding evident similar to that of zone 5. The material of this zone is very jelly-like once again. Sediments
upwards of 47 cm below the sediment-water interface were not captured. These sediments were extremely fluid in nature and could not be extracted with the coring apparatus available, despite numerous attempts.

\[
y = 0.0498x - 711.6458
\]

\[
y = 0.0308x + 23.3941
\]

\[
y = 0.0254x + 40.8941
\]

\[
y = 0.1306x - 711.6458
\]

\[
y = 0.0315x + 41.0952
\]

\[
y = 0.0752x - 346.2409
\]

\[
y = 0.0089x + 298.3606
\]

Figure 5.3 Age-depth model, physical and chemical properties and lithology of Laguna Khomme Kocha Upper sediment cores. Details of \(^{14}C\) dates given in Table 1. The sedimentary units are described in main text. Sediments above 47 cm were not retrieved due to their extremely fluid nature. Total organic carbon (TOC) plotted against depth in Figure 5.6. Wt\% = weight percent. RGB = mean value of red, green and blue color intensities. Spectral analysis axis is inverted.

5.5.2) Physical and chemical properties

Spectral properties are often controlled by organic content (Nederbragt et al., 2006), and analysis of the LKKU cores revealed that the RGB colour values and TOC show similar, but opposite overall trends, particularity in the oldest sediments (Figure 5.3). From the base of the core to 298 cm (c. 8.1 ka cal BP), RGB values show an overall decreasing trend (170 to 65) and TOC values gradually increase from 0 to 16 wt\%. Small-scale variations, more pronounced in TOC than RGB, are apparent.

From 298 to 208 cm (c. 8.1–6.6 ka cal BP) RGB values remain low (<75), before generally higher values with increased fluctuation (60–117) are recorded during the last 6 ka years. In the TOC record, values remain generally high from 298 cm, with a mean value of 15
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wt%. Superimposed on this are four maxima in TOC, where values peak at >17 wt% (95, 123, 155 and 188 cm) with a c. 900–1300 year periodicity. The RGB analysis shows the same trends as the TOC data, but the signal is less pronounced. From 2.3 ka cal BP, TOC (and RGB) values show an overall declining (increasing) trend.

CaCO₃, S and N values are low throughout the entire core (<3 wt%, Figure 5.6). Except for the penultimate basal sample (453 cm, c. 7.3 ka cal BP; 134.7 SI units), MS values remain low throughout the core (-8.3 to 9.6, mean of -0.77 SI units). After 207 cm (c. 6.5 ka cal BP) MS decreases slightly (Figure 5.6).

5.5.3) Zonation

With fire thought to be a transformative agent within the ecosystems of the tropical Andes, both as a result of human practices and natural climatic forcing (Bush et al., 2010; Gosling et al., 2009), zones were determined with reference to charcoal abundance. Optimal sum of squares partitioning (Birks and Gordon, 1985) using the software ZONE v. 1.2 (Lotter and Juggins, 1991) was performed on charcoal particulate counts to guide the position of zone boundaries. Four Khormer Kocha Upper fire stratigraphic zones were identified: KKU-F1, KKU-F2, KKU-3 and KKU-F4 (Figure 5.4).

5.5.4) Pollen, spore and charcoal description

KKU-F1. 460–428 cm (18,130–14,541 cal yr BP). 5 charcoal samples, 4 pollen samples.

Zone KKU-F1 is defined by very low total charcoal abundances throughout (<25 particulates cm⁻³; Figure 5.4B). The pollen record (Figure 5.4A) shows Polylepis/Acaena pollen as a major component of the assemblage (up to 10%). The montane forest taxa Podocarpus and Hedyosmum, also reach maximum individual values for the entire record (up to 6% and 8% respectively). Poaceae, although a major component throughout the entire pollen record (>20%), fluctuates between ~30–60%. Excluding the penultimate basal sample, which had very low pollen concentration (1400 grains cm⁻³), other major constituents include Moraceae/Urticaceae undiff. (10–15%), Acalypha (4–14%), Asteraceae (3–9%), Alnus (3–9%) and Celtis (<3–7%). The aquatic taxon Isoëtes shows a significant increasing trend from the oldest sediments, reaching abundances in excess of 40%. Spores are generally high throughout the zone. In particular, samples below 443 cm,
showed significant abundances of monolet (20–10%) and trilete (10%) spores, and the
dung fungus Sporormiella (3%). Fossil pollen concentration is low prior to 16.2 ka cal BP
(<160,000 grains cm⁻³), but subsequently increases to >550,000 grains cm⁻³.

KKU-F2. 428–389.5 cm (14,541–10,166 cal yr BP). 4 charcoal samples, 4 pollen samples.
A marked increase in the abundance of charcoal fragments (65–125 particulates cm⁻³) is
evident throughout KKU-F2 (Figure 5.4B). Polylepis/Acaena and Podocarpus pollen
debutes in abundance by at least half, reaching low values (<1%) at the upper zone
boundary (Figure 5.4A). Poaceae are highly abundant throughout this zone (20–32%).
Cecropia (3–7%) and Trema (2–7%) become important components during KKU-F2, whilst
the abundance of Hedyosmum declines to below 3%. Isoëtes shows increasing, but
fluctuating, abundance (30–65%), peaking at 394 cm (c. 10.7 ka cal BP). Fossil pollen
concentration shows a similar trend to Isoëtes with values between 430,000–1,800,000
grains cm⁻³ (Figure 5.4B).

KKU-F3. 389.5–204 cm (10,166–6415 cal yr BP). 21 charcoal samples, 19 pollen samples.
Charcoal abundances show a high level of change throughout zone KKU-F3, ranging from
100–1000 particulates cm⁻³, with peaks at 385, 320, 253 and 210 cm. The scale of these
oscillations is a unique feature of zone KKU-F3. After 385 cm (9.7 ka cal BP) Cecropia
pollen decreases in abundances by more than half to between 1–7%. A further decline in
Hedyosmum is also evident (<2.5%), whilst the abundance of Polylepis/Acaena pollen
remains at very low values throughout (<1%). From 303 cm (c. 8.3 ka cal BP) to the upper
most sediments, Chenopodiaceae/Amaranthaceae (Cheno/Ams) becomes a small, but
persistent, constituent of pollen assemblage (<2.5%). Poaceae abundances increase
(30–45%) and a peak in Plantago (16%) is evident at 225 cm (c. 6.8 ka cal BP). Isoëtes has
fluctuating abundances (25–70%), with minimum values recorded at 308 and 225 cm
(Figure 5.4B and 5.6). A peak in Isoëtes occurs between 283–253 cm (c. 7.7–7.0 ka cal BP),
which is simultaneous with a peak in Sporormiella (3–7%) and in both charcoal size
fragments. Although present in previous zones, the green alga Pediasstrum becomes an
increasingly important component of the sediment record (up to 8%) during KKU-F3.
Fossil pollen concentrations show high frequency and high amplitude variation
(230,000–1,500,000 grains cm⁻³).
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KKU-F4. 204–47 cm (c. 6415–944 cal yr BP). 16 charcoal samples, 15 pollen samples.
Charcoal particulates increase from 204 cm, peaking at 418 particulates cm\(^{-3}\) at 123 cm (c. 3.2 ka cal BP). Charcoal then decreases towards the uppermost sediments (Figure 5.4B). The pollen assemblage is characterised by an increased Alnus abundance (7–13%). Poaceae values are equivalent to those of the previous zone (KKU-F3), but with slightly increased variation (25–45%). During the zone, Polylepis/Acaena and Hedyosmum gradually increase, reaching values of 5% and 6% respectively by the uppermost sample (51 cm). Myrsine abundance increases throughout the zone (up to 3%), and sporadic occurrences of Alchornea and Plantago (both <4%) are also evident. Isoëtes shows an increasing trend prior to 133 cm (55%), followed by a decrease towards the more modern sediments (20%). For the first time, Cyperaceae reaches values >1% and an increase in Pediastrum (up to 14%) marks its highest abundance in the record. Fossil pollen concentrations show high frequency and high amplitude variation but with an overall decreasing trend towards more recent sediments (150,000–1,000,000 grains cm\(^{-3}\)).
Figure 5.4A) Percentage diagram of terrestrial pollen taxa. Taxa are grouped based on the vegetation descriptions of Navarro and Maldonado (2002), Reese and Lui (2005) and Ortuño et al. (2011) Thin lines applied to taxa with low percentage values represent a 5× exaggeration of actual values. The fire zones (KKU-F1, 2, 3 and 4) discussed in text are shown.
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Figure 5.4B) Percentage diagram of aquatic taxa, spores and algae. Percentage values calculated relative to the pollen sum and their own group abundance. Thin lines applied to taxa with low percentage values represent a 5x exaggeration of actual values. Total pollen concentration and total charcoal particulates also shown per cm$^3$. Pollen taxon richness is the number of unique pollen types identified from within the pollen sum count (300). Rate of change analysis is calculated from the Euclidean distance between adjacent sample scores in the first 3 DCA axes then divided by the intersample time (following Urrego et al., 2009). Sajama $\delta^{18}$O ice core record is also shown (Thompson et al., 2000). The fire zones (KKU-F1, 2, 3 and 4) discussed in text are shown.
5.5.5) Ordination

Detrended correspondence analysis (DCA) explored trends within the terrestrial pollen assemblage. A rescaled solution of the first 3 axes was returned with rare taxa downweighted. Sample scores for axis 1 and 2 are plotted showing KKU fire zones (Figure 5.5). The rate of change (ROC) is calculated from the Euclidean distance between adjacent samples from the 3 DCA axes then divided by the intersample time (following Urrego et al., 2009). The results suggest that the biggest change occurred during, and on the boundary transitions of zone KKU-F3 (Figure 5.4B).

Figure 5.5 Results of sample scores for the DCA (Axis 1 and 2) ordination analysis. The different symbols refer to the different fire zones.
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![Figure 5.6](image.png)

**Figure 5.6** Physical and chemical properties and charcoal abundance of Laguna Khomer Kocha Upper sediment cores plotted against age. Wt% = weight percent. The fire zones (KKU-F1, 2, 3 and 4) discussed in text are shown.

### 5.6) Environmental reconstruction and discussion

#### 5.6.1) Deglacial vegetation dynamics

Rising regional temperatures and associated deglaciation following the LGM is recorded in ice core data from the central Andes (Thompson et al., 2000). In the relatively wet Eastern Cordillera, glacial modelling suggests that temperature changes were ultimately controlling glacial dynamics during the LGM and deglaciation period (Kull et al., 2008; Zech et al., 2007). By c. 18 ka cal BP, warming had allowed the formation of an increasingly ice-free and deeper water body at LKKU. Sedimentation rates are low (<0.01 cm yr⁻¹) probably reflecting the minimal in-wash of free organic material (e.g. charcoal) and the low turnover in the terrestrial taxa, as shown by the ROC analysis (Figure 5.4B).

Increased MS and low TOC (Figure 5.3 and 5.6) represent a period of reduced productivity, and there were large inputs of sandy material from the unstable and erosive slopes above the lake. Pollen grain concentration is initially low, probably due to poor preservation of grains. Conversely, spore producing plants, which are early colonisers and
more robust to oxidation, are a relatively more important component of the late glacial assemblage (Figure 5.4B).

The abundance of *Sporormiella* fungal spores indicates the early presence of herbivores and suggests a shallow lake at this time. *Sporormiella* is a coprophilous ascomycete fungus common on the dung of herbivores (Ahmed and Cain, 1972). Although a useful proxy to indicate increased natural herbivore density (Davis and Shafer, 2006; Gill et al., 2009) and livestock intensification (Davis et al., 1977; Chapter 4; Williams et al., 2011). *Sporormiella* also has a strong positive relationship with proximity to shoreline due to its poor dispersal (Raper and Bush, 2009). At LKKU we suggest that a decreased lake depth and surface area gave herbivores access towards the more central section of the lake, thus closer to the coring site, increasing spore abundance in the sediment record.

*Isoëtes* is associated with shallow, cool water (Navarro and Maldonado, 2002), and is indicative of water levels <4 m (Bush et al., 2005; Urrego et al., 2011). However, *Isoëtes* is unable to survive persistent freezing water (Dejoux and Itis, 1992). Therefore the low abundance of *Isoëtes* in the LKKU record prior to c. 16.9 ka cal BP probably indicates a relatively shallow lake subjected to regular hard freezes (Figure 5.4B). This interpretation is consistent with local glacial modelling which suggests ~6–7°C cooling compared to modern during the LGM (Kull et al., 2008). A decrease in *Sporormiella* from c. 16.2 ka cal BP, suggests a deepening of the lake at this time as animals are restricted from the central portion of the lake. Although we interpret low water levels at LKKU between c. 18.1–16.2 ka cal BP, this is not necessarily evidence of reduced precipitation but more likely a result of moisture locked up as ice.

Prior to c. 14.5 ka cal BP fire was virtually absent from the landscape surrounding LKKU (Figure 5.4B). Within warming, but relatively moist surroundings free from fire, *Polylepis* woodland was a major component of the local landscape, more abundant that any other time over the past 18 ka years (up to 10%). Although *Polylepis/Acaena* pollen cannot be easily separated, it is most likely that the pollen recorded here is predominantly *Polylepis* rather than from *Acaena*. *Acaena* is today present in warm humid valleys and the pollen is has not been identified as capable of long-distance transporter (Ortuño et al., 2011).
Comparison to reference pollen material of several *Polyplepis* species examined at the Herbario Nacional Martín Cardenas, Cochabamba, reveals close morphological similarities to the fossil *Polyplepis/Acaena* types identified from LKKU.

The data from LKKU shows that although attaining relatively high abundances, *Polyplepis/Acaena* pollen never reached sufficiently high values to indicate complete coverage of the landscape surrounding LKKU. At lakes surrounded by *Polyplepis* woodland, pollen in sediment cores is typically >30% (Hanselman et al., 2011; B. Guido, 2011, pers. coms.). Although undoubtedly more extensive than the modern local distribution on scree slopes and gullies, *Polyplepis* woodland remained, as today, in patches within an environment dominated by Andean grassland. The palaeoecological record from the Refugio lakes (800 km northwest, 3400 m asl; eastern Peruvian Andes; Figure 5.1A) reveals that during a similar time of minimal burning, *Polyplepis* woodland was also locally abundant (~20%), but in contrast to LKKU, grassland was reduced and replaced by montane forest taxa such as *Hedyosmum* and *Vallea* (Urrego et al., 2011).

The long-distance transport of pollen in the Andes has already been observed (e.g. Ortuño et al., 2011; Reese, 2003; Reese and Liu, 2005; Weng et al., 2004). At LKKU, upslope wind provides a background signal of vegetation dynamics at lower elevations throughout the record. The pollen assemblage suggests that warming temperatures and moist conditions between c. 18–14.5 ka cal BP facilitated the expansion of montane forest vegetation upslope (e.g. *Podocarpus*, *Hedyosmum*, *Juglans*) in agreement with other palaeoecological data (e.g. Urrego et al., 2010).

The local presence of fire at LKKU from c. 14.5 ka cal BP, although minimal, altered the vegetation composition. Although there is no apparent temperature response in the pollen data, the onset of burning at this time does coincide with a peak in temperatures and aridity suggested in the Sajama ice core record (Thompson et al., 2000; see Figure 5.4B). This is also broadly concomitant with demise of palaeolake Tauca, on the Altiplano (Argollo and Mourguia, 2000; Baker et al., 2001a; Sylvestre et al., 1999). The Tauca highstand (c. 18–14 ka BP), perhaps related to Heinrich 1, is associated with cold and wet conditions that persisted in much of the southern Andes (Blard et al., 2009). An increase
in the occurrence of fire was also seen at c. 14.5 ka cal BP at Lake Titicaca (Paduano et al., 2003). These authors associate fire to increased fuel load, but considering the abundance of locally sourced pollen in the records at LKKU before the onset of burning, we do not interpret fuel load deficit prior to c. 14.5 ka cal BP to be the main cause of minimal burning on the Andean flank. Therefore, we suggest a climatic trigger (warming and drying) for the onset of burning. The impact of fire was immediately apparent on the high Andean vegetation because the data indicates that *Polylepis* woodland was reduced by two thirds of its previous abundance, as fire removed it from the most readily burnt, flatter areas around the lake which were surrounded by grasses and offered no fire protection (*i.e.* scree slopes) (Figure 5.4A).

The pollen data from LKKU supports conclusions drawn from fossil pollen records at lower elevation sites in the eastern Andes (*e.g.* Urrego et al., 2011). These data suggest that low elevation montane forests are also sensitive to changes in net moisture (temperature/precipitation) and burning during the deglaciation period. Montane *Podocarpus* and *Hedyosmum* both decline, while lowland *Trema cf. micrantha* and *Cecropia* increase as landscape disturbance, probably resulting from fire, intensified. This almost simultaneous response of vegetation from different biogeographical zones suggests that while each fire event was localised, the underlying driver of the frequency and intensity of burning was regional climate.

The LKKU pollen assemblage reveals a unidirectional transition in vegetation following the LGM, influenced by increasing fire occurrence. There are no apparent reversals to suggest a response to an interstadial or Younger Dryas-type stadial event, which has been seen in the Sajama ice core (Figure 5.4B: Thompson et al., 1998). Surface exposure dating of glacial moraines indicates that the last period of glacial advances around Cochabamba occurred at c. 11 ka cal BP (Zech et al., 2007). However, the failure to detect such events in the LKKU record may be a result of the sampling resolution for pollen being too coarse throughout this section.
5.6.2) Early and mid-Holocene climate variation

At the onset of the Holocene, the ecosystems of the eastern Andes become less constrained by the large-scale regional temperature changes (such as those recorded in the Sajama isotope record; Figure 5.4B), and show greater response and sensitivity to variation in net moisture availability. From 10.7–9.7 ka cal BP, fire frequency and intensity increased markedly once again, indicated by more than doubling of the charcoal particulate counts (Figure 5.4B). ROC analysis reveals that the turnover of terrestrial taxa at this time was greater than before (Figure 5.4B). Poaceae increased in dominance in comparison to *Polylepis* woodland (Figure 5.4A), as the aridity led to increased flammability and fire intensity that was unfavourable to woodland (Gosling et al., 2009).

Between c. 10.7–6.4 ka cal BP, *Polylepis/Acaena* pollen remained below 1% or was completely absent. However, *Polylepis* pollen does not transport far (Salgado-Labouriau et al., 1977), and therefore its persistence in the majority of samples suggests *Polylepis* remained locally present; possibly limited to small isolated pockets on the scree slopes, which act as natural fire breaks. A similar decline in *Polylepis* woodland has been observed at Lake Siberia (2920 m asl; Figure 5.1A), which today is within Andean cloud forest. The pollen record indicates that by c. 11 ka cal BP, *Polylepis* pollen at Siberia declined from >10% to zero, while a simultaneous rise in the frequency of micro-charcoal fragments indicated a intensification of burning (Mourguiart and Ledru, 2003).

At LKKU, the increased aridity and intensified burning led to large declines in several montane forests elements (e.g. *Podocarpus* and *Hedyosmum*) during the early to mid-Holocene. If increasingly warmer temperatures had occurred during this time, this would have facilitated the upslope migration of lowland taxa, as per the classic view of species movement in warmer conditions. However, the decline in montane forest elements suggests that aridity prevented this vegetation response, and supports similar interpretations at Lake Titicaca (Bush et al., 2010). Fire therefore became a key transformer of the vegetation composition, limiting the range of the montane forests.

An initial detrimental impact of fire on plant diversity around the LKKU ecosystem is apparent from the decline in the total number of pollen taxa from >35 to <25 following the onset of burning at c. 10 ka cal BP. However, species richness recovers (>35 taxa)
within c. 100 years, and remains high in the new fire-dominated ecosystem. The impact on some taxa (e.g. *Celtis*, *Trema* and *Weinmannia*) is less than on other lowland forest trees (Figure 5.4A). This may be due to their preference for more open, arid or warmer conditions. The small, but persistent, occurrence of Chenopods in the pollen assemblage from c. 8.3 ka cal BP suggests conditions had become favourable for vegetation generally preferring dry, disturbed landscapes. Increased aridity between c. 9.6–6.7 ka cal BP is also revealed in the spore assemblage. Increased *Sporormiella* fungal spores probably indicate lower water-levels, as herbivores are able to access more of the lake (Raper and Bush, 2009) or, perhaps, more animals visit LKKU as other local water bodies dry up.

This phase of increased aridity at LKKU during the early to mid Holocene is concomitant with a regional decrease in precipitation and reduced lake levels identified in numerous records across the Andes and Amazonia (Bush et al., 2010). Although varying in intensity and timing spatially, the Holocene dry event (HDE) is understood to be a drought of multi-millennial scale, but was punctuated with episodic wet events (Abbott et al., 2003; Bush et al., 2005; Grosjean, 2001; Hillyer et al., 2009; Paduano et al., 2003; Valencia et al., 2010).

The onset of the HDE caused many lakes across the Andes to either reduce in depth (e.g. Lake Titicaca; Cross et al., 2000) or completely dry out (e.g. Refugio lakes, Peru; Urrego et al., 2011). Close to LKKU (40 km southeast), although in an inter-Andean setting, the record of Lake Challacaba (Vacas Lake District, 3400 m asl; Figure 5.1A) also indicates desiccation of the lake basin prior to c. 4 ka cal BP (Chapter 4; Williams et al., 2011). However at LKKU, despite a lowering of the lake level, sediments were continually deposited throughout the height of the HDE as indicated by the presence of *Pediastrum* in all samples (Figure 5.4B). With evidence suggesting that precipitation was reduced and/or temperatures increased during this period, an explanation for the continued presence of water at LKKU is necessary. We consider that a continuation of ground-level cloud regularly covered the site as is common in the eastern Andes (Kessler, 2002b), and was observed during dry season fieldwork (Figure 5.2A). We suggest that this moisture supply, in addition to precipitation, was fundamental in maintaining an inundated lake basin. This finding is in contrast to those from the Refugio lakes where the authors report cloud
cover was insufficient to maintain the presence of open water bodies (Urrego et al., 2011). However, the Refugio lakes are today shallower than LKKU (1.5–0.5 m less), and so more susceptible to complete desiccation. While it is likely that ground-level cloud was reduced during the HDE at LKKU, it was sufficient to maintain the lake by reducing UV exposure (evaporation) and continuing to supply moisture during periods of reduced precipitation.

In the LKKU record we interpret simultaneous peaks in *Sporormiella*, Poaceae, charcoal and *Isoëtes* as indicating that greatest drought intensity occurred between c. 7.3–7 ka cal BP. The timing of aridity concurs with evidence for Holocene drought across the Peruvian/Bolivian Andes, ranging from low elevation slopes to the Altiplano: i) Lake Consuelo; 1360 m asl; c. 7.4–5 ka cal BP (Urrego et al., 2010), ii) Lake Pacucha 3095 m asl, c. 8.3–5 ka cal BP (Hillyer et al., 2009), iii) Laguna de Chochos; 3285 m asl, c. 9.5–7.3 ka cal BP (Bush et al., 2005), and iv) Lake Titicaca; 3810 m asl c. 8–5.5 ka cal BP; (Baker et al., 2001b). Increased charcoal frequency in the Siberia lake record from c. 11–4.5 ka cal BP may also indicate reduced moisture availability in the region (Bush et al., 2007; Mourguiart and Ledru, 2003).

In addition to confirming that the HDE was multi-millennial in duration, the LKKU record also supports more recent findings that suggest this dry period was punctuated with episodic wet phases (e.g. Hillyer et al., 2009). At LKKU this is indicated by: i) the non-linear direction changes in many locally growing taxa (e.g. *Plantago*), ii) high ROC scores indicating regular, large-scale, rapid terrestrial vegetation changes (Figure 5.4B), iii) high amplitude and frequency fluctuations in charcoal and *Isoëtes*, and iv) increased sedimentation rate, probably due to in-wash of material during intense period of precipitation. The increase in TOC, following onset of intensified burning from c. 10.1 ka cal BP, also suggests that the sediment being washed in had a high abundance of organic material (i.e. charcoal fragments). A peak in pollen of the high elevation bog taxa *Plantago* (Ortuño et al., 2011) at c. 6.8 ka cal BP either represents an increase in marsh habitat on the shores of the lake in response to lowered lake level, a situation observed at the lower lake today, perhaps resulting from the infilling of the basin adjacent to LKKU (Navarro and Maldonado, 2002), or the presence of a larger wetland habitat nearby.
5.6.3) Formation of the modern vegetation structure

A sharp decline in burning at c. 6.4 ka cal BP marks the end of the HDE at LKKU (Figure 5.4B). Termination of this event has been linked to a resumption of stronger ENSO activity following the "weak" El Niño regime that is thought to have dominated the mid-Holocene period (Rein et al., 2005). Concomitant with decreased burning, an increase in Alnus (Andean Alder) indicates increased moisture. Alnus is a pioneer taxon, growing in marsh and riparian transitional Punean woodland (Navarro and Maldonado, 2002). As a copious pollen producer with long-distance dispersal on upslope winds, it is present in most Andean fossil pollen records above the Andean forest treeline (Weng et al., 2004). Today Alnus occurs on slopes below the lower Khomer Kocha lake (<3800 m; D. Hertel, 2010, pers. coms.). It is therefore likely that the establishment of Alnus woodland downslope would be sufficient to provide a significant quantity of Alnus pollen to LKKU. The increase in Alnus at c. 6.4 ka cal BP indicates regionally wetter conditions. As LKKU is >600 m above the modern elevation limit of Alnus (Weng et al., 2004) it is unlikely that marsh-woodland ever colonised the slopes immediately surrounding the lake.

The return to wetter conditions after the HDE allowed Polylepis woodland to expand from the pockets in which it was restricted, suggesting that fire and climate aridity was critical in determining the niche space available for woodland growth. At Refugio, despite the return of climatically favourable conditions, the onset of human activities prevented the local expansion of Polylepis woodlands after the HDE (Urrego et al., 2011). The different dynamics of Polylepis at the two sites highlights the pitfalls in assuming all high Andean ecosystems have been impacted by humans to a similar degree. Our data suggests that it is incorrect to assume the current patchy distribution of Polylepis is solely the result of long-term human impacts as previously suggested (Ellenberg, 1958; Kessler, 2002a).

Fire reduction and increased precipitation at lower elevations also enabled the re-expansion of Andean and montane forest, as Hedyosmum, Alchornea and, to a lesser extent, Myrsine all increase in abundance. The reappearance of Hedyosmum at high abundance may also indicate cooler temperatures, as this taxon was also dominant during the early deglaciation period (c. 18–15 ka cal BP). Intriguingly Cecropia and Podocarpus do not appear to respond to the increased net moisture in the region.
The sensitivity of eastern Andean vegetation to climate and fire

Chapter 5) The sensitivity of eastern Andean vegetation to climate and fire

The increasing abundance of *Pediastrum* (*cf*. *boryanum*) throughout KKU-F4 is difficult to interpret. The taxon is restricted to freshwater habitats (Komárek and Jankovská, 2001) and *P. boryanum* var. *longicorne* appears closest to the type found at LKU. It is today common in high elevation, clear waters, and has a pH optimum of 7.2–7.4 (Jankovská and Komárek, 2000; Weckström et al., 2010). Therefore since *P. boryanum* became dominant in LKU (c. 4.4 ka cal BP, >10%), pH and other lake variables have remained close to this optimum. In addition, as *Pediastrum* does not bloom in saline conditions (Woodward and Shulmeister, 2005), its presence indicates continuous freshwater, and supports the interpretation of year-round input from ground-level clouds.

5.6.4) Potential anthropogenic impacts

Much discussion has focussed on the timing and impacts of past human populations across the Andes (e.g. Chepstow-Lusty et al., 1996; Coltorti et al., 2010; Dillehay, 2008; Ellenberg, 1979; Lynch, 1990; Mondini, 2002; Chapter 4; Williams et al., 2011). However, the heterogeneous nature of Andean topography, microclimatic and flora mean that it is unlikely that all locations experienced uniform patterns of human impact. Broad generalisations imply that ancient human cultures had no preference for climate, vegetation or resource potential; which the archaeological records suggests was not the case. For example, the favourable environmental conditions of the Cochabamba Basin led the Inca to cultivate maize, resulting in the area being known as the "granary" of the south central Andes (Lone and Lone, 1987; Zimmerer, 2000). In contrast, the palæolimnological record at Lake Challacaba, just outside these favourable agricultural lands, records no occurrence of maize despite at least 4 ka of human occupation (Chapter 4; Williams et al., 2011).

Although the appearance of Cheno/Ams pollen in the LKU record from 8.3 ka cal BP could represent the cultivation of *Chenopodium quinoa*, a staple dietary component before *Zea mays*, the low abundance (<2.5%) suggests that this is unlikely, as was also inferred at Laguna de Chochos (Bush et al., 2005). At sites where human occupation is apparent from the sediment records, Cheno/Ams pollen reaches much higher abundances, e.g. Marcococha (10-25%) and Pacucha (up to 51%) in the Peruvian Andes (Chepstow-Lusty et al., 2003; Valencia et al., 2010). The low (<2.5%) abundance of
Solanaceae pollen, the tubers of which are harvested, suggests they were not cultivated, and the absence of other crop pollen suggests that LKKU was not a site of human habitation.

5.7) Conclusions

The sediment record of LKKU represents a continuous archive of environmental change and vegetation dynamics during the past 18 ka. The proxy data suggest a relatively gradual climatic transition from the LGM, with increasing fire occurrence. There is no evidence for an interstadial or Younger Dryas-type stadial, which is apparent in the Sajama ice core record (Thompson et al., 1998).

The correlation of vegetation change to the zones established from charcoal analysis, shows that fire, governed by climatic variation in temperature and precipitation, has long been a transformative agent in high eastern Andean ecosystems. Rate of change analysis shows that the fastest vegetational change occurred during periods of high burning frequency, associated with the Holocene drought. The record confirms that the HDE was multi-millennial in duration (c. 10.1–6.4 ka cal BP) and supports evidence that this period was punctuated by episodic wet phases. The onset of generally wetter conditions from c. 6.4 ka cal BP concurs with the timing of increased moisture at other eastern Andean locations (e.g. Refugio and Siberia), and also with most Andean and Amazononia lakes (Bush et al., 2010; Mourguiart and Ledru, 2003; Urrego et al., 2011).

The LKKU pollen record provides the first opportunity to examine the dynamics of local woodland expansion and contraction in a climatically sensitive region of the eastern Bolivian Andes. Until c. 14.5 ka cal BP, the absence of fire allowed Polylepis woodland to form a major component of the local environment, when it was more abundant than any other time during the past 18 ka. However, Polylepis woodland never completely covered the landscape surrounding LKKU and remained in patches within an Andean grassland-dominated environment. The expansion of Polylepis woodland after the HDE suggests that fire and aridity was critical in determining the niche space available for woodland

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growth. However, these changes occurred in a landscape largely free from human pressures.

Long-distance transport of pollen on upslope winds to LKKU provides evidence of vegetation changes in the lower montane forests. These data highlight the sensitivity of the Yungas to changes in climate and burning regime, supporting the conclusions found at lower elevation sites in the eastern Peruvian Andes (Urrego et al., 2011). Simultaneous changes in both Andean and lowland taxa suggest that vegetation dynamics in the two environments can be linked to a common climatic driver.

The increase in human populations throughout the late Holocene does not appear to have impacted the environment around LKKU, highlighting the importance of the site in providing a record of vegetation response to climate without anthropogenic influence. In particular, there appears to have been no decline in the highly sought-after wood resource provided by both Polylepis and Alnus, which has been documented across much of the Andes (Chepstow-Lusty et al., 1998; Fjeldså and Kessler, 1996; Weng et al., 2004). Although LKKU has minimal human impacts, the record does not cover the last c. 1000 years when the Tiwanaku and Inca cultures came to prominence. To evaluate this impact, analysis of more recent sediment archives from the remote regions of the Bolivian Andes should be a future research priority.

5.8) Acknowledgements

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Chapter 6) On the identification and interpretation of Late Pleistocene and Holocene Chironomidae from the eastern Bolivian Andes

In this chapter, all subfossil Chironomidae data from both the Lake Challacaba and Laguna Khomer Kotcha Upper study sites are presented and discussed. This section highlights that the published knowledge of Andean chironomid research is in its infancy and shows how this study compliments and builds upon the existing knowledge gap. Descriptions of the chironomid types discovered are provided and discussed in reference to the data obtained from the sediment cores. A list of chironomid types is provided in Table A4.3. This chapter has been submitted for publication separately:


6.1) Abstract

This paper presents the first palaeolimnological record of chironomid remains from the Bolivian Eastern Cordillera. Taxonomic notes are provided for the 10 chironomid taxa (subfamilies: Chironominae, Orthocladiinae and Tanypodinae) identified from the lake sediments. This study highlights the role of chironomid analysis as a supporting proxy for the interpretation of Bolivian sedimentary successions when combined with palynological, charcoal and geochemical data. Analysis of the sediments from Lake Challacaba (17°33.257' S, 65°34.024'W; 3400 m asl) and Laguna Khomer Kocha Upper (17°16.514' S, 65°43.945'W; 4153 m asl) reveals new insights into the response of Chironomidae to environmental change over the last 18,000 years in the Tropical Andes biodiversity hotspot. This study shows that chironomid diversity and abundance in the Tropical Andes is sufficient to investigate the response to regional and local environmental changes, highlighting the sensitivity of chironomids to adjustments in net
moisture balance (water level fluctuations and salinity) and anthropogenic impacts (nutrient input).

At Lake Challacaba, the chironomid and geochemical data indicate periodic desiccation and hypersalinity of the basin c. 4,000–3,460 cal yr BP. The increased abundance of disturbance and high nutrient input tolerant *Chironomus* sp. at c. 1,000 cal yr BP suggests a change of human activity; this supports inferences from the pollen and spore records which indicate elevated pastoral agriculture at this time. The chironomid data provide a more complete picture of the extent to which pre-Columbian cultural groups perturbed their environment. The greatest assemblage change in the chironomid record from Laguna Khomer Kocha Upper occurred at c. 6,380 cal yr BP, concomitant with an increase in marsh woodland taxa, wetter conditions and a rising lake level. No response is recorded in the chironomid assemblage to the onset of burning at the start of the Holocene aridity (c. 10 cal yr BP) which is the major transformative agent for the terrestrial vegetation. The comparison with other proxy data suggests that within-lake processes are more important drivers of chironomid assemblages than terrestrial vegetation or fire regime. It is apparent, however, that the full potential of subfossil chironomid analysis will only be realised once more modern autecological data exists.

**6.2) Introduction**

Owing to the high chitin content, the head capsules of chironomid larvae (Insecta, Diptera, Chironomidae), are well preserved within lake sediments (Epler, 2001; Velle et al., 2010; Walker, 1987; Walker, 2001). They regularly represent the most abundant group of macro invertebrates found in fresh and brackish habitats and have a worldwide distribution, exploiting large ranges in elevation and temperature (Armitage et al., 1995; Ashe et al., 1987; Ferrington, 2008; Pinder, 1986). Within the life cycle, chironomids have four stages (instars) as larvae, with each stage culminating in moulting of an exoskeletal cuticle or head capsule (Walker, 1987; Section 3.4.3; Figure 3.7). The suitability of chironomids for palaeoecological study is not only a product of the good head capsule preservation and abundance, but also due to their sensitivity to changes in environmental conditions. During the adult stage, mobility through wind dispersal enables them to
follow climatic zones and thus track environmental changes (Brooks, 2005; Walker, 2001).

Previous studies of fossil chironomid assemblages has highlighted their potential to act as an indicator for a broad range of environmental changes (see Section 3.4.3 and Table 3.2). These include; anthropogenic land disturbance and pollution (Kansanen, 1985; Woodward and Shulmeister, 2005), volcanic activity (Araneda et al., 2007), hydrology (Hofmann, 1998), lake pH (Brodin and Gransberg, 1993; Johnson et al., 1990), lake trophic status, (Brooks et al., 2001; Gathorne-Hardy et al., 2007), oxygen regime (Quinlan and Smol, 2001), salinity (Chen et al., 2009; Walker et al., 1995), substrate type and input rate (Schakau, 1991; Verschuren et al., 2000) and water and air temperatures (Brooks and Birks, 2001; Lang et al., 2010; Porinchu et al., 2003; Walker et al., 1991).

Despite the proven value of subfossil chironomids in palaeoenvironmental reconstruction, a paucity of research in the Andes of South America remains a serious limitation to any subfossil investigation of this area. The most significant progress in using chironomids for palaeoenvironmental reconstruction has been made in the Patagonia region of Chile and Argentina (reviewed by Verschuren and Eggermont, 2006). Recent ecological and palaeoecological studies of chironomids have highlighted the improvements possible in resolving taxonomic difficulties when a research focus exists (e.g. the work of Donato et al., 2008; Massaferro et al., 2005; Massaferro and Brooks, 2002; Massaferro et al., 2009). However, nowhere else in the Andes is there an equivalent intensity of research effort and the central Andes (Bolivia/Peru) in particular remains deficient in studies. The only international published inventory of the aquatic Diptera from modern lakes in Bolivia/Peru was collected during the 1978 Catherwood Expedition. Thirty-one genera were recorded from within the subfamilies of Chironominae (6 genera), Diamesinae (1), Orthocladiinae (19), Podonominae (2), and Tanypodinae (3). More detailed modern ecological investigation of Lake Titicaca, and the smaller, separate lake of Umayo, revealed only the presence of Orthocladiinae, (9 species) and Chironominae (6 species) (see Table 6.1) (Roback and Coffman, 1983). Elsewhere in the Bolivian Eastern Cordillera, taxa from stream and lake systems have also been indentified (Table 6.1), but the modern ecologically association is largely unknown.
Chapter 6) On the identification and interpretation of Late Pleistocene and Holocene Chironomidae

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<td><em>Podonominae</em>, <em>Orthocladiinae</em></td>
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<td><em>Paratanytarsus</em>, <em>Polypedilum</em>, <em>Rheotanytarsus</em>, <em>Tanytarsus</em></td>
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<td><em>Cricotopus</em>, <em>Eukiefferiella</em>, <em>Halocladius</em>, <em>Paracricotopus</em></td>
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<td><em>Cricotopus</em> (5 species), <em>Corynoneura</em>, <em>Paracladius</em>, <em>Pseudosmittia</em></td>
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Table 6.1 Modern chironomid taxa collected from three major hydro-ecoregions of eastern Bolivia (far right 3 columns), and within two lakes situated on the Altiplano (far left column).

This study represents the first investigation into subfossil chironomid remains in the Eastern Cordillera of Bolivia. The eastern slopes of the Tropical Andes are one of the most biologically diverse areas on Earth, with high precipitation caused by the collision of moist, westerly Amazonian air colliding with the Andean mountain chain (Killeen et al., 2007; Myers et al., 2000). Increasing human occupation of the Andes and predicted future climate changes mean the ecology is highly vulnerable (Cincotta et al., 2000; Malcolm et al., 2006). We present the chironomid assemblages from two limnological records from the surrounds of the Cochabamba Basin, extending back 4,000 and 18,000 years. These data provide new insights into the chironomid genera above 3,200 m asl (meters above sea level), and changes in their distribution and abundance during the late Pleistocene and Holocene periods. With reference to previously published palynological, charcoal and geochemical/physical analysis (Williams et al., 2011; Chapter 4; Chapter 5), we explore
the relationship between turnover in the chironomid taxa in response to the impacts of climatic change and pre-Columbian societies.

### 6.3 Regional setting and study sites

Situated within the Eastern Cordillera forethrust zone of the Bolivian Orocline, the Cochabamba Basin is a Plio-Pleistocene valley formed after 5.33 Ma and is comprised of large volumes of Quaternary sedimentary deposits (Kennan et al., 1997; McQuarrie, 2002). This inter-Andean montane valley is limited on the northern and western sides by the Cordillera del Tunari, and on the east by the mountain range of Tiraque-Vacas (Figure 6.1A). Although the specific geology of this surrounding high ground is not known in detail, the bedrock material is mainly formed of Ordovician age (488.3–443.7 Ma) quartzite, lutites and sandstone, with some granite intrusions (Cassard, 1999; Kessler, 2002b).

At the heart of the central valley, the city of Cochabamba (17°40, 66°14 / 2,500 m asl) has a modern population of ~600,000. Owing to the fertile Quaternary deposits, the Cochabamba valleys are a major region of food production, and was a location of pre-Columbian agricultural practices and trading from earlier than 3,000 years ago (Hensen, 2002). This was intensified during the Tiwanaku (c. 1,500–900 yr BP) and Inca (c. 650–550 yr BP) rule, when a road network was developed to connect the Cochabamba valley to both upland and lowland areas (Higueras, 1996; Janusek, 2008; Lone and Lone, 1987; Sánchez C., 2008). See Sections 1.4 and 4.2.1 for a full discussion on the ancient road network.

Regional climate, particularly precipitation, is controlled by several systems including: movement of the Intertropical Convergence Zone (ITCZ; Leduc et al., 2009), variability of the South American summer monsoon (SASM; Zhou and Lau, 1998), and inter-annual variation of the El Niño-Southern Oscillation (ENSO; Chiang, 2009; Philander, 1990). Changes in precipitation are considered to be the predominant feature of future climatic changes (Urrutia and Vuille, 2009; Vuille and Werner, 2005).
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Figure 6.1 Maps showing study site location within Bolivia. A) Cochabamba Basin with altitudes, current city extent and study locations marked. Modified from Sánchez (2008). Inset map locates Cochabamba Basin within Bolivia. B) Lake Challacaba (also known as Pilawitu). Bathymetry shown in metres. Coring location marked (*). C) Laguna Khomer Kocha Upper. Bathymetry shown in metres. Coring location marked (*).
The topographic and climatic variation place the Cochabamba region at the confluence of four Tropical Andean ecoregions; the Bolivian Yungas, the Bolivian montane dry forests, the central Andean Puna and the central Andean dry Puna (Olson et al., 2001). Locally, several species of endemic birds, mammals, amphibians and plants exist (Navarro et al., 2005; Young, 2007), and the Cochabamba Basin is recognised as an important conservation area for the protection of high elevation *Polylepis* woodlands (Fjeldså and Kessler, 1996). High biodiversity and narrow vertical species ranges in sites of complex topography, means even small variations in temperature and precipitation can result in considerable species turnover. As a result, the fauna and flora of the region is highly sensitive to any change in environmental conditions.

Remnants of a large water body that existed within the Cochabamba Basin, together with smaller lakes created by local glaciation features in the surrounding mountain ranges, provides opportunities to obtain palaeolimnological records. In this study, two lake systems north and east of the main Cochabamba Basin are investigated.

6.3.1) Lake Challacaba (Vacas Lake District)

The Vacas Lake District, situated 60 km east of the city of Cochabamba (Figure 6.1A), is a system of six lakes located within a cold (7.2–11.3°C) and seasonally dry (2.6mm/month June–August, 114mm/month January–March), high elevation (>3,000m asl) valley (Hijmans et al., 2005; Ritter, 2000). Within the district, Lake Challacaba is a small, c. 1.5 km², freshwater system, 2.5 km from the settlement of Vacas (17°33.257' S, 65°34.024' W; 3,400 m asl; Figure 6.1B). Lake Challacaba is fed at its northernmost point by a stream from the surrounding mountains and drained via an outflow at the southeast end (Figure 6.1B). At the time of coring (June, 2007), water depth was 3 m, conductivity 332 µS/cm (microSiemens per cm), pH 9.45 and water turbidity (Secchi depth) was 0.58 m.

The Vacas Lake District is positioned within the biogeographic regions of the northern Puna/semi-humid, and sub-humid/Puna and Punean woodlands of the Tunari (Ibisch et al., 2003; Navarro and Maldonado, 2002). However, today the area is dominated by the cultivation of potatoes and other tubers, and has also been heavily impacted by grazing (Gotkowitz, 2007). Further away from direct agricultural impact, and more typical of the
natural vegetation of the Cordillera of Tiraque–Vacas, are a variety of grassland, shrubland and woodland types (Navarro and Ferreira, 2007).

Today Lake Challacaba is surrounded by actively worked agricultural land, much of which is inundated by water during the wetter months. *Myriophyllum* (Haloragaceae) is the dominant component of the aquatic vegetation in Challacaba, and many of the other Vacas lakes, which is an important food source for cattle during the dry season (Ritter, 2000). Other important aquatic vegetation of the Vacas Lake District includes *Lemna* (Lemnaceae), *Schoenoplectus* (Cyperaceae), *Zannichellia* and *Potamogeton* (Potamogetonaceae) (De la Barra, 2003; Molina et al., 2007).

Historically, the Vacas municipality was significant in regional transportation routes (Sánchez C., 2008). The current road passing through the Vacas lake district was once a principle route linking the main Cochabamba Valley and the archaeological sites of Inca Rakay in the west, to those in the southeast such as Inkallajta and Mizque (Higueras, 1996). Given the importance of camelid pastoralism and caravans for pre-Columbian peoples (Lynch, 1983) and the movement of Tiwanaku traders between the main valley and the Mizque enclave (Janusek, 2008), it seems likely that many groups of people would have had direct contact with the Vacas lakes.

*Palaeoecological summary*

In June 2007, a 297 cm long sediment core was extracted from the deepest point in Lake Challacaba. Based on three $^{14}$C accelerator mass spectrometry (AMS) dates of bulk gyttja or macrofossil plant remains, the core represents a continuous record of the last c. 4,000 years (Figure 6.2A). The full sediment structure and chronological data is detailed in Section 4.4 and Williams et al. (2011).

The sensitivity of the site to changes driven by human and climatic factors was detected in a multi-proxy analysis of the lake sediments (Williams et al., 2011; Chapter 4). Fluctuations in drought tolerant vegetation (Amaranthaceae and Caryophyllaceae) and calcium carbonate ($\text{CaCO}_3$) indicate two periods of reduced net moisture (c. 4,000–3,370 and c. 2,190–1,020 cal yr BP) compared to wetter episodes between c. 3,370–2190 and c.
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1,020 cal yr BP to present day (Figure 6.4C). The moisture fluctuations broadly correlate to the end of the mid-Holocene dry event and variations in El Niño/Southern Oscillation reported elsewhere in the Andes (Moy et al., 2002). High charcoal abundance from c. 4,000 cal yr BP indicates continuous use of the ancient road network. A decline in charcoal, and an increase in the invasive species *Ludwigia* and the dung fungus *Sporormiella* at c. 1,340-1,210 cal yr BP, suggests cultural changes, particularly increased camelid herding activity, were a major factor in shaping the modern landscape (Williams et al., 2011; Chapter 4). These can be correlated with major cultural transitions seen in the Tiwanaku archaeological record (Janusek, 2008).

6.3.2) Laguna Khomer Kocha Upper (Cordillera el Ronco)

Situated on the eastern slopes of the Cordillera el Ronco, Laguna Khomer Kocha Upper is situated above the tributaries of the Rio San Mateo, a valley which descends more than 2000 m elevation in less than 10 km. Laguna Khomer Kocha Upper is 45 km west of Cochabamba city and 35 km north of the Vacas Lake District (Figure 6.1A). Laguna Khomer Kocha Upper is a small, c. 0.1 km$^2$, glacially formed lake and its maximum depth at the time of fieldwork (June, 2007) was 3.6 m (17°16.514' S, 65°43.945' W; 4153 m asl; Figure 6.1C). During the same fieldwork season water turbidity was 3.2 m, conductivity 28 μS/cm and a pH 7.38. The lake is fed by runoff from the surrounding slopes and drains via an outflow channel at the northeast end (Figure 6.1C).

At Laguna Khomer Kocha Upper the dry season (June–August) precipitation averages 13 mm/month this increases to 138 mm/month during the wet season (January-March). Additional humidity is contributed, even during the dry season, by cloud cover which ascends from the valleys to the northwest, depositing large quantities of moisture on the sparsely vegetated slopes (Kessler, 2002b). Mean temperature varies from 4.5 °C for the wet season to 7.6 °C for the dry season (Hijmans et al., 2005) and a local lapse rate is estimated to be ~4.5°C/1000 m (Hertel et al., 2008).
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Figure 6.2 Age-depth curves and sediment stratigraphy of sediment cores. **A)** Lake Challacaba. Sedimentary units: 1) Greenish-grey sandy clay, 2) dark gyttjas with irregular brownish bands, 1-3 cm thick, 3) gyttjas with alternating dark and pale bands, 4) dark mottled gyttjas, and 5) pale to medium-gray gyttjas with progressively higher quantities of clays. **B)** Laguna Khomer Kocha Upper. Sedimentary units: 1) Greenish-gray sandy clay, 2) pale brown coarse sand, 3) dark brown gyttjas with some bands of sandy material, 4) dark brown gyttjas, 5) very dark brown gyttjas, with some strong banding evident, 6) dark brown gyttjas, and 7) very dark brown gyttjas, with some strong banding evident. Sediments upwards of 47 cm were not captured due to their extremely fluid nature. Rejected $^{14}$C dates shown by open circles. Detailed results of $^{14}$C dates previously published (Williams et al., 2011; Sections 4.4 and 5.5; Tables 4.1 and 5.1).
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Laguna Khomer Kocha Upper lies in a region of rapid spatial changes in biogeography and vegetation, associated with the steep elevation gradients present in the valley of San Mateo. The lake lies in the sub-humid Puna and transitional Punean woodlands that split the Puna and Yungas zones along the Cochabamba section of the Eastern Cordillera (Ibisch et al., 2003; Navarro and Ferreira, 2007; Navarro and Maldonado, 2002). Today the local landscape immediately surrounding the lake is dominated by Andean tussock forming grassland, within which are pockets of woodland dominated by the tree genus *Polylepis* (Rosaceae). A low (<2 m) glacial moraine separates the lake from an area of flat, waterlogged ground, which is likely to represent an infilled lake of similar size. Today there is minimal sign of human impact at Laguna Khomer Kocha Upper and examination of the *Polylepis* woodland patches surrounding the lake revealed no indications of exploitation.

**Palaeoecological summary**

A 413 cm sediment core was extracted from the deepest point of Laguna Khomer Kocha Upper during the 2007 dry season. The chronology for the succession was derived from $^{14}$C AMS dating of three bulk sediment samples and five samples comprised of picked charcoal fragments (Figure 6.2B; Chapter 5), and revealed a sedimentary succession starting at c. 18,100 cal yr BP. The uppermost 47 cm (c. 950 years) of sediment could not be retrieved due to the extremely fluid nature of the material. A full description of the sediment structure and chronological data has already been published (Chapter 5).

The sediment record from Laguna Khomer Kocha Upper shows that fire regime, governed by climatic variation, has long been a transformative agent in eastern Andean ecosystems (Chapter 5). The fossil charcoal record from Laguna Khomer Kocha Upper demonstrates that before c. 14,500 cal yr BP ago fire was virtually absent from the landscape surrounding the lake. The deglacial warming, (c. 18,000–14,500 cal yr BP) coupled with relatively moist conditions free from fire allowed locally growing high Andean *Polylepis* woodland to expand. Between c. 14,500–10,000 cal yr BP burning was minimal but still quickly began to transform the local vegetation as woodland was probably restricted to areas naturally protected from fire. A major increase in burning 10,000–6,400 cal yr BP almost completely removed high Andean woodland from around the lake. The increase in
fire was probably a function of region-wide aridity (Holocene dry event) which also caused lake water levels to fall. A sharp decline in burning at c. 6,400 cal yr BP, with an increase in marsh woodland (Alnus) marked the termination of the Holocene dry event and the return to wetter conditions. Polylepis woodland expanded from the pockets it was formerly limited to during the height of the aridity and suggests that fire, led by climate, was critical in determining the niche space available for woodland growth.

As well as recording an environmental history of local vegetation dynamics, the long-distance transport of pollen on up-slope winds into Laguna Khomer Kocha Upper provides a background signal of vegetation changes in the lower montane forests. Simultaneous adjustments in both Andean and lowland taxa suggests that vegetation dynamics in the two environments can be linked to a common climatic driver. There is no evidence in the proxy record to indicate that human activity before c. 1,000 years ago, the upper extent of the sedimentary succession, had any impact on the local landscape (Chapter 5).

**6.4) Material and methods**

Two sediments cores from each site (Challacaba B and C and Khomer Kocha Upper A and B) were recovered using a cam-modified Livingstone piston corer. Staggered, overlapping starting depths below the sediment-water interface ensured that a continuous record was recovered despite potential loss from some tube ends. All sediment cores were recovered in aluminum tubes (50 or 38 mm diameter) and sealed on site. The sediment-water interface was recovered, were possible, using a Perspex surface sample tube, attached to coring rods. The surface sampler was extruded in the field and continuous subsamples of 1 cm thickness bagged. All sediment recovered was transferred to The Open University cold store (4°C). The sediment cores were split and then sediment divided using a fine strand of wire held at tension.

Analysis of the chironomid head capsules was conducted on subsamples of 1 cm³. Following the procedure described by Brooks, Langdon and Heiri (2007), see Appendix A2.6, samples were deflocculated in 10% (KOH), heated to 70°C for 5 minutes, sieved and separated into two size fractions (90-212 and >212 μm). Head capsules were picked by
hand from a sorting tray under a binocular microscope (Olympus SZX12) at ×12.5–25 magnification and progressively dehydrated. Depending on size and fragmentation of head capsules, between 1 and 5 were mounted ventral side up under 6 mm diameter coverslips onto a microscope slide. Identification was subsequently achieved using a Nikon Eclipse 50i microscope at ×400 magnification with reference to relevant keys (Brooks et al., 2007; Dieffenbacher-Krall et al., 2008; Epler, 1995; Epler, 2001; Rieradevall and Brooks, 2001; Wiederholm, 1983). Stratigraphic diagrams were plotted using the program C2 (Juggins, 2003). The procedures for radiocarbon, palynological, charcoal, geochemical and physical analysis followed standard protocols which have been described in full elsewhere (Williams et al., 2011; Chapter 3; Sections 4.3 and 5.4; Appendix A2).

6.5) Results

6.5.1) Taxonomic notes

*Chironomus* (Figure 6.3A I)

Diagnostic features: Mentum with trifid median tooth. 6 lateral teeth. 4th lateral shorter or equal to 5th. Ventromental plates large, with smooth outer margin. Prominent striations at base. Mandible with 3 inner teeth. Occurrence: Found in Challacaba. Description based on 216 specimens.

*Parachironomus* (Figure 6.3A II)

Diagnostic features: Mentum with single median tooth. Often up to twice as broad as 1st lateral. 7 lateral teeth. 7th lateral often tiny and sometimes difficult to distinguish on degraded specimens. Ventromental plates large, triangular and with scalloped outer margin. Striations often visible. Occurrence: Found in Challacaba Upper. Description based on 10 specimens.
Tanytarsus (Figure 6.3A III)
Diagnostic features: Mentum with single notched median tooth. 5 pairs of lateral teeth evenly spaced. Short, broad, blunt spur on antennal pedestal. Post-occipital plate large and darkly pigmented but only present in final instar larvae. Mandible with 3 inner teeth, single dorsal tooth, no surficial teeth. Premandible with three apical teeth. Occurrence: Found in both Challacaba and Khomer Kocha Upper. Description based on 278 specimens.

Cricotopus / Orthocladius type I (Figure 6.3A IV)
Diagnostic features: Mentum with single median tooth. Median tooth about same width and of equal or marginally taller height to 1st lateral tooth. 6 lateral pairs. 2nd lateral often shorter with gap between 2nd and 3rd. Narrow ventromental plates. Mandible with 3 inner teeth and small indentation visible on outside edge. Occurrence: Found in Challacaba. Description based on 418 specimens.

Cricotopus / Orthocladius type II (Figure 6.3A V)
Diagnostic features: Mentum with single median tooth. 6 lateral teeth. 2nd lateral narrow and often shorter with gap between 2nd and 3rd. Narrow ventromental plates. Mandible with 3 inner teeth. Differentiated from Cricotopus / Orthocladius type I by 2nd lateral tooth width, which is narrower and positioned closer to the 1st lateral tooth in Cricotopus / Orthocladius type II. Occurrence: Found in Khomer Kocha Upper. Description based on 240 specimens.

Limnophyes / Paralimnophyes (Figure 6.3A VI)
Diagnostic features: Mentum with one pair of median teeth, and five lateral teeth. Teeth decrease in size laterally, although the outer two are of similar size. Outer edge of 5th lateral distinctly inwardly curved. Banding can often be seen, particularly in the median region. Rounded projections below outer teeth of mentum. No specimens with mandibles or premandibles found. Occurrence: Found in both Challacaba and Khomer Kocha Upper. Description based on 3 specimens.
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*Paracricotopus* (Figure 6.3B I)
Diagnostic features: Mentum with single, broad median tooth. 5 lateral teeth. Outer edge of 5th lateral distinctly inwardly curved. Setae submenti positioned centrally below mentum. Occurrence: Found in Challacaba. Description based on 8 specimens.

*Smittia / Parasmittia* (Figure 6.3B II)
Diagnostic features: Mentum with single, broad median tooth. 5 lateral teeth. 5th lateral often tiny and sometimes difficult to distinguish on degraded specimens. Outer edge of 5th lateral distinctly inwardly curved. Setae submenti positioned near to base of ventromental plates. Occurrence: Found in Khomer Kocha Upper. Description based on 1 specimen.

*Pseudosmittia* (Figure 6.3B III)
Diagnostic features: Mentum with single, broad median tooth. 4 lateral teeth. Outer edge of 4th lateral distinctly inwardly curved. Occurrence: Found in Challacaba. Description based on 2 specimens – both heavily worn.

*Apsectrotanypus* (Figure 6.3B IV)

6.5.2) Chironomid stratigraphy
After zonation analysis no statistically significant chironomid zones were identified from either site and so the chironomid assemblages for both sites are discussed with reference to the rest of the palaeo record. The zone boundaries established from the examination of the other palaeoenvironmental indicators are shown by the dashed lines in Figures 6.4 and 6.5.
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A

Depth (cm)

Age (cal yr BP)

Chironomus
Parachironomus
Tanypodinae / Orthocladiinae
Limnophyes / Paralimnophyes
Psepheninae un. diff.
Orthocladiinae un. diff.
Non-identifiable fragment
Total Head Capsules

Head capsules/gram

20 40 60 80 100 120 140 160

20 40 60 80 100 120 140 160

B

Age (cal yr BP)

Chironomus
Parachironomus
Tanypodinae / Orthocladiinae
Limnophyes / Paralimnophyes
Psepheninae un. diff.
Orthocladiinae un. diff.
Non-identifiable fragment

%
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Figure 6.4 Palaeolimnological data for Lake Challacaba. Horizontal lines represent sample points. Dashed horizontal lines indicate the position of Lake Challacaba pollen zones (VCC-P 1-4), established by optimal sum of squares partitioning (Birks and Gordon, 1985) performed using the software ZONE v. 1.2 (Lotter and Juggins, 1991). Assessment of zonal significance was subsequently completed using the broken-stick model (Bennett, 1996; Birks, 1998) in the software BSTICK v. 1.0 (Line and Birks, 1996). A; opposite page Subfossil chironomid concentration data for Lake Challacaba, counting half head capsules as one. Inner grey shaded area marks concentrations when counting half head capsules as half. B; opposite page Subfossil chironomid percentage data Lake Challacaba. C; above) Summary pollen, spore, algal, charcoal, and geochemical / physical data Lake Challacaba (Chapter 4; Williams et al., 2011).
**Lake Challacaba**

Twenty-two samples were analysed from the c. 4,000 year sedimentary succession of Lake Challacaba, at an average sampling resolution of 200 years (median: 189). Three samples (76, 284 and 295 cm) contained no head capsules (Figure 6.4A and B). Of the remaining samples, the average head capsule concentration per gram (hc/g) was 40, with a maximum of 156 hc/g at 215 cm (c. 2,520 cal yr BP), and minimum of 7 hc/g at 275 cm (c. 3,650 cal yr BP). In total seven chironomid taxa were identified: *Chironomus, Parachironomus, Cricotopus/Orthocladius type I, Limnophyes/Paralimnophyes, Paracricotopus, Pseudosmittia and Tanytarsus* (Figure 6.3A and B).

With the exception of samples containing no head capsules, the chironomid record from Lake Challacaba is dominated by *Chironomus* and *Cricotopus/Orthocladius type I*, which together constitute 75-100% of the taxa in each sample (Figure 6.4B). As other taxa were at low abundances, the percentage plot highlights only the fluctuation in the dominance between these two taxa so the data are also presented in head capsule concentrations (Figure 6.4A). *Chironomus* concentration is relatively stable from 265-150 cm (c. 3,460–1,590 cal yr BP) with abundances of 11–20 hc/g. After 130 cm (c. 1,340 cal yr BP) concentration is reduced (<9 hc/g) which is interrupted only by a maxima (30 hc/g) at 110cm (1,090 cal yr BP) and a sample containing no head capsules at 76 cm (c. 710 cal yr BP). At some point between 370 and 190 cal yr BP, *Chironomus* disappears entirely from the record and is absent in the two uppermost samples.

The *Cricotopus/Orthocladius type I* concentration curve is defined by a peak value (142 hc/g) at 215 cm (c. 2,520 cal yr BP), which is flanked either side by reduced values at 248 and 197 cm (<10 hc/g). From 175 cm (c. 1,910 cal yr BP) *Cricotopus/Orthocladius type I* displays a gradual decreasing trend in concentration from 30 to 4 hc/g, terminating at 76 cm. After this sample, which is devoid of all head capsules, concentration increases (>15 hc/g) towards the most modern sample. Concentrations of other taxa remain very low throughout the core (<3 hc/g, <18%). Noteworthy occurrences include a peak in *Parachironomus* at c. 960 cal yr BP (100 cm), and the sporadic occurrence of *Tanytarsus* from c. 560 cal yr BP (60 cm).
Laguna Khomer Kocha Upper

Chironomid analysis was conducted on 23 sample depths from the c. 18,000 year Laguna Khomer Kocha Upper record, with an average sampling resolution of 767 years (median: 633). Head capsule concentration varied from 1 hc/g at 453 cm (c. 17,350 cal yr BP) to 215 hc/g at 413 cm (c. 12,858 cal yr BP), with a core average of 33 hc/g (Figure 6.5A and B). Five chironomid taxa types were identified; Apsectrotanypus, Cricotopus/Orthocladius type II, Limnophyes/Paralimnophyes, Smittia/Parasmittia and Tanytarsus (Figure 6.3A and b).

The subfossil chironomid record at Khomer Kocha Upper is dominated by 3 taxa, Apsectrotanypus, Cricotopus/Orthocladius type II, and Tanytarsus, representing >90% in all samples (Figure 5A and B). The major feature of the sequences is a peak in concentration in all 3 of these taxa at c. 12,858 cal yr BP, which occurs after a 5,000 year period of generally lower concentrations (0–25 hc/g). From 396.4Cm (c. 10,700 cal yr BP) the concentrations of Apsectrotanypus, a carnivorous genera, remain at relatively stable, medium to low values (2–17hc/g). For the same time period, Tanytarsus concentrations are less than 11 hc/g, with higher values (17–20hc/g) observed at 376, 303-263 and 71–51 cm. From 10,700–6,380cal yr BP cal yr BP, Cricotopus/Orthocladius type II concentrations range between 5–23 hc/g. After 203 cm (6,380 cal yr BP), Cricotopus/Orthocladius type II values decrease (<2 hc/g) and are absent from 6 of the 9 uppermost samples. Concentrations of the other taxa (Limnophyes/Paralimnophyes and Smittia/Parasmittia) remain very low throughout the core (<1 hc/g, < 3 %).
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Figure 6.5 Palaeolimnological data for Laguna Khomer Kocha Upper. Horizontal lines represent sample points. Dashed horizontal lines indicate Laguna Khomer Kocha Upper fire zones (KKU-F 1-4), determined by visual examination of changes within the charcoal record. A; opposite page) Subfossil chironomid concentration data for Laguna Khomer Kocha Upper, counting half head capsules as one. Inner grey shaded area marks concentrations when counting half head capsules as half. B; opposite page) Subfossil chironomid percentage data for Laguna Khomer Kocha Upper. C; above) Summary pollen, spore, algal, charcoal, and geochemical / physical data for Laguna Khomer Kocha Upper (Chapter5; Williams, 2011).
6.6) Discussion

The analysis of the subfossil chironomid assemblages from the sediments of Lake Challacaba and Laguna Komer Kocha Upper, has, for the first time, revealed their sensitivity to long-term ecosystem changes in the eastern Bolivian Andes. Although low in diversity (5–7 taxa types per site) and average abundance (<40 hc/g), this new inventory of taxa over the last 18,000 years, provides the first step forward in the understanding of Bolivian chironomids. When placed within the framework of change already established from the analysis of the other palaeoenvironmental proxies, adjustments observed in the dominant chironomid taxa offers valuable insight into the impacts of environmental shifts and pre-Columbian cultural change, on freshwater macro invertebrates.

6.6.1) Lake Challacaba

The 4,000 year record from Lake Challacaba spans a complicated period of changes in moisture balance and human occupation. These changes resulted in shifts in the abundance of dry tolerant and aquatic plant taxa, as well as nutrient and sediment input (Figure 6.4). Although dominated by only two taxa, the chironomid assemblage from the sediments of Lake Challacaba provide new insights into the response of lake biota to these shifts.

Lake establishment and moisture/lake level fluctuations

The complete absence of chironomid head capsules in samples prior to c. 3,650 cal yr BP, supports the previous interpretation that the early basal sediments from the site represent a period of lake formation. Pollen preservation and organic sediments indicate that a permanent lake was present at Challacaba from c. 3,820 cal yr BP. However, it was not until c. 200 years later that chironomids are preserved within the lake sediments. In addition, very low concentrations (<7hc/g) of chironomid head capsules before 3,460 cal yr BP also suggest that conditions for chironomids were poor. Chironomids are known to be rapid colonisers of water bodies (Ruse, 2010) so this apparent 400 year period of minimal chironomid abundance in a permanent lake is intriguing. Chironomids are tolerant to a wide of range of salt concentrations (Armitage et al., 1995) and have been shown to be valuable in the reconstruction of changes in past water salinity (e.g. Chen et al., 2009). However, larval numbers have been shown to decline with increasing salinity.
(Ólafsson et al., 2000) and African sites have revealed chironomids to be absent from poly- to hypersaline lakes (Verschuren and Eggermont, 2006). Therefore, it is plausible that exceptionally low water levels at Challacaba before c. 3,460 cal yr BP, possibly with periodic desiccation, resulted in a hypersaline lake. This interpretation is supported by high CaCO$_3$ precipitates in the sediments (Figure 6.4C), which are known to preferentially precipitate out with heightened salinity (Baker et al., 2001).

A peak in the production of *Cricotopus/Orthocladius type I* (60-140 hc/g) at c. 2,700–2,520 cal yr BP, coincides with the decreased abundance of *Myriophyllum* pollen (Figure 6.4C). *Myriophyllum* is a genus of aquatic macrophyte which forms dense populations in lakes and has been observed to predominate in shallow waters, 0.4-4 m deep, but not in hypersaline conditions (Ritter and Crow, 1998; Ybert, 1992). As lake level increases *Myriophyllum* becomes further removed from the centre of the lake (site of core extraction) and is restricted to the shallows, thus becoming a less dominant component of the pollen record. If the decrease in *Myriophyllum* was in response to increased salinity, it is likely a peak in salt tolerant Amaranthaceae would be observed as has been seen at other sites (Bush et al., 2010). As this does not occur at Challacaba, and there are no other indications of decreased water level and thus increased salinity (e.g. CaCO$_3$), it seems likely that a deepening of the water level resulted in decreased *Myriophyllum* abundance.

The concomitant decrease in total pollen concentration at c. 2,700–2,520 cal yr BP can also be explained by an increased areal extent and deepening of the lake which may have resulted in dilution of the pollen input. Therefore, the more than doubling of *Cricotopus/Orthocladius type I* concentration, whilst *Chironomus* shows a marginally decreasing trend, appears to be in response to a factor of lake deepening. The observation that the head capsule concentrations of the two dominant chironomid types show different patterns at this point supports an interpretation that this increase in *Cricotopus/Orthocladius type I* production is not an artefact of other lake basin processes such as decreased sedimentation rate, which should cause similar effect on all taxa head capsule numbers. Although a eurytopic organism at genus level (Brooks et al., 2007), lake
deepening and the likely associated drop in salinity and temperature appears to be favourable to *Cricotopus/Orthocladius type I* abundance.

**Human impacts**

The first significant occurrence of fungal dung spores (*Sporormiella*) at c. 1,280 cal yr BP, and a marked rise in the abundance of green algal remains (*Pediastrum*) between c. 1,280–1,090 cal yr BP, has been interpreted to indicate trading and pastoralism intensification at Lake Challacaba (Chapter 4; Williams et al 2011). Analysis of the chironomid record provides further evidence for this interpretation, as a peak in abundance of *Chironomus* is seen at c. 1,090 cal yr BP, as it becomes more than 70% of the total chironomid assemblage. Although the temperature tolerance of *Chironomus* appears to vary between hemispheres (warm tolerant north, cold resistant south) and is still unresolved even within South America, the taxon does appear able to survive in highly disturbed systems (Massaferro et al., 2009). Above all, its tolerance to increased lake nutrients (eutrophication) is well documented (e.g. Armitage et al., 1995; Brodersen and Quinlan, 2006; Brooks, 2000; Brooks et al., 2007; Massaferro et al., 2008). At Lake Challacaba the peak in *Chironomus* abundance is therefore likely to be in response to increased nutrient input, caused by the arrival of substantial numbers of domesticated herbivores (camelids) at the lake site, as indicated by the rise in *Sporormiella* spores (Figure 6.4C). A change in lake trophic status is supported by the maxima in *Pediastrum* which has been shown at other sites to represent increased nutrient in-wash (Paduano et al., 2003; Woodward and Shulmeister, 2005).

After the potential desiccation or hypersaline event which leads to the elimination of chironomids at c. 710 cal yr BP, the abundances of both *Chironomus* and *Cricotopus/Orthocladius type I* recover to low values less than <8 and <20 hc/g respectively. The disappearance of *Chironomus* from the record from c. 250 cal yr BP to present is difficult to interpret but could be related to changes recent human practices, or a warming climate.
6.6.2) Laguna Khomer Kocha Upper

Although the last c. 1,000 years are not recorded at this site, the sediments from Laguna Khomer Kocha Upper represent an important record of deglaciation and Holocene environments from the wet eastern slopes of the Andes. As found in the pollen assemblage, relative stability existed within the chironomid record for much of the last 18,000 years. However, some change within the abundances of the 3 dominant taxa does provide valuable first insights into the response of high elevation chironomids to climate adjustments, from what is interpreted to be, a site of minimal human disturbance.

The largest and most significant shift in the chironomid record occurs after c. 6,380 cal yr BP when *Cricotopus/Orthocladius* type II becomes almost completely absent. In Patagonia, *Cricotopus* has been interpreted as a warm tolerant taxa (Massaferro et al., 2009), but the disappearance at Laguna Khomer Kocha Upper at 203 cm does not appear to correlate to any temperature changes detected in the other palaeoenvironmental proxies. However, the decline in *Cricotopus/Orthocladius* type II at c. 6,380 cal yr BP does coincide with a major shift in the overall terrestrial pollen taxa, as shown by higher values in the rates of change (ROC) analysis, and is associated with a marked rise in the percentage abundance of *Alnus* (Andean Alder) pollen. *Alnus* is a pioneer taxa, growing regionally in marsh and riparian transitional Punean woodland habitats (Navarro and Maldonado, 2002), and the increase at this time indicates environmental conditions became locally wetter. This interpretation is supported by a sharp decline in burning and suggests an early ending of the Holocene dry event (Chapter 5). Increased net moisture as well as restricting fire and creating an expansion of regional marsh habitat, also appears to have increased water depth at Laguna Khomer Kocha Upper. This is evidenced by a decline in the abundance of the shallow and cool water loving aquatic taxa *Isoëtes*, indicative of water levels <4 m (Bush et al., 2005; Navarro and Maldonado, 2002; Urrego et al., 2011). The decline in *Cricotopus/Orthocladius* type II with increased water depth is in contrast to the findings from Lake Challacaba, where a peak in abundance was observed with lake deepening. Although we cannot rule out the effect of other controlling factors, the opposite responses of these taxa to increased water depth supports our interpretation that the differences observed between the two *Cricotopus/Orthocladius* types are ecologically meaningful.
Intriguingly, the chironomid record from Laguna Komer Kocha Upper does not show any response to the onset of burning that was such a dominant driver of the terrestrial vegetation at the onset of the Holocene dry event at c. 10 cal yr BP (Figure 6.5). Rates of change analysis reveal this to also be a major period of turnover in local vegetation, as woodland patches are severely reduced in size. Although there is a slight decline in concentrations of all chironomid taxa at this time, this is probably related to the increase in sedimentation rate. The peak in head capsule concentration of all the taxa at c. 12,858 cal yr BP is likely to also be an artefact of sedimentary processes (i.e. decreased sedimentation rate) owing to the sub-equal responses. The lower sampling resolution in this section of the core inhibits further interpretation.

6.6.3) Application considerations

The current paucity of modern autecological data inhibits the use of chironomids as an independent proxy for central Andean palaeolimnological investigations. Only with the knowledge established from other proxies (e.g. pollen) can the chironomid data be interpreted in a meaningful way. Although the average abundance of chironomid head capsules per sample in this study was low (<40 hc/g), the low taxon richness allows for important shifts in the abundance of the most significant taxa to be rapidly assessed. The reduction in diversity observed with elevation in this study, although only based on two locations, is in general agreement with observations elsewhere, which show a hump-shaped relationship with taxon richness and elevation, with low richness at the extremes (Bigler et al., 2006; Nyman et al., 2005). As previously discovered (Walker, 1987), this study supports the conclusion that Orthocladiinae head capsules are more prone to splitting than other subfamily groups. However, in this instance, minimal difference in the interpretation, when referring to concentration data, is observed between counting split head capsules as half (0.5) or whole (1). With such low taxon richness, the use of percentage data in representing the changes observed through time should be done so with caution as it can easily result in misinterpretation. For example, in the Laguna Komer Kocha Upper record, the percentage data of *Apsectrotanybus* shows increased abundance after c. 6,500 cal yr BP, while the concentration data reveals no significant change occurred (Figure 6.5A and B).
6.7) Conclusions

The first investigation of subfossil Chironomidae from the eastern Bolivian Andes reveals their sensitivity to long-term environmental changes over the last 18,000 years, as shown by comparison to other palaeoenvironmental proxies. As a preliminary step in addressing the paucity of current chironomid research in Bolivia and the wider central Andes, our results demonstrate that chironomid communities are represented in the lake sediments of tropical, high Andean lakes above 3,200 m asl. From the analysis of sediments from Lake Challacaba and Laguna Khomer Kocha Upper, 10 chironomid taxa were identified from three subfamily groups.

This study highlights that sufficient diversity, head capsule abundance, and species sensitivity exists at high elevation sites to investigate response to regional and local environmental changes. Although preliminary, this research has revealed the sensitivity of chironomids to changes in net moisture balance, and the associated water level fluctuations and salinity. In addition, it is apparent that at sites with a history of severe human impact, as indicated by other multi-proxy analysis, the changes in chironomid assemblages are also related primarily to adjustments in anthropogenic impacts (e.g. increased nutrient input).

Limited taxon richness at high elevation sites is beneficial to the analyst and, importantly, to consistent identification between study locations. With taxonomic consistency key to the use of chironomids as a palaeoenvironmental proxy, research effort in the currently minimally investigated Tropical Andean ecosystems must be on accurate identification. Although shown in this study to be a crucial supporting proxy for the interpretation of Bolivian sedimentary sequences, the full potential of subfossil chironomid analysis will only be realised once a concerted research focus exists, particularly the establishment of a regional training set.
6.8) Acknowledgments

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This chapter draws together the palaeoecological data presented in this thesis and assesses the implications for conservation in the Cochabamba Basin, Bolivia. First, the current threats to the ecology of the Tropical Andes are summarised. Secondly, arguments in the literature related to the practicalities of using palaeoenvironmental data as a tool for conservation science are considered. Finally, following a summary of the study location and palaeoecological results, a discussion of long-term, local- to regional-scale environmental vulnerability is presented for the Eastern Cordillera of Bolivia. In this final section, the value of palaeoecological data for informing scientists, landowners and policy makers about ecosystem functions is highlighted. The implications of these data when applied to specific questions and study locations are also considered.

7.1) Threats to the ecological value of the Tropical Andes

7.1.1) Climate threats

The Tropical Andes is one of the most biodiverse regions on Earth (Myers et al., 2000) and it is under threat from predicted future climatic changes (Malcolm et al., 2006). By the end of the current century (AD 2100), it is anticipated that the region will have warmed by up to 3.5°C, with increased heating (up to 5°C) in the area of the eastern Andean flanks situated higher than 3500 m above sea level (m asl) (Gosling and Bunting, 2008; IPCC, 2007; Urrutia and Vuille, 2009). Since AD 1975, warming of the Tropical Andes accelerated, reaching values of between 0.3-0.4°C yr⁻¹ (Vuille and Bradley, 2000). In the only study of upslope plant migration rates in the Tropical Andes (eastern Peru), Feeley et al. (2011) observed rates of plant migration of 2.5–3.5 m yr⁻¹ vertically during a 4 year period (2003/04–2007/08). These rates of upslope migration are much slower than the rates required (5.5–7.5 m yr⁻¹ vertical) in order for plant species to track the predicted movements of their respective climatic envelopes.
Whilst future temperature adjustments are predicted to be reasonably uniform, predicted changes in precipitation are much less spatially consistent and uncertain (Urrutia and Vuille, 2009). The traditional view for the Andes is that precipitation variation will follow a pattern of decreased precipitation with increasing latitude (as discussed by Killeen et al. (2007)). However, for the eastern Andean flanks, a more complex pattern of precipitation change can be anticipated because the slopes today have been shown to include spatially complex and separate super-humid, humid and dry regions (Killeen et al., 2007). The modern pattern of precipitation is controlled by a variety of factors at both small- and large-scale, include the orientation of the complex topography (i.e. Andes chain and individual valleys), and wind patterns (e.g. South American low-level jet and microclimatic air movement) (Killeen et al., 2007). As well as the spatially separate super-humid, humid and dry regions, elevation gradients (often in excess of 2000 m in 20 km) allows for large changes in climate conditions over relatively little distance. This moisture and temperature variation over short lateral (horizontal) distances results in ecological sensitivity, with small niche space envelopes.

Previous research has postulated that climate stability is linked to conservation value and highlighted several regions within the eastern Tropical Andes as targets for conservation. These include: i) stable super-humid regions, because of the high species number (diversity) and, ii) stable dry valleys due to the number of endemic species they contain (Killeen et al., 2007). However, in order to ascertain the likelihood of moisture stability persisting in the future and/or assist with detailed climate modelling, evidence of environmental change over multi-millennial time scales in these locations is needed.

7.1.2) Human threats

As well as being under threat from predicted climatic changes (e.g. rapid movement of climatic envelopes), the biodiversity in the tropical Andes is also at risk from expanding human populations (Cincotta et al., 2000). Human-driven threats include increased site access (e.g. road building), landuse change (e.g. agricultural; fires and grazing) and exploration/exploitation of natural resources (e.g. mining, oil, gas) (Jarvis et al., 2010). The continuing expansion of human populations in the Andes is placing increased pressure on limited resources, which means that people, as well as biodiversity, are likely to suffer. For example, in the central Andes, glacial retreat is reducing the long-term
sustainability of water supplies (Barnett et al., 2005; Vergara, 2007) and intensive agricultural landuse has caused severe soil degradation and loss of nutrients (Kessler and Stroosnijder, 2006; Zimmerer, 1993). These types of natural provisions, known as “ecosystem services” (Costanza et al., 1987; Daily, 1997), are increasingly being valued in terms of conservation management and in support of sustainable economic growth, particularly in developing countries (e.g. Ecosystem Services for Poverty Alleviation project; http://www.nerc.ac.uk/research/programmes/espa).

The presence of, both current and historical, human populations within a landscape is seen by some as a “threat to conservation” due to their general detrimental environmental impact (Jarvis et al., 2010). Consequently it is likely that areas near to human populations, or with a long history of human occupation, are likely to present a greater challenge to conservation than more remote or pristine environments. In locations where humans already depend directly upon the ecosystems the interaction of the populations with the environment must also be considered in terms of: i) conservation management, and ii) sustainable resources, particularly with regard to food security and water availability. To complicate matters further, human impact in the Andes, like climatic change is, and has been historically, spatially non-uniform (see Dillehay, 2008). Evaluating past human impacts in these ecologically rich regions is crucial for understanding the mechanisms which contributed to the patterns of modern biodiversity distribution (Froyd and Willis, 2008).

In summary, it is clear that the current status of the ecosystems in the Tropical Andes are under threat from both climate change and human activity. Further protection and/or assistance seems likely to be required especially given that the ability of species and communities to shift with changing climatic conditions is so severely restricted today by human influence. The vastness of the Tropical Andes, together with the varied climate and associated fauna and flora (see Sections 1.1.1–1.1.2) presents a significant challenge to conservation organisations, which have limited resources and an aim of maximising return. With conservation management encouraged to focus on long-term protection (Blossey, 1999; Verissimo et al., 2002), both for economic and ecological reasons, indications of how ecosystems might respond to future change are critical. To manage
biodiversity efficiently we must fully understand the processes behind the natural observed patterns, but many of the underlying mechanisms governing these distributions have today been destroyed by humans occupation (Nogues-Bravo et al., 2008). Therefore, the only way in which to obtain quantitative data of how ecosystems may change in the short and long-term future, is to look to the past (e.g. Birks, 1996; Dearing et al., 2006). Palaeoenvironmental data, such as that presented in this thesis (Chapters 4–6), provides a means by which to examine the long-term response of ecosystems through not only naturally varying ecological stress levels (climatic changes), but also through times of changing human cultural development (changing anthropogenic impacts).

7.2) Conservation insights from palaeoecology

Examination of past environmental change, identified from fossil record, has already shown that the climatic characteristics of the Tropical Andes have long been non-uniform and/or asynchronous spatially (see Section 1.1.3 and 1.3). Examples of spatial variability include conflicting evidence related to the nature of last glacial period (wet or dry), the timing of deglaciation, the occurrence of glacial re-advance events (e.g. presence/absence of Younger Dryas cooling) and the scale of regional drought (Holocene dry event) (see Chapters 1, 4 and 5 for a fuller discussion). Responding to these climatic adjustments, fossil pollen records provide the ability to trace past movements in vegetation zones over long time scales (>100s years). Although this examination of dynamic biogeography obtained from palaeoecological records is not as precise as modern ecological survey data, it still provides valuable data of biological responses to past climate changes. As such the information gained regarding an area’s natural ecological history (Godwin, 1956; Willis and Birks, 2006) allows researchers to not have to take into account the “shifting baselines syndrome” when attempting to quantify how a system has changed (sensu; Papworth et al., 2009; Pauly, 1995). In addition, fossil pollen records can suggest species likely to act as early indicators of ecological change (Davies and Bunting, 2010), alert scientists to unexpected, non-linear changes that may occur (Bush et al., 2010), and indicate communities which are highly vulnerable or resilient to change (Willis et al., 2010).
In response to the identified threats already acting upon the Tropical Andes, some researchers have been able to use palaeoecological data to suggest how conservation in the Tropical Andes must be adjusted to optimise ecosystem protection. Gosling et al. (2009) suggested that "mimicking" natural vegetation patterns is the best conservation approach. Bush (2002) highlighted how the protection of niche space (physical features) is more critical than the transient species and populations currently occupying them, a concept that has also been supported by recent non-palaeo based researchers (e.g. Marris, 2011; Mosblech et al., 2011). However, whether protecting niche space is successful in the most extreme environments (e.g. very high elevation), when there are few species capable of surviving in the difficult conditions at these sites, has not been fully considered. In this situation there may also be a justification for species-specific conservation.

Many of the insights gained from the analysis of palaeoecological data have already begun to be integrated into current ecological understanding and the development of broad-scale conservation concepts. These are generally applicable over large regional scales, often assessing the vulnerability, risk and value of ecosystems as a whole (e.g. Tropical Andes). However, with such heterogeneity of Andean landscapes, particularly the eastern flanks, the influences of climate and human populations differ greatly over short spatial scales and thus the past and likely future changes also vary. This highlights two key questions: i) how has landscape heterogeneity, and spatial variation in climate and human impacts in the eastern Andes, ultimately determined the relative vulnerability of the biodiversity they contain? And, ii) what are the implications of palaeoecological analysis for our future conservation approach on a local scale, with specific local concerns?

With particular reference to the data gathered in this study (Chapters 4–6), the following discussion will explore how relative threats and the magnitude of impacts in the eastern Andes of Bolivia vary spatially. By focussing on the eastern Andean Cordillera, the discussion aims to demonstrate how the conservation concepts previously identified apply on a local, site-specific scale and how biodiversity, environmental conditions and human occupation are interconnected.
Chapter 7) Palaeoecology and conservation

7.3) The Cochabamba Basin, Eastern Bolivian Cordillera

As previously discussed in Section 1.4.1, the Cochabamba Basin is a Plio-Pleistocene inter-Andean valley formed after 5.33 Ma and comprises large volumes of Quaternary sedimentary deposits (Kennan et al., 1997; McQuarrie, 2002). The surrounding mountain ranges in the Eastern Cordillera forethrust zone are comprised of quartzite, lutites and sandstone bedrock material of Ordovician age (488.3–443.7 Ma), with some granite intrusions (Cassard, 1999; Kessler, 2002b). Owing to the fertile Quaternary deposits, the Cochabamba valleys today are a major region of food production, and were a location of pre-Columbian agricultural practices and trading from earlier than 3,000 years ago (Hensen, 2002). This was intensified during the Tiwanaku (c. 1,500–900 yr BP) and Inca (c. 650–550 yr BP) rule, when a road network was developed to connect the Cochabamba valley to both upland and lowland areas (Section 1.4.4, Figure 1.12 and Chapter 4; Higueras, 1996; Janusek, 2008; Lone and Lone, 1987; Sánchez, 2008).

Regional climate, particularly precipitation, is controlled by several systems (see Section 1.1.3) including movement of the Intertropical Convergence Zone (ITCZ; Leduc et al., 2009), variability of the South American summer monsoon (SASM; Zhou and Lau, 1998), and inter-annual variation of the El Niño-Southern Oscillation (ENSO; Chiang, 2009; Philander, 1990). The climatic variation and complex topography place Cochabamba at the confluence of four Tropical Andean ecoregions (see Section 1.1.2); the Bolivian Yungas, the Bolivian montane dry forests, the central Andean Puna and the central Andean dry Puna (Olson et al., 2001). Locally, several species of endemic birds, mammals, amphibians and plants occur (Navarro et al., 2005; Young, 2007).

7.3.1) Local environmental concerns

Cochabamba has a history of environmental deterioration with increases in deforested and eroded landscapes at the cost of productive agricultural lands and ecologically rich ecosystems (Zimmerman, 1993). The roots of increased soil erosion and land degradation may stem from Inca state rule (c. 650–550 yr BP), who developed the Cochabamba valley into a maize production enclave with 14,000 agricultural workers (Lone and Lone, 1987; Wachtel, 1982; Section 1.4.4). Land grabbing following Bolivia’s independence (AD 1825) further intensified cultivation and livestock production and depleted the soils of nutrients.
rapidly. Water supply problems have also impacted upon the local environment. Driven by adverse economic conditions, increased rural–urban migration caused Cochabamba’s population to grow rapidly, particularly during AD 1980’s. This influx led to increasing water shortages and as a result forced many of the inhabitants to illegally clear and claim lands on the favourable, moist, Tunari foothills, north of Cochabamba city, which are part of Tunari National Park (Sharifi et al., 2002).

Today, detrimental impacts continue upon the landscapes that Cochabamba’s residents rely upon heavily for resource sustainment. These adverse effects on the ecosystem services display a worrying trend and recurring nature. Perhaps the most famous example, common across most developing countries in both lowland and upland area is that of landscape clearance (e.g. forest clearance) and intensive use (e.g. grazing), which results in soil degradation and ultimately land abandonment as productivity declines (for discussion see Barbier, 1997). Across Bolivia, people are becoming increasingly aware of how environmental degradation and ecosystem loss is associated with adverse impacts upon population health. Indeed, in recent months environmental protection in Bolivia has reached worldwide attention following the establishment of 11 new rights for nature, which gives “Pachamama” (Mother Earth) equal rights as humans (Vidal, 2011). This new policy is a direct attempt to stem landscape damage, protect key ecosystems and prevent further escalation of the concerns of many rural populations. For the Cochabamba Basin, one of the corner-stone ecosystems fundamental to rural communities is high elevation woodlands.

The Polylepis woodlands

The arborescent genus Polylepis is considered fundamental to the biodiversity of the high Andes (Section 1.1.2). Polylepis woodland is one of South America’s most endangered ecosystems, with 15 species of Polylepis classified as vulnerable by the International Union for Conservation of Nature (IUCN) (Jameson and Ramsay, 2007; Navarro et al., 2005). Endemic to South America, with a centre of diversity and endemism from central Peru to southern Bolivia (see Chapter 1), Polylepis woodlands today are present at more than 5000 m asl (Kessler, 2002a; Navarro et al., 2005). This high altitude survival has been
facilitated by several adaptations including increased frost resistance (Graf, 1981) and protection from increased UV-radiation (González et al., 2007).

*Polylepis* woodlands are fundamental in supporting endemic and habitat specialist species in an otherwise sparse, grassland dominated, landscape (e.g. Cahill and Matthysen, 2007; Young, 2007). As well as the biodiversity *Polylepis* supports, the woodland’s social and economic importance marks them as a unique habitat. Used for firewood, construction materials (Macek et al., 2009) and cattle fodder (Fjeldså and Kessler, 1996), the *Polylepis* woodlands have also had symbolic and social significance since Inca (c. 650–550 yr BP) times (Capriles and Bedregal, 2002). Additional ecosystem services provided by *Polylepis* have also been recognised, including the potential role of the woodlands as a substantial carbon sink and future offset, in water regulation and clean water provision, and in soil protection and erosion limitation (see Section 1.1.2; Aucca and Ramsay, 2005; Fehse et al., 2002; Fjeldså and Kessler, 1996; Renison et al., 2010; Teich et al., 2005).

In 1996, the Cochabamba Basin was indicated as a top priority conservation area for protection of *Polylepis* woodland because of the endemism, and the serious problems of increasing soil erosion and water shortages associated with forest removal (Fjeldså and Kessler, 1996). Long-term management and conservation that secures the future of *Polylepis* woodland in the Cochabamba region is especially important as much of the unique flora and fauna is associated with the long-term presence of the woodlands (Fjeldså and Kessler, 1996), and that the pressures applied to the ecosystem are set to intensify as populations and resource demands increase in the future. However, as previously ascertained (Sections 7.1.2 and 7.2), to develop an effective conservation policy, a robust understanding of the region’s natural history through periods of varying stress levels is required (Godwin, 1956; Willis et al., 2010; Willis and Birks, 2006). These baseline data provides management targets and indicates how ecosystems are likely to respond to future perturbation.
7.3.2) Local palaeoecological records

In order to investigate further the questions raised and to determine the best way to facilitate the integration of palaeoecological data into local conservation issues, two locations from the eastern Bolivian Andes will be primarily used to illustrate this discussion: Lake Challacaba (LC; see Chapters 2 and 4) and Laguna Khomer Kocha Upper (LKKU; see Chapters 2 and 5). Although situated less than 35 km apart in the surroundings of the Cochabamba Basin, examination of the environmental histories at each site reveals how the current and historical circumstance of the two locations is strikingly different, both in terms of climate and human impact. As a result, the vegetation and biodiversity of each location is unique.

Laguna Khomer Kocha Upper

Laguna Khomer Kocha Upper (LKKU; 17°16.514' S, 65°43.945' W; 4153 m asl) is situated on the eastern Andean slopes above the super-humid region of the Chapare Yungas forests (Chapter 2). Although 3500 m higher than the most humid area as identified by Killen et al (2007), the LKKU region receives year round moisture input from ground-level cloudcover which ascends on upslope winds from lower elevations, depositing large quantities of moisture on the sparsely vegetated slopes (Section 5.3; Figure 5.2; Kessler, 2002b). This additional moisture input makes the area unique compared to other eastern Andean sites. Today the local area is dominated by Andean tussock-forming grassland, within which are pockets of *Polylepis* woodland. The c. 18,000 cal yr BP sediment record from LKKU, examined in this thesis, shows that fire regime, governed by climatic variation, has long been a transformative agent in eastern Andean ecosystems (see Chapter 5). A major increase in burning (10,000–6,400 cal yr BP) was probably a function of region-wide aridity (Holocene dry event; HDE), which caused lake water levels to fall and severely reduced the abundance of *Polylepis* woodland. At c. 6,400 cal yr BP an increase in marsh woodland (*Alnus*) marked the termination of the HDE and the return to wetter conditions, which allowed *Polylepis* woodland to expand from the pockets to which it was formerly limited during the height of the aridity. Long-distance transport of pollen on upslope winds into LKKU provides a background signal of vegetation changes in the lower montane forests, and shows that adjustments in both Andean and lowland taxa can be linked to a common climatic driver (Chapter 5). In contrast to many other
reconstructed palaeoenvironmental records, there is no evidence of past human influence detected from the sediments of LKKU.

**Lake Challacaba**

Thirty-five km to the south of LKKU, and within the Vacas Lake District, a 4,000 cal yr BP sediment record from Lake Challacaba (LC; 17°33.257′ S, 65°34.024′ W; 3400 m asl) has also been investigated in this thesis (Chapter 4; Williams et al., 2011). Situated within a cold (7.2–11.3°C) and seasonally dry (2.6mm/month June–August, 114mm/month January-March), inter-Andean valley (Hijmans et al., 2005; Ritter, 2000), LC is located within a landscape that is today heavily altered by cultivation and grazing (Chapter 2; Gotkowitz, 2007). Historically, the Vacas municipality was significant in regional transportation routes (Sánchez C., 2008). The importance of camelid pastoralism and caravans for pre-Columbian peoples (Lynch, 1983) and the movement of Tiwanaku traders between population enclaves (Janusek, 2008), led many groups of people to have direct contact with the Vacas lakes.

The continuous record of the last c. 4,000 years reveals sensitivity of the site to changes driven by human and climatic factors (Chapter 4; Williams et al., 2011). Fluctuations in drought tolerant pollen taxa (Amaranthaceae and Caryophyllaceae) and calcium carbonate (CaCO₃) indicate two periods of reduced net moisture (c. 4,000–3,370 and c. 2,190–1,020 cal yr BP) compared to wetter episodes (c. 3,370–2190 and c. 1,020 cal yr BP-present). A decline in charcoal, and an increase in the invasive species *Ludwigia* and the dung fungus *Sporormiella* at c. 1,340–1,210 cal yr BP, suggests cultural changes, particularly increased camelid herding activity, were a major factor in shaping the modern landscape (Chapter 4; Williams et al., 2011). These can be correlated with major cultural transitions seen in the Tiwanaku archaeological record (Janusek, 2008).
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7.4) Vulnerabilities

In the following section, a discussion of long-term, local to regional-scale vulnerability is provided, focusing on the Laguna Khomer Kotcha Upper and Lake Challacaba study sites. Although the definition of vulnerability is variable (Adger, 2006), it is here discussed in the context of three main parameters: i) the ecosystem’s exposure to stress, ii) its sensitivity (susceptibility to stress), and iii) its resilience (ability to cope with stress).

7.4.1) Exposure

All ecosystems are exposed to some globally-impacting changes (e.g. CO₂ increase and global warming). However, geographical differences (spatial variation) between sites govern the exposure of individual sites to other local stresses. In the eastern Bolivian Tropical Andes, this is primarily the differences in the relative influence of human impact and climatic fluctuation, which can vary even over short distances (see Section 7.1). Although the level and spatial variation in short-term (<50 years) stresses can be assessed through observation and examination of historical records, in order to fully understand the long-term (>50 year) impact on the local ecosystems, a knowledge of past pressures is required. This is especially important considering that biogeography of Andean biodiversity is believed to be a result of long-term impacts of climatic conditions and human intervention. The palaeoecological records from LKKU and LC testify to this spatial variation in climatic and human impacts and help to show the formation of the current ecosystem.

Long-term climate stresses

The palaeoecological evidence suggests that LKKU, which is situated close to a super-humid climate region, has, when compared to inter-Andean locations such as LC, been in general impacted less by past climate change events. Although a direct comparison can only be achieved over the period c. 4,000-1,000 cal yr BP, the data suggest that the vegetation around LKKU (Chapter 5) shows minimal response to the millennial-scale moisture fluctuations seen at LC (Chapter 4), as indicated by large-scale variation in Amaranthaceae, Caryophyllaceae and CaCO₃. Additionally, preservation of a water body at LKKU during regional-scale aridity of the mid-Holocene contrasts to the desiccation of LC before 4,000 cal yr BP. So while regional-scale (Andes and Amazon) drought events
occurred, a continuation of ground-level cloud cover at LKKU throughout this time was sufficient to contribute moisture and reduce UV exposure (evaporation), maintaining an inundated lake basin (Chapter 5). The presence or absence of this additional moisture source is directly a result of geographic and topographic location of the site. If super-humid regions are more stable due to geographic setting, as suggested by the palaeo-record of LKKU, they may be consequently less vulnerable to predicted climate changes of the future, particularly precipitation adjustments.

**Human stresses**

The records from LLKU and LC highlight how the impacts of humans are spatially variable over relatively short distances (<50 km) and are dependent on favourable environmental conditions and resource availability. Areas considered rich in biodiversity might not be under as much threat from human occupation as sites considered ecologically poor today. Moist, high elevation slopes favourable for the development of important ecosystems such as the upper Yungas, are avoided by humans due to the extremes in temperatures, heavy precipitation, difficult access and scarcity of cultivatable lands (see Bush, 2002). While the exposure to human stresses is undoubtedly the reason for the differences seen in degradation at each site, it should not be assumed that all human exposure is necessarily detrimental. Humans were probably present in the landscape around LC for the last 4,000 years (Chapter 4; Williams et al., 2011), but it is only during the last 1,000 years that major impacts of their presence can been seen.

Unless all *Polylepis* woodland clearance was completed in the Vacas Lake District prior to c. 4,000 cal yr BP, the pollen record of LC reveals no systematic or abrupt decline in woodland abundance during this time (Chapter 4; Williams et al., 2011). Although it is clear that modern human impacts are responsible for current clearance and slowing regeneration / re-establishment, predominantly via fire (Hensen, 2002; Renison et al., 2006) and increased grazing impact (Cierjacks et al., 2008; Renison et al. 2004; 2005; Teich et al., 2005), controversy still remains regarding the natural extent of *Polylepis* woodland (Section 1.1.2; Aucca and Ramsay, 2005; Kessler, 2002a). This has big consequences for the understanding of woodland dynamics and the setting of conservation targets. Fjeldså and Kessler (1996) estimated that only 10% of the original
extent remains in Bolivia today, a largely speculative assessment based upon niche-space defined models and the knowledge of a long human history in the Andes (see Section 1.1.2). However, interpolating the current level of human impact upon Polylepis forests close to inhabited areas back through history is unwise. To assume the level of detrimental impacts (exposure) that have been observed over recent times (i.e. last 50 years) also occurred since human occupation began, and civilizations formed (e.g. Tiwanaku – last 1000 years), may give misleading interpretation of the previous woodland abundance and structure. Using short-term observations to form views on long-term trends in woodland abundance is naïve and resembles the problems associated with the shifting baseline problems as previously discussed (Section 7.1). Palaeoecological analysis is the only way to resolve this problem and provide data on trends. Using this approach, the LC pollen evidence reveals that there was no significant change in woodland abundance during a time when humans were continually present upon the landscape (Chapter 4; Williams et al., 2011).

In heavily impacted “cultural landscapes” such as the Vacas Lake District, human occupation in the past has certainly been important in shaping the modern ecosystems. However, populations may well have also assisted with the preservation of ecosystems we are striving to conserve (see Froyd and Willis, 2008). For example, Polylepis woodlands were strictly protected during Inca (c. 650–550 yr BP) times who had high regard for the naturalness of the woodlands and their symbolic and social meaning, which resulted in very specific forest management (Capriles and Bedregal, 2002). Some of these beliefs are likely to have been perpetuated in modern rural cultures and some practices do exist in modern communities that protect local forest patches as valuable resources (Fjeldså, 2007). If this type of forest stewardship can be developed and expanded, the exclusion of humans from woodland patches would be unnecessary and, perhaps, detrimental to biodiversity conservation. The passing of the new rights for nature laws (Section 7.3.1), inspired by the indigenous Andean spiritual view (Vidal, 2011), may represent a significant step in reintroducing this type forest stewardship.
7.4.2) Sensitivity

The susceptibility and sensitivity of an ecosystem to the stresses imposed upon it are complex. Regionally, *Polylepis* has been shown to be highly sensitive to fire (Gosling et al., 2009), and data from LKKU has shown that when fire increases *Polylepis* woodland is rapidly reduced in abundance (Chapter 5; Figure 5.4). However, while this relationship appears straight-forward, ecosystem responses are complicated by feedback mechanisms which can introduce non-linear changes (see Bush et al., 2010). Palaeoecological data which records species and community-level sensitivity to change is a potentially useful tool in assessing these ecosystem responses.

*Ecological indicators*

Mountainous regions have already been identified as sensitive to changes in environmental processes and climate change, so much so that they have been labelled as “early warning indicators” (Ørbæk et al., 2004; Tiberti et al., 2010). However, the changes to expect following future warming are unknown and are certain to be site specific. If sensitive ecological indicators of past environmental change can be identified from the palaeoecological records, they have the potential to be useful markers of future ecosystem shifts.

From the analysis of the Cochabamba records some ecological indicators of change can be suggested. *Hedyosmum*, a genus of tree and shrubs occurring in the Bolivian montane forests below LKKU, shows rapid expansion upslope as climate warms during the deglaciation period (Chapter 5). Modern analysis of upslope migration rates from the eastern Peruvian Andes showed that *Hedyosmum* had one of the fastest (16-25 m yr$$^{-1}$$) during a four year period when temperatures were warming at around 0.04°C yr$$^{-1}$$ (Feeley et al., 2011). As one of the few taxa potentially able to keep pace with climate changes, *Hedyosmum* is therefore likely to persist and perhaps is less vulnerable to future extinction.

At LC, in a landscape dominated by human occupation, the palaeoecological record shows that the arrival of an invasive plant (*Ludwigia*), associated with human occupation, had the most influence of the lake margin vegetation over the last 4,000 years (Chapter 4;
Williams et al., 2011). With increasing human impact predicted in the region, it seems logical to suggest that additional arrivals could feature in the future, as humans alter the ecosystems, create new niche spaces and act as a transport mechanism (either accidental or deliberate). If, as with the case at LC, species currently present can be shown to have arrived in response to human impacts, it highlights the usefulness of palaeoecology as a tool for addressing many questions regarding biological invasions (Froyd and Willis, 2008). This includes examining the impacts, rates of spread and how we classify species (e.g. how long does a species need to have been present to be classified as a natural ecosystem component?).

7.4.3) Resilience

The ability of an ecosystem to cope with stress and absorb disturbance (Holling, 1973), is another topic for which where palaeoecology offers great potential to provide data useful for conservation practice (Froyd and Willis, 2008). Understanding the limits of species/community resilience identifies key ecological thresholds of ecosystem change. Without palaeoecological analysis the critical point of change would remain unidentifiable and unexpected. From the Cochabamba palaeo-records several examples can be cited. Two examples will be discussed, one from changes seen in the terrestrial vegetation, and one in the chironomid assemblage.

**High Andean woodland resilience**

Polylepis has already been shown to be regionally and locally highly sensitive to fire (see Section 7.4.2), with a rapid reduction at LKKU during the Holocene dry event (HDE) which elevated burning. Despite the decline of Polylepis pollen in the record during the HDE (10,100–6,400 cal yr BP) (to less than <1%), woodlands remained present in the locality (probably on the scree slopes, which act as natural fire breaks). The local persistence through the HDE would have helped the re-establishment of larger woodlands once the climate had changed to more favourable wetter and consequently less frequently burnt landscape at 6,400 cal yr BP (see Chapter 5). Although reduced in abundance during the HDE the ability of Polylepis to endure unfavourable conditions and not become locally extinct is evidence of its natural resilience to arid climate condition. Small groups of trees preserved in niches governed by micro-climates allowed Polylepis to quickly re-establish
at the onset of more favourable conditions. The rapid expansion of *Polylepis* has also been observed periodically in the 370 ka cal BP pollen record from Lake Titicaca, which indicates maximum abundance during transitional warm and wet periods (Gosling et al., 2009; Hanselman et al., 2011).

Although *Polylepis* returned to LKKU after the HDE, the pollen record from Lake Refugio in the eastern Peruvian Andes revealed that woodlands did not re-establish there. The failure of *Polylepis* woodland to re-establish at Refugio has been associated with the arrival of people in the landscape (Urrego et al., 2011). Human activities provided a source of fire ignition in the area, which extends to today and prevents expansion of the woodlands after their 'natural' suppression during the HDE. It is therefore apparent, that *Polylepis* has developed a natural resilience to aridity (persisting in small ecological niches) but is not necessarily adapted to endure elevated human impacts which effectively cut the natural cycle of woodland expansion and contraction.

The palaeoecological record can also provide information on the impact of landscape degradation by human activity, *(i.e. where woodland taxa are not sufficiently resilient to withstand the climate and human stresses)*. At LC human populations responded to changes in resource availability by switching from the collection and burning of fuelwood, to the utilization of dried dung as camelid numbers in the area increased rapidly (Chapter 4; Williams et al., 2011). Dried cattle/camelid dung has long provided an alternative fuel to wood fires (Janusek, 2008), and in many rural Andean regions today dung acts as an important energy source and in Bolivia accounts for 19% of total biofuel use (Winterhalder et al., 1974; World Bank, 1994; Yevich and Logan, 2003). This cultural adjustment at c. 1,300-1,000 cal yr BP had apparently no major detrimental effects on the human population of the area *(e.g. no abandonment)* and may have possibly even had positive effects, as the time spent gathering fuel wood could be allocated to other tasks (Chapter 4; Williams et al., 2011).
Lake macro-invertebrates

From the analysis of subfossil chironomids from the sediments of LKKU and LC, the decline of *Cricotopus / Orthocladius* type in LKKU from c. 6,500 cal yr BP is a key shift observed in the record (Chapter 6; Figure 6.4). Throughout the previous 12,000 years, this taxon had been continually present at the LKKU, through periods of regionally recognised temperature amelioration and decreasing wetness. Even during the height of the HDE, *Cricotopus / Orthocladius* persisted, as did all other taxa identified in the record (Figure 6.4). However, a rapid onset of wetter conditions marked by an expansion of marsh woodland (*Alnus*) at lower elevations, and a fire frequency decline, coincided with a decline in *Cricotopus / Orthocladius* from the lake after c. 6,500 cal yr BP. Because of the infancy of chironomid research in Bolivia, and generally across the Andes (Section 6.2), causes for this decline are speculative. However, there is no indication of any human impact at the site during this time (Chapter 5) and, with the evidence available, this shift in the chironomid assemblage appears linked to moisture increase and the associated impacts of lake deepening and increased in-wash. These findings are further indication that moisture is a key driver of biotic organisation in the Tropical Andes.

7.5) Implications

7.5.1) Conservation and vulnerability

Undisturbed super-humid locations in Tropical Andes have been identified as critical for conservation targets due to the high biodiversity they maintain (Section 7.1.1; Killeen et al., 2007). Evidence from the palaeo-records from the Cochabamba Basin suggests that moisture balance does indeed underpin the spatial variation in biodiversity (Chapters 4–6). Therefore, while the palaeoecological data support the interpretation that conservation of these “wet spots” is important, it should not be at the expense of those areas which are already impacted by humans. Indeed, some plant species thrive in disturbed landscapes (Kessler, 1999) and there is a close relationship between avian biodiversity and ancient population centers, which possibly stimulated the development of rich, co-adapted, species and communities (Fjeldså, 2007).
The protection of sites such as LKKU are likely to be deemed more important to non-local groups due to the current, more natural status of the associated ecosystems, often a result of remoteness and limited accessibility. However, the management at sites such as LC and the Vacas Lake District are more valuable to local populations. These locations pose a greater conservation challenge as policy must balance biodiversity and yet continue to support a population that, as with the whole Andes, is expected to increase in the future. Maintaining ecosystem services requires careful assessment of the ecology and examination of the complex impacts of increasing human populations. For example, increasing water shortages due to growing populations will deplete the freshwater input to valuable lakes such as LC, limiting the provision of drinking water and food (aquatic vegetation) important for cattle (Section 4.2.1).

The adaptability of human populations is also apparent in the palaeoecological records. As well as highlighting how ecosystems, communities and species adjust to environmental changes, the palaeoecological data also shows that past human populations are able to absorb changes occurring in the landscape and adapt practices accordingly. Examples of such adjustments include: i) switching fuel source (Chapter 4; Williams et al., 2011), and ii) developing agroforestry (Chepstow-Lusty and Winfield, 2000). However, in order to facilitate future adjustments it is essential that the opportunity and ability of both ecosystems and people to adapt is maintained.

7.5.2) The future of *Polylepis* woodlands

Considering the ecosystems services provided by *Polylepis* woodlands for the communities of the high Andes (Section 7.3.1), it is imperative that their importance is highlighted to landowners. If the benefits of woodland protection can be promoted, local forest stewardship can result in improving ecosystem services whilst simultaneously supporting the local biodiversity.

The palaeoecological data discussed here demonstrates that if given the opportunity, following times of unfavourable conditions, *Polylepis* woodlands will recover and their history of expansion and contraction as climate changes, highlights the woodland’s resilience (Chapter 5; Section 7.4.3). As previously discussed, there is evidence from
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Palaeo-records and non-palaeo research that highlights the need for the protection of niche space and physical features over the transient species and communities that inhabit them (see Section 7.2). For high Andean Polylepis woodland this is also crucial, as there is need to maintain features such as boulderfields, scree slopes and protected gulleys which act as natural fire breaks allowing Polylepis to remain locally present even during the most unfavourable climatic times (chapter 5). However, there is no evidence that other tree/shrub communities expanded to fill the niche-space made available when Polylepis woodland was most restricted (Figure 5.4). In contrast, grasses, which have already been shown to be abundant on the landscape, appear to have been the main beneficiary of a reduction in woodland. With high Andean woodland clearly crucial for supporting biodiversity and for providing ecosystem services to local human populations, and with no other arboreal taxa able to survive in such harsh environments as Polylepis, there is justification for a species-based, as well as niche-based, conservation approach. Ultimately, removal of Polylepis woodland, either by natural landscape transformative processes (e.g. aridity-initiated fire) or by more selective human processes (e.g. cutting for timber or fuel), will reduce the biodiversity of the area.

To address the importance of Polylepis woodlands in supporting biodiversity, land managers in the high Bolivian Andes are already encouraged to use Polylepis over exotic tree species for the control of erosion and for the provision of firewood (Fjeldså and Kessler, 1996). While this practice should continue, land managers must start to take into account the findings established from local and regional palaeoecological records. Current projects such as the Asociación Ecosistemas Andinos (ECOAN) in Peru have initiated the planting of 60,000 Polylepis racemosa trees, in a direct attempt to join up fragments of existing woodland (Aucca and Ramsay, 2005). But if the ultimate conservation aim is to restore the natural ecosystem state, we must “mimic” the vegetation structure seen in the palaeoecological records.

From the currently available records across the eastern central Andes, there is no evidence that Polylepis woodland ever formed a continuous forest habitat (Chapters 4 and 5). This suggests that even in the absence of human impacts, woodlands always remained in isolated stands within an Andean grassland matrix. Planting project such as
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ECOAN, which aim to link up woodland patches, take no account of how the modern vegetation structure was formed. Indeed, it has been shown that species endemism is highest at woodland patches and not in the continuous forest belts (Fjeldså and Irestedt, 2009) and so linking up woodland patches may actually be detrimental to the overall biodiversity.

7.6) Conclusions

Palaeoecological data are a valuable source of information for conservation-related questions and provide a tool which can provide data relevant for policy makers. However, to determine conservation priorities, objectives must already be set (e.g. maintain as much naturalness as possible, help balance human-environment interactions, or provide much needed resources). Assessing local risks to vulnerable biotopes is crucial and one which conservation policy makers must engage with local people. However, background information regarding the impact and duration of past human intervention there has been in an area is also essential and there is urgent need for evidence-based conservation. In this respect, the multi-proxy analysis of palaeo-records, such as those presented in this research, are fundamental for conservations managers who must make informed decisions based on the data available to them from across the whole scientific community.
Chapter 8) Conclusions

In this chapter, the main findings of the thesis are summarised. First, the thesis rationale is reviewed before concluding remarks are made specifically addressing the original research goals outlined. Secondly, suggestions for future work and further application of this research are discussed.

8.1) Summary of thesis rationale and objectives

Population growth and predicted global climate change are applying new, and increasing, pressure to Andean environments, but the consequences of these changes upon the biodiverse and vulnerable Tropical Andean ecosystems are poorly understood. Past environmental shifts can be used to obtain empirical data that demonstrates how these ecosystems are likely to respond to future change. Via the use of palaeolimnological studies, the sensitivity of the Tropical Andean ecosystems to historical environmental changes allows the evaluation of long-term ecological adjustments.

The last c. 21 ka is a critical time period for understanding human and climate interactions in the Andes because it contains: i) the last major global climatic change (full glacial to interglacial transition, and ii) the arrival and subsequent spread of humans throughout South America (see Chapter 1). The deglaciation period and early Holocene represents the most recent time when the ecosystems of the Tropical Andes were not substantially influenced by human practices, but were exposed to naturally varying ecological stress levels. The subsequent development of human culture through the Holocene lead to changes in resource uses and practices, such as land use change, agricultural and animal domestication, which placed a unique set of pressures upon the ecosystems they occupied.

Due to the complex human-climate-ecosystem interactions (Chapters 1 and 3), a history of climatic changes and human impacts is essential before we can fully understand the threats imposed upon ecosystems today, and demonstrate how they are likely to respond to future change. However, the history of the Tropical Andes, as with much of the
Neotropics is still insufficiently understood and fragmentary due to a paucity and uneven spread of archaeological and palaeoenvironmental records. The correlation of changing environments and human cultures, together with assessing the scale and nature of human-environment interactions, is an important issue that warrants continued discussion and debate.

The intent of this thesis was to improve understanding of human-ecosystem-climate interactions by tracing Tropical Andean ecosystem adjustments of the past using the sediment records from two lakes in the eastern Bolivian Andes. How the three specific research aims, detailed in Chapter 1 (Section 1.3) and reproduced below, have been addressed are summarised in the following sub-sections.

The research aims were:

i. To determine the scale and impact of climatic events, climate system adjustments and ecosystem responses in the Bolivian Andes since deglaciation, and to examine the uniformity and correlation of these changes to other Andean locations.

ii. To determine how pre-Columbian population enclaves, distant from the civilization centres of Cusco and Tiwanaku, impacted the landscape that they occupied, via the exploitation of agricultural development, domestication of animals and fire. To examine if these impacts were wholly detrimental to the biodiversity of the Tropical Andean region in which they existed.

iii. To assess the drivers governing the current distribution of Polylepis woodland and Andean grassland, and determine if the historic growth patterns suggests a previous, more widespread dominance. To provide new data useful for conservation policies and management strategies to assist with the replication of the natural ecosystem structure.
8.2) Specific research findings

8.2.1) The scale and impact of climatic adjustments

To determine the scale and impact of climatic events, climate system adjustments and ecosystem responses in the Bolivian Andes since deglaciation, and to examine the uniformity and correlation of these changes to other Andean locations.

The complete paleolimnological histories of Laguna Khomer Kotcha Upper and Lake Challacaba have revealed that ecosystem adjustments in the Cochabamba Basin, Bolivia, have been driven by climatic factors during the last c. 18 ka (Chapters 4-6). The multi-proxy analysis, particularly the combination of pollen, charcoal and chironomid assemblages, has, for the first time, identified biological changes within the lake system and in the local and regional terrestrial vegetation of the eastern Bolivian Andes. This research has explored the sensitivity of the preserved ecological markers (fossil pollen, spores, charcoal, chironomids) in the detection of both major and subtle environmental changes, including temperature, net moisture availability and the associated variations in vegetation, fire regime, water level and salinity.

The sediment record from Laguna Khomer Kocha Upper, dating back c. 18 ka cal BP shows that climatic variation and the associated changes in fire regime, have long been a transformative agent of local and regional vegetation in the high Andes. The deglaciation period during the Late Pleistocene (c. 18-10 ka cal BP), was a relatively gradual climatic transition in the eastern Andean flanks (Section 5.6.1). In contrast to palaeo-records from the Altiplano, as discussed in Sections 1.1.3, there is no evidence for the occurrence of globally known climatic events such as an interstadial or Younger Dryas-type stadial in the proxy data from Laguna Khomer Kocha Upper (Section 5.6).

The onset of the fire activity from c. 14.5. ka cal BP, with a major increase at c. 10.1 ka cal BP (Section 5.6.2), steadily transformed the local vegetation (i.e. decreased abundance of high elevation woodland) but had only minor impacts on lake biota (Section 6.6.2). The change in burning regime was driven by an increase in regional climate aridity, and the fluctuations observed confirms that the Holocene dry event was multi-millennial in
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duration (c. 10.1–6.4 ka cal BP) and was punctuated by episodic wet phases (Section 5.6.2). In contrast to other central Andean lake basins, the continuation of the ascending ground-level cloud cover from lower elevations was sufficient to maintain an inundated lake basin at Khomer Kocha, highlighting both the importance and spatial variation in Amazon derived moisture input (Chapter 5). Increased moisture availability at c. 6.4 ka cal BP, caused a decline in burning, a rapid adjustment in local and lower elevation vegetation (Section 5.6.3) and an increase in lake depth (Section 6.6.2; Figure 6.5). This onset of generally wetter conditions concurs with the timing of similar adjustments at other eastern Andean locations (as discussed in Chapter 5).

From the 4 ka cal BP record of lake Challacaba, fluctuations in the abundance of drought tolerant plants (e.g. Caryophyllaceae, Chenopodiaceae/Amaranthaceae; Chapter 4; Figure 4.), shifts in chironomid assemblages (Section 6.6.1.; Figure 6.4) and variation in the geochemical data (Figure 4.3), indicate two periods of reduced moisture availability and increase salinity (c. 4–3.3 and c. 2.1–1 ka cal BP) compared to adjacent wetter episodes (c. 3.3–2.1 and c. 1 ka cal BP to the present day). These moisture fluctuations can be correlated to variations in the El Niño/Southern Oscillation. The aridity before c. 3.3 ka cal BP is also linked to the latter stages of the region wide Holocene dry event (Chapter 4; Williams et al., 2011). As previously discussed, the timing of lake formation at Lake Challacaba, is concomitant with those seen in other dry, inter-Andean locations across the Andes (Section 4.5.1). However, in comparison to the closest alternative study site, Laguna Khomer Kotcha Upper (35 km north), the occurrence and timing of climatic adjustments are non-uniform. This finding highlights the spatial variation of climatic change and ecosystem vulnerability in the biodiversity hotspot of the Tropical Andes, a factor of the heterogeneity induced by the complex Andean topography (Chapter 7).

As well as recording the environmental history of local vegetation dynamics, long-distance pollen transport provides evidence of changes in more distal vegetation zones. At Laguna Khomer Kotcha Upper, the sensitivity of the lower elevation montane forests to burning regime changes is identified (Chapter 5). The simultaneous changes in both Andean (local) and lowland (distal) taxa (Figure 5.4), suggests that vegetation dynamics in the two environments can be linked to a common climatic driver.
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8.2.2) Pre-Columbian populations

ii. To determine how pre-Columbian population enclaves, distant from the civilization centres of Cusco and Tiwanaku, impacted the landscape that they occupied, via the exploitation of agricultural development, domestication of animals and fire. To examine if these impacts were wholly detrimental to the biodiversity of the Tropical Andean region in which they existed.

With the limited number of archaeological sites in, and around, the Cochabamba Basin, this thesis has provided important new findings relevant to expanding the current knowledge of pre-Columbian cultures (i.e. those present in South America prior to the arrival of Christopher Columbus during AD 1492). The research presented here has explored patterns of perceived vegetation change attributed to human activity (i.e. landscape exploitation), and suggests how ancient human populations may have responded and adapted to environmental change (Chapter 4; Williams et al., 2011).

The multi-proxy analysis of the sediments from Lake Challacaba has revealed the importance of the Vacas Lake District as a site of human occupation during the last c. 4 ka (Chapter 4; Williams et al., 2011). Although the ancient road network passing through the Vacas district had previously been identified as important during Incan times (c. 0.6-0.5 ka cal BP), little was known about the longevity or history of this trade route (Sections 1.4.4 and 4.2.1). From the examination of fossil pollen and spores (e.g. the dung fungus *Sporormiella*) from the Lake Challacaba record (Chapter 4; Williams et al., 2011; Figure 4.4), this research provides evidence indicating that the road network was in use by at least c. 1.2 ka cal BP, suggesting that Andean and lowland areas were connected, by trade routes through the Cochabamba valleys, before the end of Tiwanaku state (1.5–0.9 ka cal BP).

The charcoal record indicates that the local ecosystem has been under anthropogenic influence for the duration of the Challacaba record (c. 4 ka; Figure 4.4). Despite the presence of human activity, there appears to have been no decline in highly sought-after wood resources (e.g. *Polylepis* and *Alnus*) regularly documented in many other Andean
records (Section 4.5.4). This has highlighted the danger of directly linking human presence in the landscape with degradation of high Andean ecosystems (Section 7.4).

A marked change in the preserved ecological assemblages between c. 1.3 and 1 ka cal BP, has been one of the most intriguing findings of the Challacaba record and of this thesis as a whole (Section; 4.5.6; Figure 4.4). A decline in charcoal and an increase in camelid numbers (*Sporormiella*), lake nutrient input and landscape disturbance (*Pediastrum* and *Chironomidae*), and the arrival of an invasive plant (*Ludwigia*), indicate elevated pastoral agriculture from this time (Chapters 4 and 6). The timing of this shift is broadly coeval with the fragmentation and later collapse of the Tiwanaku state (c. 1000-900 cal yr BP), which is linked to prolonged drought on the Altiplano (Section 1.1.4). The data from the Challacaba record, demonstrates that the development and fragmentation of the Tiwanaku civilisation had knock-on-effects for the distance populations in the Cochabamba Basin, providing strong evidence that this region was under Tiwanaku control and within their sphere of influence (Chapter 4; Williams et al., 2011).

In summary, the ecological assemblages (pollen, spore, charcoal, algal and chironomid) from the Lake Challacaba record during the last 1 ka differ to those from any other time during the preceding 3 ka. This environmental change is likely to be associated to cultural adjustments lead by the development and subsequent declines of the Tiwanaku and Inca states (as discussed in Section 1.1.4). Over this period, we also have an indication of how human populations adapted to changing conditions and were able to utilise new, readily available, resources, such as the inferred increase in the use of camelid dung as a fuel source (Sections 4.5.3 and 7.7.4.3). In addition, the landscape scale spatial variability of change within the Andes has been explored (Chapter 7). While the effects of human impact were obvious at Lake Challacaba, there is no evidence for their impacts in the environment around Laguna Khomer Kotcha Upper during the entire duration of the recovered record (c. 18-1 ka cal BP; Section 7.4.1). Although the lack of a human occupation signal at the this site limits the conclusions that can be made regarding pre-Columbian impacts on the moist eastern ranges, it does signify the importance of Laguna Khomer Kocha Upper in providing a record of vegetation response to climate without anthropogenic influence, a rare situation in Tropical Andean palaeoecological records.
8.2.3) The natural history of the *Polylepis* woodlands

*iii.* To assess the drivers governing the current distribution of *Polylepis* woodland and Andean grassland, and determine if the historic growth patterns suggests a previous, more widespread dominance. To provide new data useful for conservation policies and management strategies to assist with the replication of the natural ecosystem structure.

As *Polylepis* woodlands are such an important component of the high Andean ecosystems of Bolivia (Sections 1.1.2 and 7.3.1) they have had a prominent role in the discussions throughout this thesis (Chapters 1–8). The analysis of the c. 18 ka cal BP sediment record from Laguna Khomer Kocha Upper (Chapter 5), demonstrated that fire regimes were critical in determining the niche-space available for *Polylepis* woodland growth and that fire has long been a transformative agent of eastern Andean vegetation as a whole (Section 5.6). In a local environment free from human intervention, fire, controlled by climatic aridity, facilitated the expansion and contraction of *Polylepis* woodland patches in a landscape otherwise dominated by Andean grassland (Figure 5.4).

While there can be no doubt that in recent times (i.e. last 50 years) human practices are, in general, detrimental to *Polylepis* woodland (Sections 1.1.2 and 7.3.1), harmful human impacts over longer time scales are more variable. High resolution analysis of the last four millennia from the sediments Lake Challacaba shows non-uniform human impacts, both in occurrence and effect. Also at Lake Challacaba, there is no evidence that human occupation in the Vacas area resulted in either abrupt or gradual woodland clearance (Chapter 4; Williams et al., 2011).

The palaeoecological data presented in this thesis supports a conclusion that, during the last 18 ka, *Polylepis* woodlands never formed a continuous forest belt at high elevations (> 3000 m asl) in the eastern Bolivian Andes. Contrary to perceived ecological understanding (see Section 1.1.2), the palynological data from Laguna Khomer Kocha Upper and Lake Challacaba both suggest that the woodlands maintained a patchy distribution both before and during human arrival (Chapter 4 and 5). There is no
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indication that human impact alone was responsible for creating the woodland structure observed today. Instead, palaeoecological analysis of the sediments from Laguna Khomer Kocha Upper highlights the role of *Polylepis* woodland’s long-term sensitivity to fire regime and moisture availability and identifies these as the key drivers of the woodland/grassland matrix (Section 5.6).

The importance of maintaining woodland patches for biodiversity and ecosystem services, both near and remote from human populations, has been identified from the literature (Section 1.1.2) and extensively discussed in this thesis (Chapter 7). This research supports the importance of *Polylepis*, by highlighting it’s unique resilience and ability to survive under harsh environmental conditions that are associated to the high elevations of the eastern Andes (Section 7.3.4). The palynological data shows, that in these harsh environments, no other arboreal taxon was able to replace *Polylepis* woodland when it’s abundance was reduced (Chapter 5; Figure 5.4). These findings have major implications for conservation, as loss of high elevation woodland would have severe consequences for the biodiversity of the associated plants, birds and mammals supported (see Section 1.1.2). Therefore, there is clear justification for a species-based, as well as niche-based, conservation approach (Section 7.5.2).

Although justifying a species-based conservation approach and supporting the ongoing *Polylepis* re-establishment projects underway in the Andes (e.g. ECOAN; Section 7.5.2), the palaeoecological data from the Laguna Khomer Kocha Upper and Lake Challacaba study sites has provided new baseline data of woodland distribution patterns. These data indicate that the woodlands never formed a continuous habitat and therefore planting strategies, such as ECOAN, must aim to recreate and mimic the natural patchy distributions observed from the palaeoecological records (as discussed in Section 7.5.2).
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8.3) Suggestions for future work

8.3.1) Data collection

Much progress has been made over recent decades in the identification and interpretation of Andean/Amazonian pollen records, including the modern transport mechanisms and the spectra typical of a variety of tropical ecosystems (Sections 1.2 and 3.4.1; Chapters 4 and 5). However, as highlighted by this thesis, the paucity of modern autecological chironomid data and taxonomic keys for the Andes remains a large stumbling block in the interpretation of subfossil Chironomidae from paleolimnological records (Section 6.2). As demonstrated by this research, at present, subfossil chironomid analysis has to be combined with other proxy data (e.g. palynological, charcoal and geochemical) that quantify the variables in order to provide meaningful conclusions (Section 6.6.3). However, data presented here (Section 6.5; Figures 6.4 and 6.5) suggest that changes in the chironomid assemblages can indicate environmental changes not detected by other proxies. Therefore, a research focus must be developed to advance the analysis and interpretation of subfossil Chironomidae from the central Andes of Bolivia/Peru. Primary steps in addressing the current knowledge gap must include: i) an inventory of species present in central Andean water bodies, and ii) the association of these species to water properties, terrestrial climatic conditions and lake basin vegetation. Examining the distribution of species under modern conditions will unlock the full potential of subfossil chironomid analysis and allow researchers to pursue a previously under exploited tool in the examination of new and existing palaeoenvironmental records from the region.

Perhaps one of the more obviously lines of future research, which will build upon the findings of this thesis, is the extraction of longer and more complete limnological records from the study region. The sediment cores obtained from Lake Challacaba have provided a detailed analysis of human-climate-vegetation interactions over the past 4 ka highlighting that the Vacas Lake District was an important location on a pre-Columbian roadway network (Chapter 4; Williams et al., 2011). However, preliminary investigation at the other lakes in the area indicate that a much longer record is likely to be available (Section 1.4.1; Table 1.2; Figure 2.1). The deep (>13 m) glacial scour lake of Acerokocha, 3 km west of Lake Challacaba, is anticipated to contain a record dating from at least the last
glacial maximum (c. 21 ka cal BP). Analysis of the surface sediments from Acerokocha have already revealed that chironomid and pollen is persevered (not shown in the thesis), and with the lake easily accessible by an off-road vehicle, a coring attempt should be made a future priority. Obtaining a record of equal length to Laguna Khomer Kocha Upper from the Vacas Lake District would allow new and fuller comparisons to be made between two sites dominated by opposing geographic location, precipitation regimes and human histories. Extending the record from the Vacas Lake District would also allow testing the conclusion made in this thesis: that no large scale Polylepis clearance occurred with the arrival of humans. With a scarcity of pre-Incan archeological sites in Bolivia (see Sections 1.1.4 and 1.4.4), the examination of palaeoenvironmental records has the potential to continue to fill a void in our knowledge of how early humans adapted to changing environmental conditions and how they may have shaped the modern landscape.

Obtaining additional sedimentary records from the surrounds of Laguna Khomer Kocha Upper should also be a future target. As the uppermost 1 ka of sediment could not be collected from the lake itself during the fieldwork of 2007, returning with additional surface sampling equipment may allow these sediments to be captured. An alternative for obtaining this recent time-period would be to core the area of waterlogged ground adjacent to the lake (see Section 2.2.1; Figure 2.6). Tracing the environmental history through the last 1 ka would allow better understanding of the recent vegetation dynamics and provide a pollen spectra that can be directly related to the modern Polylepis woodland structure and abundance. The surprisingly long record extracted from Laguna Khomer Kocha Upper (413 cm; c. 18,000 ka cal BP), suggests that older sediments could possibly be contained within the larger and deeper (>10 m) basin of Laguna Khomer Kocha (Lower), situated at 3900 m above sea level (Sections 1.4.1 and 2.2.1; Table 1.2; Figure 2.6). Even if the sediment record from this lower site only extends to a similar time, the comparison between the locations could potentially allow assessments such as plant migration rates, pollen transport mechanisms and the scale of burning events.
8.3.2) Data application

Examining the natural and human histories of Lake Challacaba and Laguna Khomer Kocha Upper has revealed how the vulnerabilities of each site are ultimately driven by the complex topography of the eastern Andes (Chapter 7). Moisture balance and environmental stability was shown to underpin the biodiversity of each location, and also influence human settlement over very small spatial scales. With several other pairs of lakes existing along the length of the Andes (Ecuador and Peru) which are situated in opposing dry and wet spots, there is the opportunity to further investigate these findings by using the palaeoecological records already extracted from these sites. If differences in climatic stability of these sites in the past, due to their geographic setting, can be associated to the vulnerability of each location today, there are major implications for conservation strategies. Comparison of long-term climatic stability at these sites will help to further assess the vulnerabilities of these locations to climatic changes predicted regionally. Developing a fuller understanding of the importance of spatial scale and a better knowledge of the impacts of global versus local scale environmental changes, will assist ecological conservation management in these biodiverse areas.

The early warning potential of mountain regions is yet to be fully appreciated or understood. Although this thesis represents a significant forward step, the future research targets outlined above would continue to address unresolved questions and lead to better understanding of human and climatic threats upon the biodiverse Tropical Andes. Continuing to learn lessons from the past provides a rare opportunity to examine how these valuable ecosystems are likely to cope with future environmental change. Palaeoenvironmental data provides a means in which to examine the long-term response of ecosystems through not only naturally varying ecological stress levels, but also through times of changing human cultural development, examining the amplitude of changes, lag times and tipping points. Such data helps to produce better conservation and resource strategies, assisting the preservation of the unique ecological wealth and helping to secure the future of regionally growing human populations.


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References


References


References


References


References


References


References


References


References


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References


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References


References


References


Appendix A1) Initial core description

This appendix presents the detailed core description for all sediments analysed for this thesis. The methods of description are discussed, followed by images of all core drives extracted.

A1.1) Description methodology and key

In the following initial core descriptions (Plates A1.1 and A1.2), depths are displayed in reference to the individual drive lengths and also to the relative depth below the lake floor (blf). All depths are presented as centimetres and sections of fine banding are expanded for easier viewing. Radiometric dates obtained from cores are marked. Detailed information for each radiometric date is provided in Appendix A3.

Initial core description was completed with reference to the Troels-Smith sediment description system (Birks and Birks, 1980), and the Munsell Soil Colour Charts (Munsell Soil Color Charts, 2000). An explanation of the codes utilised in this thesis is provided in Tables A1.1 and A1.2

<table>
<thead>
<tr>
<th>Sediment composition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>As</strong> Argilla steatodes - clay</td>
</tr>
<tr>
<td>Particles &lt; 0.002 mm</td>
</tr>
<tr>
<td><strong>Dh</strong> Detritus herbosus - plant material</td>
</tr>
<tr>
<td>Fragments &gt; 2 mm</td>
</tr>
<tr>
<td><strong>Ga</strong> Grana arenosa - fine sand</td>
</tr>
<tr>
<td>Particles 0.06 - 0.002 mm</td>
</tr>
<tr>
<td><strong>Ld</strong> Limus detrituosus - lake mud, elastic, non-sticky</td>
</tr>
<tr>
<td>Fragments &lt; 0.1 mm</td>
</tr>
</tbody>
</table>

Table A1.1 Key to sediment compositions codes used in core profile logs. Following the Troels-Smith sediment description system (Birks and Birks, 1980).
APPENDIX A1) Initial core description

<table>
<thead>
<tr>
<th>Sediment colour</th>
<th>Gley 1: 2.5/N</th>
<th>black</th>
</tr>
</thead>
<tbody>
<tr>
<td>10YR: 2/1</td>
<td>Gley 1: 3/10Y</td>
<td>very dark greenish grey</td>
</tr>
<tr>
<td>10YR: 2/2</td>
<td>Gley 1: 3/N</td>
<td>very dark grey</td>
</tr>
<tr>
<td>10YR: 3/1</td>
<td>Gley 1: 4/10Y</td>
<td>dark greenish grey</td>
</tr>
<tr>
<td>10YR: 3/2</td>
<td>Gley 1: 4/N</td>
<td>dark grey</td>
</tr>
<tr>
<td>10YR: 4/1</td>
<td>Gley 1: 5/10Y</td>
<td>greenish grey</td>
</tr>
<tr>
<td>10YR: 4/2</td>
<td>Gley 1: 5/N</td>
<td>grey</td>
</tr>
<tr>
<td>10YR: 5/1</td>
<td>Gley 1: 6/10GY</td>
<td>greenish grey</td>
</tr>
<tr>
<td>10YR: 5/2</td>
<td>Gley 1: 6/N</td>
<td>grey</td>
</tr>
<tr>
<td>10YR: 6/1</td>
<td>Gley 1: 7/10Y</td>
<td>light greenish grey</td>
</tr>
<tr>
<td>10YR: 6/2</td>
<td>Gley 1: 7/N</td>
<td>light grey</td>
</tr>
<tr>
<td>10YR: 7/1</td>
<td>Gley 1: 8/1</td>
<td>white</td>
</tr>
<tr>
<td>10YR: 8/1</td>
<td>Gley 1: 8/N</td>
<td>grey</td>
</tr>
</tbody>
</table>

Table A1.2 Key to sediment colour codes used in core profile logs. Following the Munsell Soil Colour Chart system (Munsell Soil Color Charts, 2000).

Plate A1.1 A–H (following pages 248–255) Initial core descriptions for Lake Challacaba.

Appendix A1) Initial core description

A1.2) Lake Challacaba

Vacas Lake District. 17° 33.257 S, 65° 34.024 W; 3419 m asl.
Appendix A1) Initial core description

Lake Challacaba
Core site: B
Drive number: 1
Start depth: 46 cm b.l.f

Radiocarbon Analysis
Code: SUERC-22351
Depth: V2B 1 45 cm
Bulk Sediment
Lake Challacaba
Core site: B
Drive number: 2
Start depth: 100 cm b.l.f

110 cm
120 cm
130 cm
140 cm
150 cm
160 cm

0cm
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100

Slumped Material
Gley 1: S/10Y
As

Gley 1: 3/10Y
As

Gradual

10YR: 3/N
Ld
Appendix A1) Initial core description

Lake Challacaba
Core site: B
Drive number: 3
Start depth: 160 cm b.l.f

Radiocarbon Analysis
Codes: SUERC-21929
SUERC-22352
Depth: V2B 3 52 cm
Macrofossil / Bulk

Plate A1.1
Lake Challacaba
Core site: B
Drive number: 4
Start depth: 245 cm b.l.f

Radiocarbon Analysis
Code: SUERC-32100
Depth: V2B 4 20 cm
Bulk Sediment

Radiocarbon Analysis
Codes: SUERC-21930
SUERC-22355
Depth: V2B 4 39 cm
Macrofossil / Bulk
Lake Challacaba

Core site: C

Drive number: 1

Start depth: 27 cm b.l.f
Lake Challacaba

Core site: C

Drive number: 2

Start depth: 103 cm b.l.f
Appendix A1) Initial core description

Lake Challacaba
Core site: C
Drive number: 3
Start depth: 203 cm b.l.f

Depth b.l.f
203 cm
210 cm
220 cm
230 cm
240 cm
250 cm
260 cm
270 cm
280 cm
290 cm
300 cm
303 cm
0cm
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100

10YR: 4/1 Ld
Gradual
Mottled Sediments
10YR: 2/1 with inner shaft of 10YR: 4/1 Ld
Alternate bands of 7/1 & 2/1 (1mm)
Ld
Sharp
Gradual
10YR: 5/1 Ld
Undulated
Mottled / Banded Sediments
10YR: 3/2 with 5/1 Ld
Gradual
Moderate
10YR: 5/1 Ld
10YR: 3/2 Ld
Undulated
10YR: 7/1 Ld
Gley 1: 4/N Ld
10YR: 5/1 Ld
Gradual
10YR: 3/2 Ld
10YR: 4/1 Ld
Gradual
10YR: 3/2 Ld
10YR: 4/1 Ld
Gradual
10YR: 3/2 Ld
10YR: 4/1 Ld
Gradual
10YR: 3/2 Ld
10YR: 4/1 Ld
10YR: 4/1 grading to Gley 1: 4/10Y
Ld
Gley
Slumped Material
Gley 1: 4/10Y
Missing Sediments

Plate A1.1 H
A1.3) Laguna Khomer Kocha Upper

Cordillera el Ronco. 17° 16.514 S, 65° 43.945 W; 4144 m asl

<table>
<thead>
<tr>
<th>Drive 1</th>
<th>Drive 2</th>
<th>Drive 3</th>
<th>Drive 4</th>
<th>Drive 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Khomer Kocha Upper A</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drive 1</td>
<td>Drive 2</td>
<td>Drive 3</td>
<td>Drive 4</td>
<td>Drive 5</td>
</tr>
<tr>
<td>Khomer Kocha Upper B</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Appendix A1) Initial core description

Laguna Khomer Kocha Upper
Core site: A
Drive number: 1
Start depth: 47 cm b.l.f

Radiocarbon Analysis
Code: SUERC-22356
Depth: KKUA 1 30.5 cm
Bulk Sediment
Appendix A1) Initial core description

Laguna Khomer Kocha Upper
Core site: A
Drive number: 2
Start depth: 108 cm b.l.f

Radiocarbon Analysis
Code: SUERC-32101
Depth: KKUA 2 15 cm
Charcoal Fragments
Appendix A1) Initial core description

Laguna Khomer Kocha Upper
Core site: A
Drive number: 3
Start depth: 229cm b.l.f

Radiocarbon Analysis
Code: SUERC-37126
Depth: KKUA 3 55 cm
Charcoal Fragments

Material still of 'jelly' like nature but less so than previous core
Slightly coarser than previous core but still very uniform
Laguna Khomer Kocha Upper
Core site: A
Drive number: 4
Start depth: 308 cm b.l.f

Radiocarbon Analysis
Code: SUERC-22357
Depth: KKUA 4 13 cm
Bulk Sediment

Radiocarbon Analysis
Code: SUERC-31727
Depth: KKUA 4 55 cm
Charcoal Fragments

Radiocarbon Analysis
Code: SUERC-32102
Depth: KKUA 4 85 cm
Charcoal Fragments
Appendix A1) Initial core description

Laguna Khomer Kocha Upper

Core site: A

Drive number: 5

Start depth: 308cm b.l.f

Radiocarbon Analysis

Code: SUERC-22358

Depth: KKUA 5 37.5 cm

Bulk Sediment
Appendix A1) Initial core description

Laguna Khomer Kocha Upper
Core site: B
Drive number: 1
Start depth: 41.5 cm b.l.f
Appendix A1) Initial core description

Laguna Khomer Kocha Upper
Core site: B
Drive number: 2
Start depth: 144 cm b.l.f

Radiocarbon Analysis
Code: SUERC-31725
Depth: KKUB 2 70 cm
Charcoal Fragments
Appendix A1) Initial core description

Laguna Khomer Kocha Upper
Core site: B
Drive number: 3
Start depth: 260 cm b.l.f
Appendix A1) Initial core description

Laguna Khomer Kocha Upper
Core site: B
Drive number: 4
Start depth: 360 cm b.l.f

Plate A1.2

Missing/ Slumped Material

Partially Intact Material
Gley: 3/N

Start depth: 360 cm b.l.f

360 cm

Feint Banding
Gley: 3/N with 5/10Y

370 cm

Gradual
Distinct Band - 10YR: 6/2 Ga

Moderate
Distinct Band - 10YR: 6/2 Ga

Feint Banding
Gley: 3/N with 5/10Y

380 cm

Band width decreasing from 0.3 - 0.1 mm
Micro laminations present

390 cm

Banding
10YR: 4/1 with 3/2 and 6/1
Band width decreasing from 0.3 - 0.1 mm

400 cm

Distinct Band - 10YR: 6/2 Ga

410 cm

Banding
10YR: 4/1 with 3/2 and 6/1
Band width decreasing from 0.3 - 0.1 mm

420 cm

Distinct Band - 10YR: 6/2 Ga

Banding
10YR: 4/1 and 4/2
With several distinct bands of 10YR: 6/2 Ga

430 cm

Distinct Band - 10YR: 6/2 Ga

Banding of 10YR: 4/1 with 3/2 and 6/1
Band width decreasing from 0.3 - 0.1 mm

440 cm

Distinct Band - 10YR: 6/2 Ga

Banding of 10YR: 4/1 with 3/2 and 6/1

444 cm

Distinct Band - 10YR: 6/2 Ga

Banding of 10YR: 4/1 and 4/2

0cm 6 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 105 110 115 120

Depth b.l.f
Appendix A1) Initial core description

Laguna Khome Kocha Upper

Core site: B

Drive number: 5

Start depth: 442 cm b.l.f

Plate A1.2 K

Depth b.l.f

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>442 cm</td>
<td>Gley 1: 6/N As</td>
</tr>
<tr>
<td>450 cm</td>
<td>Gley 1: 4/N As</td>
</tr>
<tr>
<td>460 cm</td>
<td>Gley 1: 6/N grading to 5/N As</td>
</tr>
<tr>
<td>463 cm</td>
<td>Sandy material and possibly disturbed during core splitting; water was released from this section</td>
</tr>
</tbody>
</table>

Plate A1.2 K

Depth b.l.f

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>442 cm</td>
<td>10YR: 4/1 with 3/2 and 6/1 Ld</td>
</tr>
<tr>
<td>460 cm</td>
<td>10YR: 6/2 with inner 3/2 mottle Ga</td>
</tr>
<tr>
<td>463 cm</td>
<td>Gley 1: 6/N As</td>
</tr>
<tr>
<td>466 cm</td>
<td>Gley 1: 4/N As</td>
</tr>
<tr>
<td>470 cm</td>
<td>Gley 1: 6/N grading to 5/N As</td>
</tr>
</tbody>
</table>
Appendix A2) Analytical protocols

This appendix presents detailed procedures for the analytical techniques used in this thesis, including the laboratory sample preparation undertaken. Magnetic susceptibility and colour analysis methods are provided fully in Chapter 3.

A2.1) pH, conductivity and temperature analysis – Hanna 991300 Probe

A2.1.1) pH
Switch on meter ('On/Off Mode' button). Press 'set hold' button until pH appears. Submerge probe into water and circulate thoroughly. Note pH and temperature. Switch probe off and repeat twice more. Use a mean average of the 3 readings.

A2.1.2) Conductivity (mS/cm)
Switch on meter. Press 'set hold' button until mS. Submerge probe into water and circulate thoroughly. Note conductivity. Switch probe off and repeat twice more. Use a mean average of the 3 readings.

A2.1.3) Calibration
Every 2 to 4 days test pH. This is done by inserting the probe into pH4 and pH7 calibration solutions provided. Check the reading is within ± 0.1. If not then calibrate:
In pH mode, press and hold 'On/Off Mode' for 3 seconds until 'CAL' appears. Release the button, LCD display shows 'pH 7.01 USE'. Place probe into pH7 solution, and gently agitate. When the LCD display shows 'pH 4.01 USE', take the probe out of the pH7, gently shake any drops and place probe into pH4 solution. Once 'OK' is displayed, calibration is complete.

Check conductivity by agitating probe in 1413 solution for 20 seconds. If reading differs by >10 mS/cm then calibrate:
Appendix A2) Analytical protocols

In mS mode, press and hold ‘On/Of Mode’ button for 3 seconds, until ‘CAL’ appears. Release the button, LCD display shows ‘mS 1413 USE’. Place probe into 1413 solution. Once ‘OK’ is displayed, calibration is complete.

This protocol was adapted from one provided by S.J.Brooks.

A2.2) Core tube splitting

A2.2.1) Set up

Ensure that work surface and plastic bed to hold tube are secure and clean. Secure and check that the titanium bit is correctly fitted to the router. Set router speed to “1” and ensure router slides freely along the plastic bed in both directions (lubricate if necessary). Attach vacuum cleaner to router ensuring hose of cleaner does not impede the movement of router along plastic bed. Place the core tube in to the plastic tube bed securing both ends firmly with the inserts appropriate for the core tube diameter.

A2.2.2) Cutting

Set height limiter on router against the highest point on the core tube wall ensuring that the depth adjuster is extended to its maximum position. Lubricate router bit and lower plastic guard into place. With the vacuum cleaner on, start the router and depress the blade until you reach the limit set. Starting from one end, push the router slowly and smoothly along the length of the core continue until the cutting bit is beyond the other end of the core tube. Check the cut and note any points where the core tube wall has been penetrated. Push the router back along the length of the core to the start position. Lower the cutting bit ¾ of a turn on the depth adjuster and repeat cutting process until tube wall is penetrated along its entire length. Once one side of the core tube has been cut to the point where only a sharp knife is required to separate the two halves rotate the core 180° and repeat cutting process until the second side of the core tube has been cut.

A2.2.3) Splitting the sediment

Remove the two inserts that are holding the tube into the plastic bed. Keeping the core tube horizontal carefully remove it from the plastic bed, ensuring that the two halves stay
Appendix A2) Analytical protocols

together, and place on bench surface. Ensure that the two halves of the core tube are completely separated using a sharp knife. With the cuts in the core tube lined up horizontally, place cheese wire across sediment at one end of the tube and move slowly and smoothly through the sediment through the cuts in the tube wall. Rotate the core tube so that the cuts in the core tube are lined up near horizontal and separate the sediment into the two separate halves of the core tube. A pallet knife may be necessary to prise apart sticky sediments, be sure not to smear sediment up or down the core. The core splitting protocol was developed by J.J. Williams and W.D. Gosling.

A2.3) Photographic set up

Photographs of each core section were taken and overlapped together to provide one image per core drive (c. 1 m). To ensure maximum clarity and detail of core photographs, several methodologies of photography were tested prior to two methods being utilised. The method used for composite photographs are described below (Table A2.1). Test were conducted on the different methodologies in order to select those which maximise colour details recorded, consistency between photographs and minimise any limitations of the camera. The full protocol for the photographic setup has already been described in Chapter 3.

<table>
<thead>
<tr>
<th>Method</th>
<th>Resolution (megapixel)</th>
<th>Optical zoom</th>
<th>Background sheet colour</th>
<th>Lighting</th>
<th>Exposure (seconds)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>6.1</td>
<td>3x</td>
<td>None</td>
<td>Fluorescent &amp; Spot</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>6.1</td>
<td>3x</td>
<td>None</td>
<td>Fluorescent</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>6.1</td>
<td>3x</td>
<td>None</td>
<td>None</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td>6.1</td>
<td>3x</td>
<td>Black</td>
<td>Spot</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>6.1</td>
<td>3x</td>
<td>White</td>
<td>None</td>
<td>2</td>
</tr>
<tr>
<td>6</td>
<td>6.1</td>
<td>3x</td>
<td>Black</td>
<td>Fluorescent</td>
<td>3</td>
</tr>
</tbody>
</table>

Table A2.1 Photographic methodologies tested during core cataloguing. Photographs were taken of all cores using both methods 5 and 6. Method 6 was chosen for final publications.
Appendix A2) Analytical protocols

A2.4) Fossil pollen and spore analysis

A2.4.1) Sample set up

Measure

A typical sample size of 1 cm$^3$ is measured (maybe reduced to 0.5 cm$^3$ when using material from smaller diameter tubes) using a water displacement method in a small (c. 5 cm$^3$) measuring cylinder. Samples are then transferred to 15 ml plastic centrifuge tubes labelled appropriately. The tubes are centrifuged at 3,000 rpm for 3 minutes, ensuring first that tubes are balanced. Decant off the supernatant in one fluid movement from tubes into a waste container; the solid pellet should be left in the bottom of the tubes. This applies for all centrifuge use throughout the schedule.

Spike

As Lycopodium is a possible component of the natural aquatic taxa, a spike suspension of polystyrene microspheres are used to enable the calculation of fossil pollen concentration during identification. 0.5 cm$^3$ (or half the quantity of sediment) is added to each tube using a glass pipette. Check the manufactures information for the number of microspheres per cm$^3$. It is important that the spike suspension is thoroughly mixed prior to use. This is achieved by using a stir plate for 2 hours at a medium speed setting. The magnetic slug should remain in the solution, which should be stored at 3°C (refer to manufacturer notes).

A2.4.2) Solution and removal of carbonates and humic compounds

HCL Treatment

To remove carbonates from the samples a hydrochloric acid treatment is used which acidifies the samples to c. pH 1. First, add 1 ml of 10% HCL and stir using a wooden stick. Once any violent reactions have occurred a further 6 ml of 10% HCL can be added to each tube. The tubes are then placed in the water bath (inside the fume cupboard) for 30 minutes at 90°C. Once complete, balance, centrifuge and carefully decant off the yellow/brown coloured supernatant. Unless noted to the contrary, all chemicals may be discarded into the fume cupboard sink with water running continuously.
Appendix A2) Analytical protocols

\( \text{H}_2\text{O Wash} \)

Whirlimix the sample until fully mobilised and top up with distilled or deionized (DI) water. Balance and centrifuge tubes and decant off supernatant as before.

\( \text{KOH Treatment} \)

To deflocculate the sediments and remove humic acids a potassium hydroxide procedure is performed which bringing the samples up to pH 14 (alkaline). First, mobilise the sample on the whirlimix and top up the tube with 7 ml of 10% KOH. The tubes are then placed in the water bath in fume cupboard for 10 minutes.

\( \text{Sieving} \)

Label up a second batch of corresponding tubes in a rack with funnels and 180 \( \mu \)m sieves. Using a little DI water washout the contents from the original sample tubes ensuring all material is removed. Using a washbottle with restricting nozzle, wash the material through sieve thoroughly working across the sieve mesh surface. The original tube can also be used to catch material being washed through once the 2\( ^{nd} \) one is full. Centrifuge, decant, whirlimix and refill tubes as necessary (at least 3 times each – equates to c. 90 ml of water being washed through each sieve) as any extra washing here will help towards the next step. From this step onwards each sample is split between two tubes. This particularly aids the following steps of washing.

\( \text{H}_2\text{O Washes} \)

This step removes any remaining organic acids and fine clay particles. Follow the washing procedure as previously described, and repeat until liquid is clear (usually 6-10 times). Record the total number of washes. The addition of 4% sodium pyrophosphate (\( \text{Na}_4\text{P}_2\text{O}_7 \)) may help to break up the electrostatic bonds of any clay rich samples (heat for 5 minutes in water bath).

\( \text{HCL Wash} \)

To assist the action of HF on samples and to make sure there is no residual carbonate, sample are acidified prior to HF treatment. This is achieved by washing in HCL following the same procedure as previously described except using HCL instead of \( \text{H}_2\text{O} \).
A2.4.3) Solution and removal of silicates and sulphides

HF Treatment
To removed silicates from the samples a hydrofluoric acid treatment is used. Samples are first thoroughly mobilised using the whirlimix before 5 ml of HF is added to each tube and stirred with wooden sticks. Avoid drips were possible and dip lower parts of tube into the saturated Sodium Carbonate solution to remove drips of HF from the tube.

Prior to January 2010 and the construction of the new laboratories and backwash fume cupboards, HF treatment was conducted cold during a period of 1 - 2 days depending upon the sample. Once the new labs were operational, samples were placed into a hot water bath at 80°C for 3 hours, with particularly silicate rich samples left overnight. Once complete, tubes are centrifuged and carefully decanted into a labelled collector vessel, not down the sink. The solution is then either disposed of into a waste HF container or neutralised with sodium carbonate before being emptied into the sinks connected to marble chip traps.

HCL Treatment
To remove siliceous colloidal clumps and fluorosilicate that form during silica digestion, a hot HCL treatment is needed. Follow the procedure as outlined previously.

Examine the sediment packed in the bottom of the tubes at this point. If a small separate gray layer or area is present then there are still silicates in the sample. If unsure, it may also be worthwhile making up a quick slide of material to examine under a microscope. If remaining crystalline materials inhibit pollen counting then the HF treatment needs to be repeated. Two hot HF treatments are generally enough for even very silicate rich samples.

HNO₃ Treatment
If samples are known to contain sulphides (appear as tiny black cubes about 1–4μm on a side that collect within pollen grains) then a wash in 10% Nitric Acid may be required. To do this, follow the washing procedure as outlined previously but use 10% HNO₃ instead of H₂O.
Appendix A2) Analytical protocols

H₂O Wash
Follow the procedure as previously described.

A2.4.4) Removal of cellulose and polysaccharides - acetylation

CH₃COOH Wash
Removal of water is essential before acetolysis can be conducted. This is achieved by washing in Concentrated (glacial) Acetic acid. Follow the washing procedure as previously described except using CH₃COOH and decanting into a waste beaker.

Acetolysis Treatment
To remove some organic matter and clean the surface of the grains acetolysis is used. It is important that the mixture is prepared fresh just before use. Using a graduated measuring cylinder mix acetic anhydride and concentrated sulphuric acid (H₂SO₄) in a proportion of 9:1. Carefully pour out the acetic anhydride amount required before slowly adding the H₂SO₄ stirring to prevent heat build-up. Remember, volumetric measurements are made with the bottom of the meniscus touching the required gradation line. Make sure the waterbath is preheated (80 - 90°C) before adding 5 ml of the mixture to each tube. Put samples into water bath and heat for exactly 3 minutes and stir once.

CH₃COOH Wash
Remove from water bath and cool immediately by adding 3 ml glacial acetic which neutralises the reaction. Centrifuge and decant into the beaker containing the waste acetic acid. Empty beaker contents down the sink with plenty of water.

H₂O Wash
Follow the procedure as previously described.

A2.4.5) Slide preparation

Transfer to microtubes
Whirlimix remaining material in tubes with a small amount of DI water. Then carefully transfer into appropriately labelled microtubes; centrifuging, decanting and repeating until all residue is transferred.
Appendix A2) Analytical protocols

Slide mounting
To preserve the material until ready to count, it is imperative not to let it dry out. Add equal quantity of glycerol to each sample residue and stir well. With caps left open, any unwanted excess H₂O will evaporate off. When ready, place a small amount of a sample onto a slide using a cocktail stick cover with coverslip.

This protocol was developed with guidance from W.D. Gosling.

A2.5) Charcoal analysis

A2.5.1) Sample set up

Measure
A typical sample size of 1 cm³ is measured using a water displacement method in a small (c. 5 cm³) measuring cylinder. Samples are then transferred to 15 ml plastic centrifuge tubes labelled appropriately. The tubes are centrifuged at 3,000 rpm for 3 minutes, ensuring first that tubes are balanced. Decant off the supernatant in one fluid movement from tubes into a waste container; the solid pellet should be left in the bottom of the tubes. This applies for all centrifuge use throughout the schedule.

A2.5.2) Wet lab preparation

KOH Treatment
To deflocculate the sediments prior to sieving, a potassium hydroxide procedure is performed. First, mobilise the sample on the whirlimix and top up the tube with 7 ml of 10% KOH. The tubes are then placed in the water bath (75°C) in fume cupboard for 5 minutes. They are then removed from the bath and left for 24 hours.

Sieving
Nest an 180 μm and 100 μm sieve together in a large sink with the 180 μm mesh on top and the 100 μm underneath. Using a cold tap with hose attachment, wash sediments through thoroughly. Wash sievings into two labelled sample tubes, keeping the two size fractions separate as a distinction will be made between the two size fractions when counting.
Appendix A2) Analytical protocols

A2.6) Subfossil chironomid analysis

A2.6.1) Sample set up

Measure

A typical sample size of 1 g of wet sediment is used for chironomid analysis but the amount of sediment required to obtain substantial numbers of head capsules for analysis varies greatly with each lake and, often, each depth. However, the low sediment budget available for the Bolivian samples results in only 1 g being used for all samples. Samples are placed into 50 ml sample tubes.

A2.6.2) Wet lab preparation

KOH Treatment

To deflocculate the sediments a potassium hydroxide procedure is performed. 10 ml of 10% KOH is added and samples are placed in a water bath at 75°C for 5 minutes, do not keep in for longer than this time. Mobilise the samples gentle periodically.

H₂O Treatment

To dilute the KOH and further deflocculate the sample, top up each sample tube with water and continue in water bath for 15 minutes.

Sieving

Nest a 212 μm and 90 μm sieves together in a large sink with the 212 μm mesh on top and the 90 μm underneath. Using a cold tap with hose attachment, wash sediments through thoroughly but do not use excess pressure, as this will damage the head capsules. Wash sieving into two labelled Petri dishes, keeping the two size fractions separate as this will aid picking.

A2.6.3) Picking and mounting procedure

Picking

Pipette a small amount into a grooved Perspex sorting tray. Pick out head capsules using fine forceps under a ×25 binocular microscope; do not actually touch the head capsules with the forceps as this will damage them, but instead trap them in a bubble of liquid just behind the tip (practice). Place head capsules into 80% ethanol in a wide necked screw lid...
Appendix A2) Analytical protocols

vial which can then be labelled and stored in the fridge until ready to mount up. Allow the forceps to dry after placing in the ethanol as if placed directly into the sorting tray this will cause the sample to rapidly disperse.

Dehydrating
Progressively dehydrate head capsules by passing through 90% ethanol and Euparal Essence (about 5 minutes in each). Use the staining blocks to do this but remember to cover them with the glass covers to prevent excess evaporation. Do not use too much Euparal Essence and remember not to try and process too many head capsules at once. Depending on size and the ease of picking, 10–20 at a time is about right.

Mounting
Using a slide template (see Figure A2.3), arrange six drops of Euparal mountant evenly spaced on each side. Carefully place into each drop two head capsules, ventral side up. Once checked for appropriate positioning, cover each drop with a 6 mm diameter coverslip and store slides flat.

As a rule, it is best to do as little chemical steps to the samples as possible. Do not bring samples to the boil and avoid stirring samples too vigorously with wooden sticks, as this will begin to damage and disintegrate the head capsules.

This protocol was developed with guidance from S.J. Brooks

A2.7) Elemental determination
A2.7.1) Instrumentation
The abundance (wt%) of total carbon (TC), total inorganic carbon (TIC), Sulphur (S) and Nitrogen (N) was determined using the in-house LECO CNS-2000 elemental analyzer. The LECO CNS-2000 comprises of an auto-sampler, capable of holding 49 samples, and a furnace kept at 1350°C. Samples are weighed into inert ceramic boats, which have been preconditioned by placing them in a separate furnace for 1 hr at 1000°C, and then stored in a desiccator before use. The auto-sampler introduces boats into the furnace in turn for
combustion. CO\textsubscript{2} and SO\textsubscript{2} gases are then analysed and abundance of C and S determined via the use of infrared detector cells, and processed by the LECO CNS-2000 computer system. TOC is calculated as by the subtraction of TIC from TC. All TIC is assumed to be in the form of CaCO\textsubscript{3}, which is obtained by multiplying the TIC values by 8.33.

A2.7.2) Measurement protocol

TC, S and N

For TC, S and N, 0.2 g of dried, finely ground sediment samples were weighed into the boats. 1 g of the combustion catalyst ComCat is added to the sample and mixed with the sample thoroughly to ensure, a rapid, complete combustion.

TIC

Measurements for TIC were established using sample weights of 0.15 g. These sample were first “ashed” at 450°C to remove all organic carbon and then mixed with ComCat and run as per the TC, S and N measurement.

Standards

The auto-sampler accepts a total of 49 boats. 40 sediment samples are loaded, with the remaining 9 spaces occupied with a range of other readings. Two empty boats (blanks) and 2 pure ComCat (1.0 g) are measured at the start of run, and intermittent standards of known values are measured every 10 samples to allow for any long-term drift to be assessed. The standard used for all analysis was The Open University’s in house Oxford Clay (OX-12g). The reproducibility of these standards is shown in Table A2.2.

This protocol was established with guidance from A.L. Coe.

<table>
<thead>
<tr>
<th>Dates</th>
<th>Number run</th>
<th>Carbon (wt%)</th>
<th>Sulphur (wt%)</th>
<th>Nitrogen (wt%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>8 – 15\textsuperscript{th} Oct 09</td>
<td>45</td>
<td>4.475 ± 0.179</td>
<td>1.213 ± 0.092</td>
<td>0.116 ± 0.067</td>
</tr>
</tbody>
</table>

Table A2.2 Mean values for in house Oxford Clay standard (OX-12g). Uncertainties calculated as 2 standard deviation.
### Fossil Pollen Preparation Tick Sheet – Andean Sediments

<table>
<thead>
<tr>
<th>Step</th>
<th>In</th>
<th>Out</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Worker:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sheet No:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sediment Quantity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Microspheres Quantity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hot 10% HCl (30mins)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>In:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Out:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H₂O Wash</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hot 10% KOH (10mins)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stale x3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H₂O Wash (until clear)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Add Na₂P₂O₇ to clay rich samples</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10% HCl Wash</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HF</td>
<td></td>
<td></td>
</tr>
<tr>
<td>In:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Out:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hot 10% HCl (30mins)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>In:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Out:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10% HNO₃ Wash</td>
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<td></td>
</tr>
<tr>
<td>H₂O Wash</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CH₃COOH Wash</td>
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<td></td>
</tr>
<tr>
<td>Acetolysis (3mins)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9 parts Acetic Anhydride</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 part Sulphuric Acid</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CH₃COOH Wash</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H₂O Wash</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vial</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Version 1.1 – Joseph J Williams

**Figure A2.1** Fossil pollen preparation tick sheet for Andean lake sediments.
### Pollen Count Sheet – Eastern Bolivia Cordillera (Cochabamba Basin)

<table>
<thead>
<tr>
<th>Sample Code:</th>
<th>Analyst:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative Depth:</td>
<td>Date:</td>
</tr>
<tr>
<td>Sediment Quantity:</td>
<td>Microsphere Quantity:</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Pollen</th>
<th>Spores</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alnus</td>
<td>Monolete</td>
</tr>
<tr>
<td>Amaranthaceae</td>
<td></td>
</tr>
<tr>
<td>Anacardiaceae</td>
<td></td>
</tr>
<tr>
<td>Apiaceae</td>
<td>Trilete (cf Lyco)</td>
</tr>
<tr>
<td>Araceae</td>
<td></td>
</tr>
<tr>
<td>Asteraceae</td>
<td></td>
</tr>
<tr>
<td>Brassicaceae</td>
<td></td>
</tr>
<tr>
<td>Bromeliaceae</td>
<td>Sporomielia</td>
</tr>
<tr>
<td>Caryophyllaceae</td>
<td>SpyraG (HHT 374-5)</td>
</tr>
<tr>
<td>Chloranthaceae (cf Hedyosmum)</td>
<td>Other</td>
</tr>
<tr>
<td>Chenopodiaceae</td>
<td></td>
</tr>
<tr>
<td>Compositae</td>
<td></td>
</tr>
<tr>
<td>Ericaceae</td>
<td></td>
</tr>
<tr>
<td>Euphorbiaceae (cf Acalypha)</td>
<td></td>
</tr>
<tr>
<td>Euphorbiaceae (others)</td>
<td></td>
</tr>
<tr>
<td>Fabaceae</td>
<td>Non-Pollen</td>
</tr>
<tr>
<td>Flacourtiaceae</td>
<td>Microspheres</td>
</tr>
<tr>
<td>Gunneraceae</td>
<td>Pediasturum (Simplex)</td>
</tr>
<tr>
<td>Juglandaceae</td>
<td>(Duplex)</td>
</tr>
<tr>
<td>Loganiaceae</td>
<td>Chironomid Parts</td>
</tr>
<tr>
<td>Melas / Comb</td>
<td></td>
</tr>
<tr>
<td>Mora / Urti</td>
<td></td>
</tr>
<tr>
<td>Onagraceae (cf Ludwigia)</td>
<td>Unknown Types</td>
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<tr>
<td>Papaveraceae</td>
<td></td>
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<tr>
<td>Piperaceae</td>
<td></td>
</tr>
<tr>
<td>Poaceae</td>
<td></td>
</tr>
<tr>
<td>Podocarpus</td>
<td></td>
</tr>
<tr>
<td>Ranunculaceae</td>
<td></td>
</tr>
<tr>
<td>Rosaceae (cf Polylepis)</td>
<td></td>
</tr>
<tr>
<td>Rubiaceae</td>
<td></td>
</tr>
<tr>
<td>Solanaceae</td>
<td></td>
</tr>
<tr>
<td>Ulmaceae (cf Trema)</td>
<td></td>
</tr>
<tr>
<td>(cf Celtis)</td>
<td></td>
</tr>
</tbody>
</table>

| Cyperaceae | |

<table>
<thead>
<tr>
<th>Isoetes</th>
<th>Damaged Grains</th>
</tr>
</thead>
<tbody>
<tr>
<td>Myriophyllum</td>
<td>Broken</td>
</tr>
<tr>
<td>Typhaceae</td>
<td>Crumpled</td>
</tr>
<tr>
<td></td>
<td>Corroded</td>
</tr>
<tr>
<td></td>
<td>Obscured</td>
</tr>
<tr>
<td></td>
<td>Degraded</td>
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</tbody>
</table>

Created by JJW. Version 1 (March 2009)

Figure A2.2 Fossil pollen count sheet for Andean lake sediments.
### Chironomid Slide Count Sheet

<table>
<thead>
<tr>
<th>Site and Depth:</th>
<th>Date:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short Code:</td>
<td>Analyst:</td>
</tr>
<tr>
<td>Relative Depth:</td>
<td>Sheet number: CHIRON</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Slide Number:</th>
</tr>
</thead>
<tbody>
<tr>
<td>i)</td>
</tr>
<tr>
<td>ii)</td>
</tr>
<tr>
<td>iii)</td>
</tr>
<tr>
<td>iv)</td>
</tr>
<tr>
<td>v)</td>
</tr>
<tr>
<td>vi)</td>
</tr>
<tr>
<td>vii)</td>
</tr>
<tr>
<td>viii)</td>
</tr>
<tr>
<td>ix)</td>
</tr>
<tr>
<td>x)</td>
</tr>
</tbody>
</table>

Slide Layout:

<table>
<thead>
<tr>
<th>V</th>
<th>IV</th>
<th>III</th>
<th>II</th>
<th>I</th>
</tr>
</thead>
<tbody>
<tr>
<td>VI</td>
<td>VII</td>
<td>VIII</td>
<td>IX</td>
<td>X</td>
</tr>
</tbody>
</table>

Created by JJW. Version 1. May 2009

**Figure A2.3** Subfossil chironomid count sheet for Andean lake sediments
Appendix A3) Bolivian lake sediment data

This appendix presents the data collected from the sediments of Lake Challacaba and Laguna Khomer Kocha Upper which have been discussed in this thesis (Chapters 4–6). Data is presented here in tabulated form, with large data sets on compact disc (Enclosure CD1). Sample codes refer to lake, core site, drive, drive depth.

A3.1) Radiometric dates

A chronological framework for all cores was established using radiocarbon dating ($^{14}$C) of either plant macrofossils, Lake sediments (gyttja) or macroscopic charcoal and seed cases (see Chapter 3). All dates were obtained via the Scottish Universities Environmental Research Centre (SUERC) Radiocarbon Facility (Environment) administered by the Natural Environment Research Council (NERC). Two rounds of funding were awarded by the NERC Radiocarbon Facility-Steering Committee (RCF-SC), reference numbers 1287.0408/2008 and 1463.0410/2010.

A3.1.1) Sample pre-treatment and analysis

All chemical pre-treatment and analysis was conducted at the SUERC Facility, East Kilbride. Samples were digested in 1M HCl ($80^\circ$C, 30 mins), washed free from mineral acid with deionised water then digested in 0.2M KOH ($80^\circ$C, 20 mins). The digestion was repeated using deionised water until no further humics were extracted. The residue was rinsed free of alkali, digested in 1M HCl ($80^\circ$C, 1 hour) then rinsed free of acid, dried and homogenised. The total carbon in a known weight of the pre-treated sample was recovered as CO$_2$ by heating with CuO in a sealed quartz tube. The gas was converted to graphite by Fe/Zn reduction. Sample graphite's were analysed using Accelerator Mass Spectrometry (AMS). See Freeman et al. (2007) for facility information.

While all samples were pre-treated and prepared to CO$_2$ identically, SUERC-32100, -32101 and -32102 contained <500 µgC and required analysis at low current and preparation of additional standards which matched the sample carbon weights. $\delta^{13}$C/$^{12}$C ratios for samples <500 µgC were measured on the SUERC AMS during $^{14}$C determination and used to model $\delta^{13}$C values by comparison to the Craig (1957) $^{13}$C/$^{12}$C value for PDB standard.
These $^{13}$C values are shown in brackets and were considered the most appropriate to normalise $^{14}$C data to $\delta^{13}_{\text{CVPDB}} = -25$, but are not necessarily representative of the $\delta^{13}$C in the original sample material. The $\delta^{13}$C values not in brackets were measured on a dual inlet stable isotope mass spectrometer (VG OPTIMA) and are representative of $\delta^{13}$C in the original, pre-treated sample material.

A3.1.2) Reported results

Original results reported by the SUERC AMS Laboratory, together with calibration calculations, are given in Table A3.1. The position of each date is marked on the initial core description (Appendix 1).

For reference purposes, a complete list of all depths (per cm) and associated ages (cal yr BP) is provided in a spreadsheet file on Enclosure CD1. The data is divided by study site into the following files:

- Lake Challacaba Depth vs Age Data.xls
- Laguna Khomer Kocha Upper Depth vs Age Data.xls
### Table A3.1


<table>
<thead>
<tr>
<th>Publication code</th>
<th>Sample code (type)</th>
<th>Depth (cm bbl)</th>
<th>$^{14}$C Enrichment (% Modern $\pm 1\sigma$)</th>
<th>Conventional Radiocarbon Age (years BP $\pm 1\sigma$)</th>
<th>Carbon content (% by wt.)</th>
<th>$\delta^{13}$C$_{vppm}$ $\pm 0.1$</th>
<th>Calibrated dates Range (cal yr BP)</th>
<th>Curve used</th>
</tr>
</thead>
<tbody>
<tr>
<td>SUERC 21929</td>
<td>V2B 3 52 cm (MF)</td>
<td>197</td>
<td>74.79 $\pm 0.35$</td>
<td>2333.19 $\pm 37.75$</td>
<td>16</td>
<td>-21.8</td>
<td>2155 - 2270</td>
<td>SHcal04</td>
</tr>
<tr>
<td>SUERC 21930</td>
<td>V2B 4 39 cm (MF)</td>
<td>284</td>
<td>63.79 $\pm 0.29$</td>
<td>3611.33 $\pm 36.96$</td>
<td>30</td>
<td>-14</td>
<td>3616 - 3933</td>
<td>SHcal04</td>
</tr>
<tr>
<td>SUERC 22351</td>
<td>V2B 1 45 cm (BS)</td>
<td>91</td>
<td>88.49 $\pm 0.40$</td>
<td>982 $\pm 37$</td>
<td>3.2</td>
<td>-24.2</td>
<td>770 - 925</td>
<td>SHcal04</td>
</tr>
<tr>
<td>SUERC 22352</td>
<td>V2B 3 52 cm (BS)</td>
<td>197</td>
<td>72.24 $\pm 0.31$</td>
<td>2,612 $\pm 35$</td>
<td>6.1</td>
<td>-24.3</td>
<td>2490 - 2643</td>
<td>SHcal04</td>
</tr>
<tr>
<td>SUERC 22355</td>
<td>V2B 4 39 cm (BS)</td>
<td>284</td>
<td>57.31 $\pm 0.25$</td>
<td>4471 $\pm 36$</td>
<td>4.2</td>
<td>-27.2</td>
<td>4864 - 5071</td>
<td>SHcal04</td>
</tr>
<tr>
<td>SUERC 22356</td>
<td>KKUA 1 30.5 cm (BS)</td>
<td>61.5</td>
<td>84.43 $\pm 0.38$</td>
<td>1359 $\pm 37$</td>
<td>9.6</td>
<td>-24.6</td>
<td>1148 -1300</td>
<td>SHcal04</td>
</tr>
<tr>
<td>SUERC 22357</td>
<td>KKUA 4 13 cm (BS)</td>
<td>321</td>
<td>36.54 $\pm 0.18$</td>
<td>8086 $\pm 41$</td>
<td>13.5</td>
<td>-24.5</td>
<td>8661 - 9029</td>
<td>SHcal04</td>
</tr>
<tr>
<td>SUERC 22358</td>
<td>KKUA 5 37.5 cm (BS)</td>
<td>445.5</td>
<td>17.26 $\pm 0.13$</td>
<td>14112 $\pm 61$</td>
<td>7.6</td>
<td>-24.2</td>
<td>16363 - 16645</td>
<td>FairB</td>
</tr>
<tr>
<td>SUERC 32100</td>
<td>V2B-4-20 cm (CHAR)</td>
<td>265</td>
<td>63.56 $\pm 0.73$</td>
<td>3640 $\pm 92$</td>
<td>N/A</td>
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<tr>
<td>SUERC 32101</td>
<td>KKUA-2-15 cm (CHAR)</td>
<td>123</td>
<td>67.79 $\pm 0.75$</td>
<td>3123 $\pm 89$</td>
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<tr>
<td>SUERC 32102</td>
<td>KKUA-4-85 cm (CHAR)</td>
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<td>33.74 $\pm 0.53$</td>
<td>8727 $\pm 125$</td>
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<td>SUERC 31725</td>
<td>KKUB-2-70 cm (CHAR)</td>
<td>210</td>
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<td>5910 $\pm 38$</td>
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<td>KKUA-3-55 cm (CHAR)</td>
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<td>6190 $\pm 38$</td>
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<tr>
<td>SUERC 31727</td>
<td>KKUA-4-55 cm (CHAR)</td>
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<td>35.14 $\pm 0.17$</td>
<td>8400 $\pm 40$</td>
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A3.2) Geochemical and physical data

All non-ecological data obtained from the sediments of both study sites is presented in Table A3.2 (Lake Challacaba) and Table 3A.3 (Laguna Khomer Kocha Upper). Magnetic susceptibility values are given in both initial corrected susceptibility (\(k\)) and mass specific susceptibility value (\(\chi\)). Colour intensity values are provided for the colour channels red (R), green (G) and blue (B), and an averaged value of the 3 is also given (mean RGB). The abundances of total carbon (TC), calcium carbonate (\(\text{CaCO}_3\)), total organic carbon (TOC), Sulphur (S) and Nitrogen (N) are given as weight percent (wt%). Depth are provided in centimetres below the lake floor (cm blf). Detailed analytical methodologies are described in Chapter 3 and Appendix A2.

Table A3.2 Full listing of Lake Challacaba geochemical and physical data. V2B = core site B. V2C = core site C. SS = Sediments from short core (sediment/water interface).

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Appendix A3) Bolivian lake sediment data

| V2C SS 50cm | 50  | 8.200  | 41.837  | 148.702  | 120.720  | 109.956  | 126.462  | 2.609  | 0.289  | 2.574  | 0.131  | 0.341  |
| V2B 1 5cm  | 51  | 3.350  | 24.632  | 158.829  | 133.320  | 120.343  | 137.497  | 1.858  | 0.391  | 1.811  | 0.062  | 0.255  |
| V2C SS 55cm | 55  | 8.700  | 40.465  | 155.735  | 127.377  | 115.627  | 132.916  | 2.258  | 0.289  | 2.223  | 0.106  | 0.279  |
| V2B 1 10cm | 56  | 4.050  | 29.348  | 170.033  | 144.967  | 129.928  | 148.316  | 1.285  | 0.381  | 1.239  | 0.049  | 0.212  |
| V2C SS 60cm | 60  | 5.350  | 34.516  | 139.271  | 109.410  | 100.368  | 116.354  | 3.788  | 0.290  | 3.753  | 0.228  | 0.442  |
| V2B 1 15cm | 61  | 4.200  | 26.752  | 167.686  | 141.921  | 126.627  | 145.414  | 1.197  | 0.399  | 1.149  | 0.108  | 0.204  |
| V2C 1 20cm | 66  | 4.700  | 29.375  | 161.124  | 132.976  | 118.081  | 137.392  | 1.587  | 0.503  | 1.527  | 0.151  | 0.237  |
| V2B 1 25cm | 71  | 5.350  | 29.558  | 161.404  | 133.367  | 118.483  | 137.751  | 1.666  | 0.444  | 1.613  | 0.050  | 0.242  |
| V2B 1 30cm | 76  | 5.500  | 41.045  | 162.832  | 135.480  | 119.281  | 139.197  | 1.125  | 0.393  | 1.078  | 0.040  | 0.184  |
| V2B 1 35cm | 81  | 4.350  | 31.752  | 157.370  | 132.498  | 121.075  | 136.980  | 1.840  | 0.448  | 1.786  | 0.069  | 0.259  |
| V2B 1 40cm | 86  | 4.450  | 36.179  | 155.489  | 128.041  | 116.965  | 134.948  | 2.220  | 0.511  | 2.159  | 0.140  | 0.275  |
| V2B 1 45cm | 91  | 4.800  | 37.209  | 146.447  | 118.460  | 110.089  | 125.000  | 3.169  | 0.443  | 3.116  | 0.088  | 0.382  |
| V2B 1 50cm | 96  | 3.550  | 29.098  | 140.116  | 111.508  | 104.127  | 118.580  | 3.607  | 0.681  | 3.525  | 0.131  | 0.414  |
| V2C 1 55cm | 97  | 3.450  | 30.000  | 141.703  | 113.072  | 103.379  | 119.389  | 3.787  | 0.338  | 3.746  | 0.150  | 0.427  |
| V2B 2 40cm | 100 | 4.200  | 36.522  | 145.357  | 117.573  | 107.067  | 123.336  | 2.895  | 0.508  | 2.834  | 0.059  | 0.146  |
| V2C 1 75cm | 103 | 3.000  | 29.412  | 134.753  | 106.609  | 99.293   | 113.551  | 5.135  | 0.338  | 5.094  | 0.202  | 0.588  |
| V2B 2 45cm | 105 | 3.100  | 31.633  | 138.001  | 108.745  | 98.899   | 115.215  | 3.690  | 0.452  | 3.636  | 0.154  | 0.341  |
| V2C 2 5cm  | 108 | 0.800  | 9.524   | 124.083  | 94.307   | 90.495   | 102.962  | 8.591  | 0.387  | 8.545  | 0.377  | 0.784  |
| V2B 2 50cm | 110 | 3.400  | 31.193  | 134.408  | 105.642  | 97.939   | 112.664  | 4.126  | 0.501  | 4.066  | 0.178  | 0.415  |
| V2C 2 10cm | 113 | 0.800  | 10.811  | 122.667  | 93.591   | 90.335   | 102.199  | 9.246  | 0.387  | 9.200  | 0.679  | 0.958  |
| V2B 2 55cm | 115 | 1.700  | 18.085  | 128.356  | 99.163   | 93.347   | 106.944  | 6.284  | 0.502  | 6.224  | 0.493  | 0.459  |
| V2B 2 60cm | 120 | 0.750  | 9.036   | 124.930  | 96.053   | 92.881   | 104.624  | 7.727  | 0.510  | 7.666  | 0.557  | 0.661  |
| V2B 2 65cm | 125 | 0.950  | 12.025  | 102.919  | 72.875   | 82.192   | 10.920   | 0.513  | 10.858 | 0.644  | 0.733  |
### Appendix A3) Bolivian lake sediment data

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### Appendix A3) Bolivian lake sediment data

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### Appendix A3) Bolivian lake sediment data

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### Appendix A3) Bolivian lake sediment data

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|------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|------------|------------|------------|--------|---------|---------|---------|---------|---------|---------|---------|------------|---------|---------|---------|
|            | 362       | 367       | 371       | 376       | 380       | 385       | 389       | 394       | 398        | 403        | 407        | 413     | 418     | 423     | 428     | 433     | 438     | 443     | 445.5     | 448      | 453     | 458     |
|            | -0.050    | -0.050    | 0.200     | 0.100     | -0.250    | 0.050     | 0.700     | 0.150     | -0.150     | 0.200      | -0.150     | 0.100    | 0.000   | 0.150   | 0.200   | 0.200   | 0.800   | 0.550   | 0.000   | 1.850      | 19.35    | 5       |
|            | -0.649    | -0.658    | 1.905     | 0.980     | -3.378    | 0.532     | 4.965     | 1.546     | -2.143     | 2.247       | -2.459     | 1.220    | 0.000   | 1.667   | 2.128   | 5.926   | 4.741   | 4.741   | 0.000   | 7.582      | 134.37   | 5       |
|            | 103.363   | 100.041   | 92.775    | 81.285    | 103.683   | 78.549    | 78.013    | 104.456   | 99.494     | 107.973     | 102.865    | 118.759  | 132.040 | 137.397 | 141.404 | 135.057 | 148.104 | 151.270 | 134.498  | 146.999   | 134.37   | 9.615   |
|            | 78.082    | 74.483    | 65.969    | 55.475    | 85.252    | 54.263    | 78.103    | 104.456   | 99.494     | 82.021      | 82.232     | 118.759  | 132.040 | 137.397 | 141.404 | 135.057 | 148.104 | 151.270 | 134.498  | 146.999   | 134.37   | 9.615   |
|            | 82.894    | 79.770    | 72.016    | 62.170    | 89.152    | 60.558    | 52.920    | 104.456   | 99.494     | 87.251      | 83.060     | 95.002   | 132.040 | 137.397 | 141.404 | 135.057 | 148.104 | 151.270 | 134.498  | 146.999   | 134.37   | 9.615   |
|            | 88.120    | 84.767    | 76.920    | 66.310    | 12.760    | 64.660    | 59.391    | 104.456   | 99.494     | 92.422      | 88.049     | 97.378   | 132.040 | 137.397 | 141.404 | 135.057 | 148.104 | 151.270 | 134.498  | 146.999   | 134.37   | 9.615   |
|            | 0.575     | 0.749     | 0.518     | 0.631     | 0.517     | 0.461     | 0.517     | 0.518     | 0.518      | 0.461       | 0.461      | 0.461    | 0.461   | 0.461   | 0.461   | 0.461   | 0.461   | 0.461   | 0.461    | 0.461      | 0.461    | 0.461   |
|            | 0.460     | 0.998     | 0.361     | 0.424     | 0.451     | 0.218     | 0.320     | 0.319     | 0.319      | 0.221       | 0.293      | 0.234    | 0.248   | 0.253   | 0.185   | 0.385   | 0.367   | 0.224   | 0.367    | 0.414      | 0.416    | 0.404   |
|            | 0.997     | 1.076     | 0.838     | 0.811     | 1.010     | 0.646     | 0.734     | 1.044     | 0.823      | 0.694       | 0.957      | 0.823    | 0.690   | 0.772   | 0.551   | 0.534   | 0.284   | 0.367   | 0.284    | 0.367      | 0.312    | 0.002   |
A3.3) Ecological proxies data

A3.3.1) Pollen and spore

The original data obtained from fossil pollen and spore analysis, including percentage and concentration calculations, is provided as an electronic spreadsheet file in Enclosure CD1. Taxa list provided in Appendix A4. The data is divided by study site into the following files:

- Lake Challacaba Pollen Data.xls
- Laguna Khomer Kocha Upper Pollen Data.xls

A description of the methodology used is provided in Sections 3.4.1, 4.3 and 5.4 and the protocol is presented in Appendix A2.4. Plots are pollen and spore abundance against time/depth are shown in the respective discussions (Chapters 4 and 5; Figures 4.4. and 5.4).

A3.3.2) Charcoal

The full charcoal particulate data for Lake Challacaba and Laguna Khomer Kocha Upper is shown in Tables A3.4 and A3.5. A description of the methodology used is provided in Sections 3.4.2, 4.3 and 5.4, and the protocol is presented in Appendix A2.4. Plots are charcoal abundance against time/depth are shown in the respective discussions (Chapters 4 and 5; Figures 4.4. and 5.4).

A3.3.3) Chironomid

The original data obtained from subfossil chironomid analysis, including percentage and concentration calculations, is provided as an electronic spreadsheet file in Enclosure CD1. Taxa list provided in Appendix A4. The data is divided by study site into the following files:

- Lake Challacaba Chironomid Data.xls
- Laguna Khomer Kocha Upper Chironomid Data.xls

A description of the methodology used is provided in Sections 3.4.3 and 6.4, and the protocol is presented in Appendix A2.4. Plots are chironomid abundance against time/depth are shown in Chapter 6 (Figures 6.4 and 6.5).
### Appendix A3) Bolivian lake sediment data

<table>
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<th>Sample code</th>
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<th>Type 1</th>
<th>Type 1</th>
<th>Type 2</th>
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Table A3.4 Full listing of Lake Challacaba charcoal data. A description of charcoal type morphology is provided in Chapter 3. V2B = core site B. V2C = core site C. SS = from surface sampler.
### Table A3.5 (below and opposite) Full listing of Laguna Khomer Kocha Upper charcoal data. A description of charcoal type morphology is provided in Chapter 3. KKUA = core site A. KKUB = core site B.

<table>
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<th>Sample code</th>
<th>Depth (cm blf)</th>
<th>Charcoal counts (particulates/cm³)</th>
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Appendix A3) Bolivian lake sediment data

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A3.3.4) Ordination

The ordination data used to calculate rates of change analysis in Chapters 4 and 5 is shown in Tables A3.6 and A3.7 (overleaf). A description of the ordination methodology is provided in the relevant chapter along with ordination plots and rates of change scores against time/depth.
### Appendix A3) Bolivian lake sediment data

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<th>Intersample time (yr)</th>
<th>Non-metric multidimensional scaling (NMDS) axis scores</th>
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<td>1593.19</td>
<td>126.39</td>
<td>-0.39 0.19</td>
<td>1.01</td>
<td>0.0039</td>
</tr>
<tr>
<td>V2C 2 25cm</td>
<td>158</td>
<td>1694.31</td>
<td>101.11</td>
<td>-0.63 0.50</td>
<td>0.39</td>
<td>0.0043</td>
</tr>
<tr>
<td>V2B 3 30cm</td>
<td>175</td>
<td>1909.17</td>
<td>214.86</td>
<td>-0.52 0.17</td>
<td>0.35</td>
<td>0.0049</td>
</tr>
<tr>
<td>V2B 3 40cm</td>
<td>185</td>
<td>2035.56</td>
<td>126.39</td>
<td>-0.51 0.54</td>
<td>0.37</td>
<td>0.0052</td>
</tr>
<tr>
<td>V2B 3 50cm</td>
<td>197</td>
<td>2187.22</td>
<td>151.67</td>
<td>-0.28 0.03</td>
<td>0.56</td>
<td>0.0055</td>
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<tr>
<td>V2C 2 55cm</td>
<td>198</td>
<td>2193.54</td>
<td>6.31</td>
<td>-0.42 0.01</td>
<td>0.14</td>
<td>0.0068</td>
</tr>
<tr>
<td>V2B 3 60cm</td>
<td>205</td>
<td>2326.29</td>
<td>132.75</td>
<td>-0.40 -0.72</td>
<td>0.73</td>
<td>0.0073</td>
</tr>
<tr>
<td>V2B 3 70cm</td>
<td>215</td>
<td>2515.94</td>
<td>189.65</td>
<td>-0.25 -0.67</td>
<td>0.16</td>
<td>0.0079</td>
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<tr>
<td>V2B 3 80cm</td>
<td>225</td>
<td>2705.58</td>
<td>189.65</td>
<td>-0.50 -0.93</td>
<td>0.36</td>
<td>0.0080</td>
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<tr>
<td>V2B 3 90cm</td>
<td>235</td>
<td>2895.23</td>
<td>189.65</td>
<td>-0.38 -0.41</td>
<td>0.53</td>
<td>0.0082</td>
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<tr>
<td>V2B 3 95cm</td>
<td>244</td>
<td>3065.91</td>
<td>170.68</td>
<td>-0.46 -0.31</td>
<td>0.13</td>
<td>0.0086</td>
</tr>
<tr>
<td>V2B 4 3cm</td>
<td>248</td>
<td>3141.77</td>
<td>75.86</td>
<td>-0.27 -0.43</td>
<td>0.24</td>
<td>0.0087</td>
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<tr>
<td>V2B 4 10cm</td>
<td>255</td>
<td>3274.52</td>
<td>132.75</td>
<td>-0.51 -0.40</td>
<td>0.25</td>
<td>0.0093</td>
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<tr>
<td>V2B 4 20cm</td>
<td>265</td>
<td>3464.17</td>
<td>189.65</td>
<td>-0.71 1.09</td>
<td>1.51</td>
<td>0.0097</td>
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<tr>
<td>V2B 4 30cm</td>
<td>275</td>
<td>3653.82</td>
<td>189.65</td>
<td>-0.37 0.16</td>
<td>0.99</td>
<td>0.0145</td>
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<tr>
<td>V2B 4 39cm</td>
<td>284</td>
<td>3824.50</td>
<td>170.68</td>
<td>-1.03 1.47</td>
<td>1.46</td>
<td>0.0223</td>
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<tr>
<td>V2B 4 50cm</td>
<td>295</td>
<td>4033.11</td>
<td>208.61</td>
<td>0.48 1.63</td>
<td>1.51</td>
<td>0.0277</td>
</tr>
</tbody>
</table>

**Table A3.6 (above)** Full listing of the Lake Challacaba ordination data. A description of the ordination methodology is provided in Chapter 4. V2B = core site B. V2C = core site C. SS = from surface sampler.

**Table A3.7 (opposite page)** Full listing of the Laguna Khomer Kocha Upper ordination data. A description of the ordination methodology is provided in Chapter 5. KKUA = core site A. KKUB = core site B.
Appendix A3) Bolivian lake sediment data

Sample

Depth

code

(cm blf)

Sample

Intersample

Age

time

(cal yr BP)

(yr)

Detrended

correspondence

analysis (DCA) axis scores

AXIS 1

AXIS2

AXIS3

3 way axis

Rate of

Euclidean

change

distance

value

KKUA 1 20 cm

51

1024.56

N/A

65.26

19.12

25.78

N/A

N/A

KKUA 140 cm

71

1543.52

518.96

48.99

9.95

29.33

19.01

0.0366

KKUA 1 60 cm

82

1900.17

356.65

48.12

19.85

15.88

16.73

0.0469

KKUA 185 cm

93

2256.82

356.65

53.96

26.31

27.64

14.64

0.0410

KKUA 195 cm

103

2581.04

324.23

50.77

37.12

30.64

11.66

0.0360

KKUA 2 5 cm

113

2905.27

324.23

35.23

20.90

5.50

33.71

0.1040

KKUA 2 15cm

123

3229.50

324.23

32.06

0.00

35.98

37.10

0.1144

KKUA 2 25 cm

133

3622.83

393.33

32.68

7.46

29.71

9.76

0.0248

KKUA 2 35 cm

143

4016.17

393.33

51.78

27.15

23.01

28.24

0.0718

KKUA 2 45 cm

153

4409.50

393.33

36.07

10.26

32.20

24.83

0.0631

KKUA 2 55 cm

163

4802.83

393.33

26.58

1.87

34.64

12.90

0.0328

KKUA 2 65 cm

173

5196.17

393.33

28.06

5.75

15.84

19.25

0.0490

KKUA 2 75 cm

42.70

8.60

34.81

24.13

0.0613

183

5589.50

393.33

KKUA 2 85 cm

193

5982.83

393.33

25.36

5.80

8.00

32.05

0.0815

KKUA 2 95 cm

203

6376.17

393.33

45.57

12.31

20.75

24.77

0.0630

KKUB 2 65 cm

205

6454.83

78.67

20.63

9.61

32.85

27.85

0.3540

KKUB 2 75 cm

215

6687.58

232.75

13.20

6.27

29.30

8.89

0.0382

KKUB 2 85 cm

225

6759.75

72.17

13.89

11.99

58.79

30.04

0.4163

KKUA 325 cm

233

6817.49

57.74

16.59

8.19

0.30

58.68

1.0163

KKUA 3 35 cm

243

6889.66

72.17

35.85

54.14

24.76

55.50

0.7691

72.17

9.18

12.07

0.00

55.63

0.7708

KKUA 345 cm

253

6961.83

KKUA 355 cm

263

7034.00

72.17

23.31

26.39

35.38

40.70

0.5640

KKUA 365 cm

273

7350.98

316.98

6.48

21.04

15.49

26.60

0.0839

KKUA 375 cm

283

7667.97

316.98

40.45

56.56

22.05

49.58

0.1564

KKUA 385 cm

293

7984.95

316.98

0.33

29.22

26.85

48.79

0.1539

KKUA 3 95 cm

303

8301.93

316.98

9.08

25.76

43.09

18.77

0.0592

KKUA4 5 cm

313

8618.91

316.98

33.89

67.31

5.45

6l.31

0.1934

cm

331

9005.47

386.56

14.48

27.38

63.04

72.71

0.1881

KKUA 4 35 cm

340

9125.15

119.68

15.54

38.56

25.78

38.91

0.3252

KKUA 425

KKUA4 45 cm

349

9244.82

119.68

33.39

64.79

48.06

38.77

0.3239

KKUA 4 55 cm

358

9364.50

119.68

9.34

30.20

19.30

51.01

0.4262

KKUA 465

cm

367

9482.33

117.83

20.15

19.08

43.78

28.97

0.2459

KKUA4 75 cm

376

9600.17

117.83

0.00

20.90

8.28

40.86

0.3468

KKUA 4 85 cm

385

9718.00

117.83

16.96

77.34

25.20

6l.31

0.5203

KKUA 4 95 cm

394

10727.49

1009.49

14.69

46.15

11.07

34.32

0.0340

403

11736.98

1009.49

41.98

43.84

31.84

34.37

0.0340

1121.65

35.84

32.09

23.75

15.53

0.0138

KKUA 4105

em

KKUA 55 cm

413

12858.63

KKUA 515 cm

423

13980.28

1121.65

66.50

64.53

30.23

45.10

0.0402

KKUA 525 cm

433

15101.93

1121.65

90.00

17.68

36.82

52.82

0.0471

KKUA 5 35 cm

443

16223.59

1121.65

87.72

34.91

18.48

25.27

0.0225

KKUA 5 45 cm

453

17345.24

1121.65

66.20

0.44

35.53

44.06

0.0393

458

17906.07

560.83

73.60

1.35

24.69

13.16

0.0235

KKUA 5 50 cm

297


Appendix A4) Identified ecological remains

This appendix presents details of the fossil pollen, spore, algal and chironomid types identified from the analysis of the Lake Challacaba and Laguna Khomer Kocha Upper sediments cores. Pollen, spore and algal images are provided on the enclosed CD (Enclosure CD1).

A4.1 Pollen, spore and algal types

A list of the fossil pollen, spore and algal taxa identified from the analysis of the Lake Challacaba and Laguna Khomer Kocha Upper sediments cores are given in Tables A4.1 and A4.2. In addition, a total of 80 unknown taxa (Unknown 1–80), which only had minimal occurrences, were identified. Twenty-four of these unknowns where later identified to family/genus level. Photographs of the taxa (including the unknowns) are provided in the Enclosure CD1.

<table>
<thead>
<tr>
<th>Spore types</th>
<th>Algal types</th>
</tr>
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<td>Isoëtes type 1</td>
<td>Pediostrum duplex type</td>
</tr>
<tr>
<td>Isoëtes type 2</td>
<td>Pediostrum simplex type</td>
</tr>
<tr>
<td>Joined spore</td>
<td>Pediostrum mini type</td>
</tr>
<tr>
<td>Neurospora HHT361</td>
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</tr>
<tr>
<td>Monolete Psilate</td>
<td></td>
</tr>
<tr>
<td>Monolete Verrucate</td>
<td></td>
</tr>
<tr>
<td>Monolete type 1</td>
<td></td>
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<td>Monolete type 6</td>
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<td>Rugby-ball shaped spore</td>
<td>Trilete type 12</td>
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<tr>
<td>Rugby-ball shaped (smooth) spore</td>
<td>Trilete type 13</td>
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<td>Spore HHT 354</td>
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Table A4.1 Spore and algal taxa identified from Lake Challacaba and Laguna Khomer Kocha Upper sediment cores.
### Table A4.2 Pollen taxa identified from Lake Challacaba and Laguna Khormer Kocha Upper sediment cores.

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<td><strong>Type 1</strong></td>
<td><strong>Moraceae / Urticaceae</strong></td>
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<td><strong>Type 21</strong> c.f. Cuphea**</td>
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*Note: Type indicates the type of pollen grain identified.*
A4.2) Chironomid types

A list of the subfossil chironomid taxa identified from the analysis of the Lake Challacaba and Laguna Khomer Kocha Upper sediments cores is given in Table A4.3. Line drawings, photographs and taxonomic notes of the subfossil chironomid taxa are provided in Chapter 6.

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<th>Subfamily</th>
<th>Tribe</th>
<th>Genus</th>
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<td>Chironomus</td>
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<td>Tanytarsus</td>
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<td>Tanypodinae</td>
<td>Macropolpi</td>
<td>Apsectrotanypu</td>
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<td>Orthocladiinae</td>
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<td>Smittia / Parasmittia</td>
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<tr>
<td></td>
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<td>Pseudosmittia</td>
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Table A4.3 Chironomid taxa identified from Lake Challacaba and Laguna Khomer Kocha Upper sediment cores.