Interactions between Climate, Megafauna, Humans and Fires in Western Amazonia

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(Urrego et al, 2010)

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

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Acknowledgements

Abstract

South America, and more specifically Western Amazonia has a lack of data regarding ecosystem changes that have occurred over the last 30,000 years. Even though ecological changes during the Late Pleistocene have been documented, including ice-age plant migrations and the extinctions of 80% of megafauna species at continental scale, there is uncertainty on the role that fire has played in these ecosystems. Controversy exists over fires natural role in parts of Amazonia, as high humidity and precipitation are thought to supress natural fires. This has created an assumption that fire in Western Amazonia occur largely a result of anthropogenic activities.

This study aims to gain a deeper understanding of the interactions between climate, fire activity, megafauna, and humans in Western Amazonia. This research is the first attempt to investigate the impacts of fire activity and Megafauna extinctions from a hotspot of biodiversity in Western Amazonia: Lake Consuelo. By analysing microparticles of charcoal, spores of *Sporormiella* and the pollen record this research aims to detect the changes in: fire activity, megafauna presence and vegetation changes over the last 28,000 years.

The results showed that fires have occurred since the Late Pleistocene (28,0000 years ago) and thus have been a natural feature of this ecosystem. It was also found that megafauna survived into the Mid-Holocene, suggesting that Lake Consuelo may have provided a refuge for megafauna. Lake Consuelo remained forested and relatively humid during the Mid-Holocene; a period known to be as pervasively dry in Western Amazonia. Lake Consuelo's ecosystem showed to be highly resilient to the changes in climate, fire activity, and megafauna with a relatively high degree of environmental stability throughout the past 28,000 years. Given the high biodiversity concentration found in Western Amazonia, long-term understanding of ecosystem functioning in this region is vital to manage and conserve this biodiversity in the future. As unprecedented climate change and rapid population increases are predicted, areas like Lake Consuelo may be crucial to preserve high biodiversity levels if managed appropriately.

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Abbreviations

Word	Abbreviation Used
Antarctic cold reversal	ACR
NGRIP	North Greenland Ice Core Project
Oxygen isotopic ratios	δ18O
El Niño-Southern Oscillation	ENSO
Sea surface temperatures	SST
Antarctic Oscillation	AAO
Atlantic meridional overturning circulation	AMOC
Above Sea Level	ASL
South American Summer Monsoon	SASM
South American Low-Level Jet	SALLJ
Mid Holocene Dry Event	MHDE
Mid Holocene Dry Period	MHDP

Chapter 1 Introduction

Chapter 1 will start by presenting the aims and objectives of the project. The chapter aims to then provide a contextual overview of the ecosystem changes that occurred from the Late Pleistocene to the present within South America, specifically for Western Amazonia. The proxies used in the project to determine the ecosystem changes will be explained and their importance and role will be addressed. Finally, the chapter will outline the project rationale and the scientific approach that will be taken to answer the project aims, objectives and the research question.

1.1 Project Overview

Ecosystems and their biodiversity are constantly changing and adapting to prevailing environmental conditions in time and space. Fire regimes and animal extinctions can have both short- and long-term lasting impacts on an ecosystem functioning. Recently, studies have reported on the effects of fire activity and megafauna extinctions on ecosystems across South America. Such studies have highlighted that fires are not only linked to regional influences (climate) but also local factors (fuel load) (Power et al, 2008, Roman-Cuesta et al, 2014). They have also highlighted that time and duration of extinction events varies over space and are also driven by differing factors locally (Barnosky and Lindsey, 2010).

This project will take a holistic ecosystem approach aiming to determine relationships between fire activity, the decline of megafaunal abundance, and vegetation change over the past 28,000 years. As well as understanding how these changes relate to the climatic shifts and human's arrival into South America. This data will contribute to the understanding of the resilience of Amazonian biodiversity in a period of large ecological change. The data from Lake Consuelo will be compared against other regional records to better comprehend ecosystem functioning, and megafauna extinctions in Western Amazonia during the Late Pleistocene.

1.2 Project Objectives/Aims

a. To identify and quantify sedimentary charcoal abundance using two charcoal fraction sizes >180µm and 106-63µm to produce a high-resolution analysis of fire activity at the local and regional scale over the past 28,000 years around Lake Consuelo.

b. To identify and quantify the abundance of *Sporormiella,* a coprophilous fungi that is a marker for megafauna presence over the past 28,000 years around Lake Consuelo.

c. To quantitatively explore relationships between the fire record, climate and megafauna abundance, human appearance, and vegetation changes, using both novel data and published records.

d. Relate all five variables to examine the drivers of ecological change in Western Amazonia.

1.3. Environmental change in Western Amazonia during the last 30,000 years

1.3.A Late-Pleistocene Climate Change

Late Pleistocene climate change in South America is characterised by lower precipitation levels and decreased atmospheric CO_2 levels which reduced evapotranspiration (Monnin et al, 2001). Glaciers in the Andes had reached maximal extent by 27,000 cal yr BP (Clapperton, 1993) at a time when the temperature was ~5ºC cooler than the present (Guilderson et al, 1994, Thompson et al, 1998). Amazonian temperature reconstruction using oxygen isotopic ratios (δ18O) highlights that during the LGM temperatures were colder in this period than at present (Thompson et al, 1998). With mean annual temperatures in the high Andean areas reduced by 4-6ºC at the maximum of the Late Pleistocene glaciation (Seltzer et al, 2002).

The deglaciation onset and the transition from a glacial to an interglacial period vary between regions in South America. Dates from moraines ranging from 27,000 to 12,000 cal yr BP (Seltzer, 1990). The deglaciation occurred in Southern areas later than in Northern areas and the climate markedly changed in this deglaciation period (Clark et al, 2012). Generally, this period is shown to be a time of general warming with rapid climatic oscillation occurring (Poveda and Mesa, 1997). During the deglacial period many millennial-scale oscillations

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occurred including the ACR and the Younger Dryas (Clark et al, 2012). Cold SST in the Southern Hemisphere in this period was key to the glacier movement. Atlantic meridional overturning circulation (AMOC) variability and atmospheric CO_2 concentration also helped drive glacier advancement (Jomelli et al, 2014).

South America's climate in this period was controlled by varying moisture sources and the patterns of change were not temporally uniform. Data from models show there were, for example, marked differences between the Altiplano and the Bolivian Amazon Lowlands in the LGM (Rowe et al, 2002). The Altiplano was wetter and Bolivian Amazon drier because of the contrasting moisture sources between the regions (Vuille et al, 2003). Regional climatic differences are a result of multiple factors, these alter temporally and spatially to create such contrasts. Factors include: the Milankovitch precession cycles, the ITCZ position and Sea Surface Temperatures (Hillyer et al, 2009).

1.3.B. The Pleistocene - Holocene Transition

The transition from the Late Pleistocene into the early Holocene occurred between 13,000 – 8000 cal yr BP across South America (Borrero, 1996). In this time after the end of the glaciation temperatures rose (Seltzer et al, 2000, Paduano et al, 2003). Across South America there is evidence for a rapid and pronounced cool period (Urrego et al, 2009), and in North America this period has been termed the Younger Dryas (12,900 – 11,550 cal yr BP) (Barnosky and Lindsey, 2010, Urrego et al, 2009), which was followed by rapid warming thus marking the beginning of the interglacial period (Jomelli et al, 2014, Haug et al, 2001).

However, within South America the timing of these climatic events is highly debated, varying across the continent in both their timing and magnitude. The YD signal is shown in various Andean locations, but the signal contrasts between Central and North Andean records (Urrego et al, 2016). Despite this signal being present in most locations, some South American data sets do not record a pronounced event and the signal varies across different studies (Cruz et al, 2009, Peterson and Haug, 2006, Urrego et al, 2009). Rather the warming trend generally followed into the early Holocene period (10,000-8000 cal yr BP).

1.3.C. Holocene Climate Change

The climate in the Holocene on a continental scale has greater regional similarly in terms of climate change trends than identified over previous times. Holocene temperatures were generally warmer and the Amazonia drier. However, the Mid-Holocene was a climatically unstable period. Generally consisting of phases where shorter dry episodes alternated with humid episodes (Argollo and Mourguiart, 2000). Within the Holocene period, there is a well-recognised climate event of reduced precipitation, the Mid-Holocene Dry Event (MHDE). The Oxygen Isotopic ratio from speleothems in Huagopo Cave, central Peruvian Andes, identifies the Mid-Holocene as a dry/warmer period, higher δ18O % thus indicating a warm period (Kanner et al, 2012). However, this was not a continentally synchronous event. The MHDE was controlled by many factors, including a weakened ENSO and thermal optimum as well as changes in insolation (Bush et al, 2007a), occurring between latitudes of 0-25⁰ South in a period between 10,000-4400 cal yr BP across the Andes region (Bush et al, 2005). Many researchers now identify the event to be time-transgressive from the North to the South, and is commonly described as a period of increased drought frequency interrupted with episodic wet events (Hillyer et al, 2009). The MHDE has been linked to a decrease in the wet season precipitation, temperature increase, the low-pressure system in South America (SASM) as well as changes in the Pacific Ocean circulation and ENSO frequency. (Urrego et al, 2010) This event is recorded in vegetation records in Western Amazonia, with the dry period occurring between 9500 and 5000 cal yr BP (Urrego et al, 2010).

1.3.D. Climate change and vegetation shifts

Climate has played a key role in temporal changes in Amazonian forest ecosystems. Amazon rainforests have existed in South America for the last 55 million years, since the late Cretaceous period (Silman, 2011). These forests cover vast areas, stretching from the Colombian eastern lowlands down to Peru/Bolivia and through the Andes to the Atlantic Ocean (Silman, 2011). They are commonly regarded to be heterogeneous in nature with extremely high biodiversity and a vast range of different and endemic plant species (Pitman et al., 2001). The elevation is the key structuring gradient that affects the diversity and biomass of the forests in this region of South America. Vegetation's

distribution both temporally and spatially is controlled by climatic functions including temperature, CO_2 and precipitation levels (Maslin et al., 2005). Andean montane forests are found up to 3,600m elevation, encompassing both montane and temperature rainforests (Bush et al., 2007). The forest line has shifted over time via glacial and interglacial phases (Weng et al., 2006). However, species present currently are not necessarily the same species found there over time, as forest composition varies due to individualist migration of species. Therefore, future extinction events are highly plausible if temperatures rise, as species would be forced to migrate further to stay in their optimum environmental range (Urrego et al, 2009). Making these forests of high study value.

Although similarities exist within the Amazon region as a whole there are unique differences found between lowland and higher elevation forests. Due to these differences, forests are classed as ecologically distinct from each other (Malhi et al., 2010). Elevation plays a determining role in the type of forests formed along the Andean flank. Both temperature and rainfall vary across elevational gradients and the variation acts to create the differences in plant distributions and species (Silman, 2011). The lowland and mid-elevation mesic forest of the Andean flank generally have the highest diversity (Pennington et al., 2010). Lowland forests tend to exist at a lower elevation, 300-1200m on flat ground. Characterised by: high canopy vegetation, high rainfall, low seasonality (Homeier et al., 2010) and high concentrations of biodiversity and species richness (Homeier et al., 2010, Butler, 2012). Whereas, higher Andean forests tend to have lower diversity levels, trees with decreased stature, and more bryophytes (Foster, 2001). These forests lower limit is determined by clouds/fog level, meaning the air is humid and with a wetter and colder environment (Frahm and Gradstein, 1991).

However, species migrate due to changes in the environment to allow them to stay in their bioclimatic envelope. For example, in the LGM Amazon lowland species distribution moved from 1000-1500m, but migrated upwards in the subsequent deglaciation (Liu and Colinvaux, 1985). Forests at higher elevations are impacted more than lowland areas by changes in the environment (climate and moisture patterns). As there is restricted space in which species can migrate to and still remain in their optimum climatic envelope, relating to the

cone shape of the Andes mountains (Urrego et al., 2009). Consequently, they are more vulnerable to environmental changes and so more likely to face extinction (Fadrique et al., 2018).

Cloud Forest is another classification of forest type distinguished in Amazonia found around elevations of 1200-3600m on the Eastern Andean Flank. They are ecosystems of hydrological significance as they are highly influenced by the frequent ground-level cloud immersion and mist, making them sensitive to changes in climate (Foster, 2001). If temperature increases, as predicted by models, these systems will be threatened. As warming can cause the cloud base to lift and thus change the environmental conditions, causing forests species to migrate upslope (Bush et al., 2008). Cloud forests are normally situated in isolated patches on tropical mountains which gives them a unique environment within terrestrial ecosystems (Still et al., 1999). The clouds form at ground/canopy level creating a persistent fog, reducing the amount of sunlight and evapotranspiration they receive (Hamilton et al., 1995). Cloud level is controlled by the atmospheric temperature and humidity (Urrego et al., 2005). The combination of mist, convective rainfall and orographic clouds, that are derived from trade winds, allow these conditions to prevail (Still et al., 1999), allowing the forests to have an extra source of moisture that even during dry seasons permits the forest wetness to be maintained.
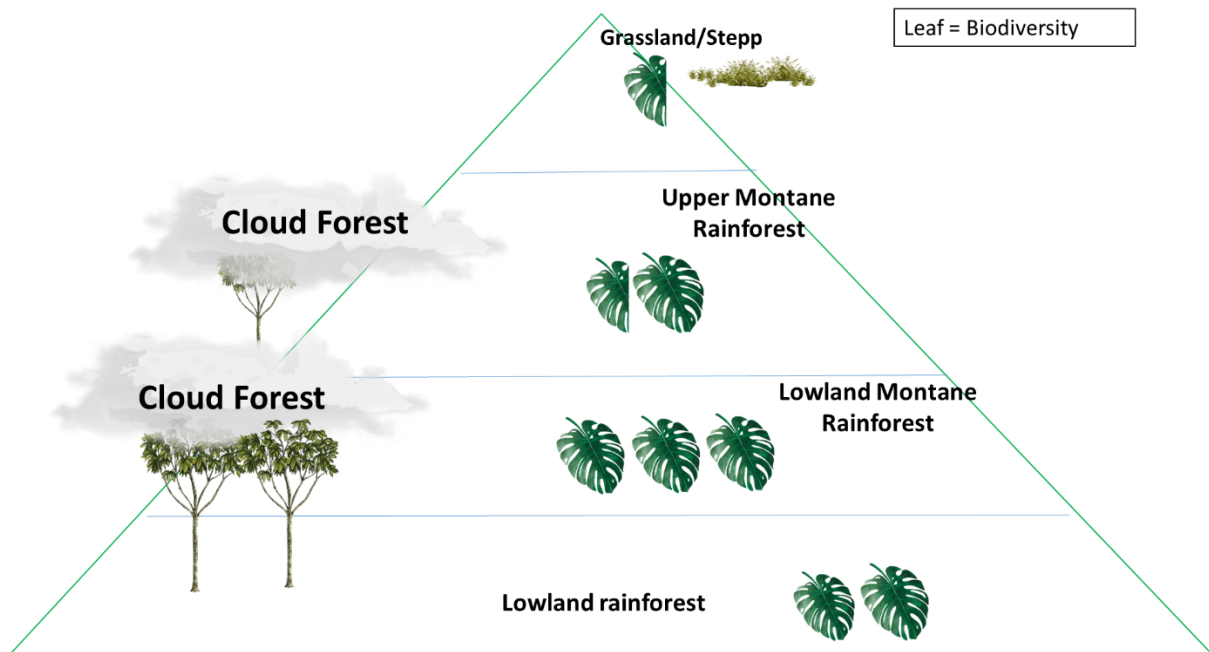
Figure 1. 1 Ecotone zonation diagram. Different forests types and their associated biodiversity levels found at different elevations in tropical South America (tropical mountains). From lowland Rainforest to Stepp land.

1.4 Fire activity

Fires are controlled by multiple factors with complex links at different spatial and temporal scales. Important factors include vegetation type, fuel load, local climate, moisture balance, relative humidity and human activities (Whitlock et al., 2007). Optimal conditions for fires include droughts, increased temperatures, greater fuel load, increased atmospheric CO_2 levels and level of available moisture, hence soil moisture (Nepstad et al., 2004). When the favourable conditions are met fires are more likely to be promoted.

A highly important factor determining the magnitude and extent of a fire is the fuel quantity/load (Pausas and Fernández-Muñoz, 2012). The greater the amount of dry fuel load there is the higher the chance of a fire to ignite and be higher in its intensity. A positive feedback loop can form after an initial fire making it more likely for another fire to start. As post-burn, invasive species growth (e.g. invasive grasses) is promoted due to their fast recolonization times. In turn altering fuel properties, the load quantity and flammability level, thus the fire characteristics (Brooks et al., 2004). The type and structure of the vegetation is also important to fire activity because it constitutes the primary fuel source (Power et al., 2008). Certain vegetation types are adapted to fires and thus have an increased chance of survival via regeneration, while other

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vegetation types are more flammable and so can enhance fire spread (Brooks et al., 2004). Studies have identified that immediately after a fire events there can be changes in ratios of the canopy to understorey pollen (Minckley and Shriver, 2011), in turn this can alter further fire activity.

Climate is also an important driver in determining fires. Regional climate variability influences fire through major climatic oscillations including: ENSO, SAM and AAO (Holz and Veblen, 2012). These phenomena alter the dynamics of fires through changing regional climate conditions and fuel load (Mariani et al., 2016). For example ENSO events can increase droughts severity and decrease rainfall, which leads to soil moisture deficit and increase forest flammability (Nepstad et al., 2004).

Fires have not been static, data from the Neotropics shows clear differences between fires activity in the late glacial period compared to interglacials. During the late glacial period fire in the Neotropics was infrequent due to the lower temperatures, drier conditions and CO_2 causing less biomass burning (Power et al., 2008). However, in the Holocene (interglacial) due to increased atmospheric CO_2, summer insolation, moisture availability and increased temperatures, fire increased, as these conditions favour vegetation growth and thus increased the fuel load. Fossil pollen and charcoal analysis from Lake Titicaca (Bolivia/Peru border) suggested an age for the fire in the region as old as 320,000 years (Hanselman et al., 2011), highlighting fire as a natural component in Andean ecosystems, and it occurs even without humans, and can be influenced by climate conditions. This data also identifies fire to have been greater in interglacials and lower in glacial periods. Drought conditions also are important to fire (Urrutia-Jalabert et al., 2018) when the Orbital precession length is increased the length of the dry season is intensified, which promotes drought conditions and leads to burning (Rowe et al., 2002).

Humans alter natural fires, for example, to open areas for agriculture. Human-induced fires can be greater in magnitude and frequency than natural ones. Data from the Upper Beni, Amazonia, demonstrates that the largest observed changes in forests structure is highly linked to peaks in human occupation. These vegetation changes are due to human-induced fires, and these fires are

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suggested to have a larger impact than previous natural fires recorded (Urrego et al., 2013).

Moreover, when environmental conditions are optimum for fires to spread these anthropogenic fires can develop easily into wildfires. Humans using fire to alter the land has been documented back to the Late Pleistocene. Possibly to ~14.5ka in the Altiplano (Hanselman et al., 2011) and to 13,000 cal yr BP in the Amazon rainforest where evidence of early foragers from archaeological sites has been discovered (Roosevelt, 2013). Humans used fire mainly for activities, such as: land clearance, crop cultivation and deforestation through slash and burn practices. Unlike other environmental factors, fire is not uniform over tropical South America, and records show that fires are unique to a particular area (Power et al, 2010). The differences within paleorecords make it evident that both local ecosystem conditions, as well as humans, influenced fires across Amazonia. Bush et al, (2007b) compared four lakes in Peru within a 50km radius. The results demonstrate how even locations in close proximity have different fire histories. For example, at Lake Gentry from 6200-6000 cal yr BP there is a significant peak in charcoal, but even though Lake Parker is situated merely 9.5km away the same peak was not identified. Although fire is present in both areas, contrasting human occupation might have resulted in these differences.

Therefore, current data on fire activity in tropical South America clearly indicates that fires are both natural and anthropogenically driven and their impacts are becoming an increasing environmental threat. Past records of fire in tropical South America are especially vital to understand the role of moisture balance, burning, deforestation and climate in controlling fires (Power et al., 2010). Fires affect ecosystems through releasing tons of Carbon, CO_2 and other dangerous gases into the atmosphere. Current models show that Amazonia in the near future will face increased burning due to drought (Malhi and Phillips, 2004). In 2010, the fire season was caused by a combination of natural and anthropogenic sources, but it was ultimately the anomalously dry conditions that facilitated their extent and allowed the fire to develop to uncontrollable wildfires (Earth Observatory, 2010).Therefore, it is an important research focus to further comprehend fire activity both pre and post colonisation to assess both natural and anthropogenic impacts of fires.

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1.4.A. Charcoal Transportation Processes

The main natural trigger source for fire is via lighting strikes hitting vegetation, the impact of this depends on the climate of the environment. Anthropogenic actions are also important in starting fires. Particulate charcoal is a direct signal of burning as it is formed from organic matter and plant tissues that have gone through incomplete combustions (Conedera et al., 2009).

After fires happen, charcoal particles go through a variety of different taphonomic processes during transport. Wind and water are the main agents of dispersal. Slope wash is the main transport mechanism when transported by water (Clark, 1988). However, the wind has a more significant role in the transportation process. In large fires, charcoal particles, depending on their size and the velocity of the wind can be lofted 1-5km into the air. This is due to the effects of thermal buoyancy which allows charcoal to reach levels above the canopy. They are then carried via: suspension, saltation or traction, or a mixture of methods depending on the size of the particle (Clark, 1988). The relationships between particle size and transportation method and distance are identified in Table 1.1. Finally, the particles are deposited into a body of water. Either after primary transportation, airborne fall-out or secondary transportation such as reworking of the particles by redepositioning or slope run-off (Figure 1.2). After the initial fire event, it can take a few years for the particles to settle before they become entrapped in the sediment and preserved as fossil charcoal (Whitlock and Larsen, 2002).

Table 1. 1 Different sizes of charcoal particles and their transportation distances, defined by different researchers.

Particle Size	Transport Distance	Reference
> 500μm	Local to fire source. Macroscopic particles not transported far; low amount identified outside the very local area.	(Ohlson and Tryterud, 2000)
10-200 μm	Found 20-100km away from the source	(Conedera et al., 2009)
>125 μm	Were abundant in sites <7km from fire after this distance accumulation fell rapidly.	(Whitlock and Millspaugh, 1996)
60-2000 μm	Not normally suspended, carried less than meter above surface. Carried by process of saltation. Locally found.	(Clark, 1988)
<60 pm	Transport by suspension	(Clark, 1988)
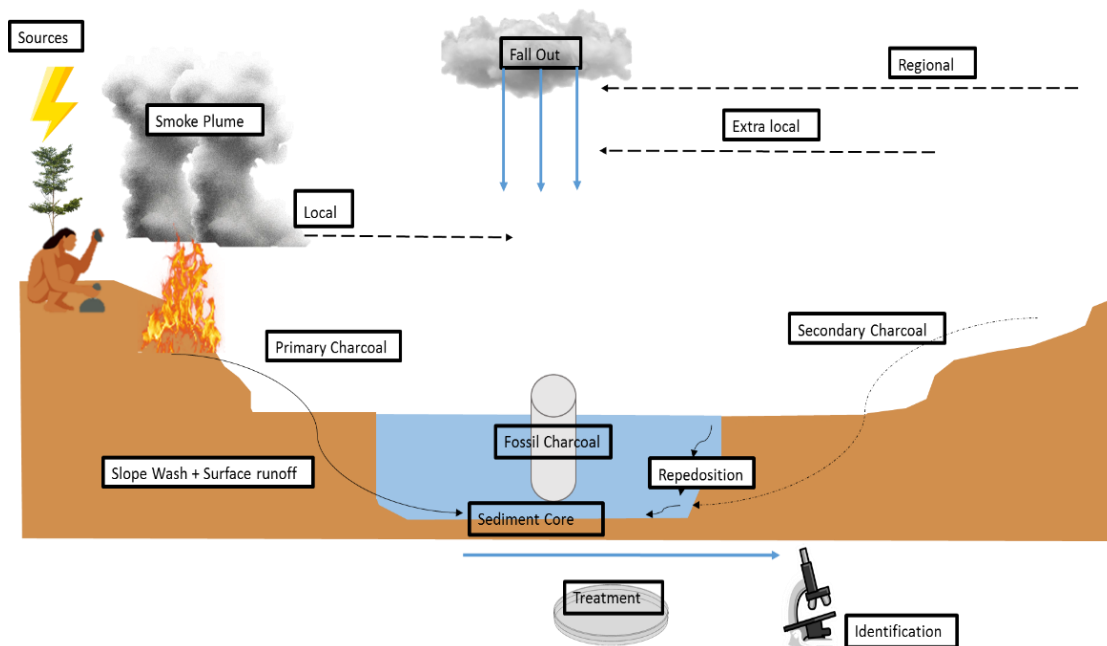
Figure 1. 2 illustration of Charcoal particle transportation. Based on diagrams from Whitlock and Larsen (2002), Patterson III et al. (1987) and Conedera et al. (2009). Depicting the process from the initial fire to the fossil charcoal assemblage. Including the transportation methods and taphonomic processes involved.

Charcoal particles are not uniform in size and so are divided into different size classes. These size boundaries are used to differentiate between signals from local and regional fires because particle size determines how far from the fire source charcoal particles can travel (Whitlock and Larsen, 2002). Small particles are defined generally as micro particles <100 µm and have a wider source area. They are transported for longer distances (Table 1.1) and therefore are interpreted as a representation of regional-scale fires (Whitlock and Larsen, 2002). Large particles are generally defined as macro particles >100 µm and indicate a local fire event. These macro particles generally stay within the watershed and travel no more than 1000m from the source (Clark, 1988). The size boundaries used to classify local and regional fires are not standardized across studies (Appendix 6). Despite differences in classification across literature, the transportation process is generally similar following the pattern described above.

The source area also depends on the fire's properties. The larger the height of the fire's smoke plume the greater distance the particles can possibly travel,

making the source area greater. Micro-particles are lighter so they can be lofted higher up in the smoke plum, thus have a greater chance of traveling a further distance from the location of the fire. The amount of charcoal that is produced also depends on a range of factors, such as the type of vegetation in the ecosystem. But charcoal production also depends on the duration, temperature and the intensity of a fire (Patterson III et al., 1987).

Distinguishing between local and regional fire signals can help to identify the main factors behind the recorded fires. It can indicate if they were a result of human or climatic factors.

1.5 South-American Human occupation

It is well documented that humans have significant impacts upon ecosystem dynamics. Yet, there is still no clear consensus in South America regarding the time, method, or entry route of humans nor the extent and impact of their activities on the environment (Borrero, 2008). Dated archaeological evidence (bones/artefacts) of humans is scarce, especially in tropical South America, and is largely clustered towards the southern cone (Figures 1.3/1.6) (Barnosky and Lindsey, 2010). Evidence of human occupation also comes from charcoal records, specific pollen taxa and shell remains found in soils (Capriles et al., 2019).

It has been largely accepted that around 14,000 years ago humans had occupied parts of South America. For a prolonged time the occupation was thought to have followed the 'Clovis-First model', suggesting that migration occurred ~13,000 years ago (Dillehay et al., 2015). However, recent archaeological research has revealed data to debunk this theory, suggesting some pre-Clovis humans existed in South America. These first settlers existed in small units, were highly seasonally adapted and very mobile, moving locations when new resources were required (Capriles et al., 2019). Employing a hunter-gather method to survive which did not largely include the selective killing of large animals. Thus, initially their overall environmental impact was minimal (Gutiérrez and Martínez, 2008) but when environmental conditions improved more permanent settlement became favoured (Lombardo and Prümers, 2010). Dillehay et al, (2015) concludes that at Monte Verde site,

anthropogenic activity was evident from as early as 18,500 cal yr BP. This finding implies that humans entered the continent after the LGM, becoming more sustained from 14,500 cal yr BP. This is the earliest sound date for human arrival in South America. Overall, most data suggests humans arrived in South America much later than this towards the late Pleistocene period (Delgado et al., 2015).

In Western Amazonia there is limited direct evidence of anthropogenic activity due to difficulties of data collection (Capriles et al., 2019). Evidence from Palaeoecological records and archaeological data from Bolivia lowlands suggests humans were present in the region from ~10,000 cal yr BP (Lombardo et al., 2013). Moreover, in Pubenza (Colombia) dates from tools and mastodon remains suggests humans extend back to 20,300-15,600 cal yr BP (Van der Hammen and Urrego, 2001). However, these dates are unconfirmed and provide only an ambiguous date for human's existence (Borrero, 2016). Records from Peru based on *Zea mays* and charcoal highlight sustained human presence after 3380 cal yr BP (Bush et al., 2016). Although evidence of human occupation is available in Western Amazonia, the data is inconclusive. A recent study from forest islands in Llanos de Moxos area concludes that this area is likely to have been the earliest area of human occupation in SW Amazonia region, dating humans in the area from 10,600 cal yr BP (Capriles et al, 2019). However, the main development/settlement age ranges from 8700 to 5800 cal yr BP (Capriles et al., 2019). Overall, the current literature strongly indicates that within Western Amazonia the ages for human occupation is generally concentrated after 10,000 cal yr BP, the Late Holocene period.
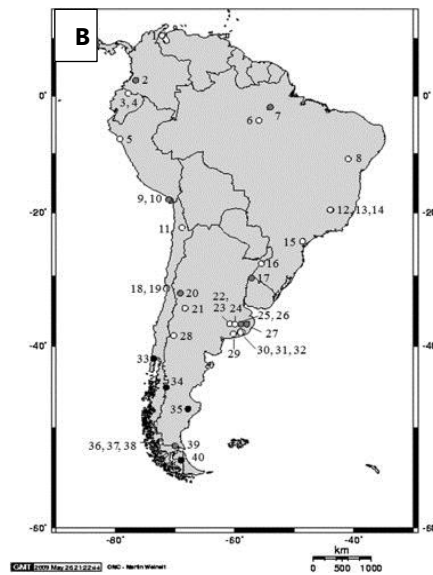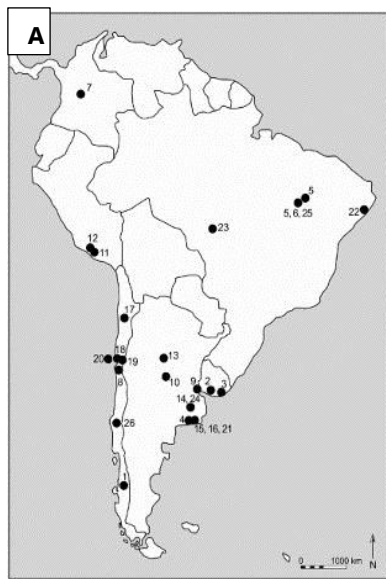
Figure 1. 3 Maps from studies using multiple records to anlayse humans and megafauna in south america. A) Map of the archeological sites in South America that identify human occupation and Megafauna remains (Borrero, 2016). B) Map of robust dates sites of megafaunal (white dots) and Archeological Sites (Grey) and where both (Black) (Barnosky and Lindsey, 2010).

1.6 Megafauna

Megafauna animals are generally defined as oversized mammals both herbivores and carnivores that once populated most continents. However, towards the end of the Pleistocene epoch, an extinction event occurred causing a substantial loss of many megafauna species. Today, large herbivores are mostly constrained to Africa where a significant proportion of species have prevailed (Barnosky et al., 2004b). Examples of these extant African megafauna animals include elephants (*Loxodonta africana*) and giraffes (*Giraffa*). The megafauna that once lived in South America included giant ground sloths (*Mylodon darwinii*) the giant short-faced bear (*Arctotherium sp.*) and the sabre-toothed cat (*Smilodon populator*) (Metcalf et al., 2016).

Within the literature, weight thresholds are a commonly employed way to distinguish megafauna apart from other animals. However, discrepancy exists regarding the threshold size for megafauna (Owen-Smith, 1987, Bakker et al, 2016). The most common boundary limits for modern herbivores are defined as animals weighing between 44 and 100kg (Gill, 2014). This weight class includes keystone animals, these are animals that would have had significant environmental impacts. However, other research has used different boundaries, such as a 1000kg limit which would consider extinct Pleistocene megaherbivores (Owen-Smith, 1987). Or the study by Berzaghi et al. (2018) who uses a >5kg threshold. This research will consider species >44kg meaning

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very small taxa are excluded as these could convolute the results and interpretations and large extinct taxa are included.
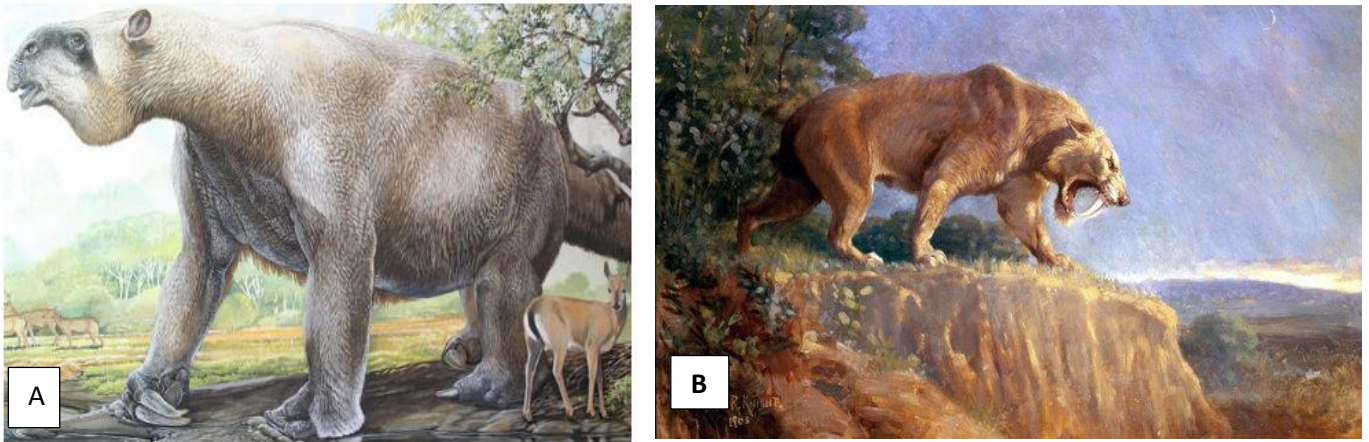
*Figure 1. 4 Images of possible extant species from South America **A**. Reconstruction of a Giant Ground Sloth (Megatherium americanus) (Schouten, 2019). **B**. Reconstruction of a Smilodon populator (Knight, 1903).*

1.6.A. Reconstructing Megafauna abundance

The presence of megafauna and their abundance in a given ecosystem can be determined through a range of methods each having their advantages and limitations. One direct method is via fossil analysis, which involves identification and examination of fossilised megafauna remains (Metcalf et al, 2016). The foremost problem with this method is the lack of samples and the expense associated with direct dating (Walker and Walker, 2005). Alternatively, obligate coprophilous fungi (dung fungi) found in the sedimentary record are becoming increasingly used to identify megafaunal presence and abundance in past environments (Baker et al, 2013). A range of coprophilous fungi varieties, especially those from the genus *Sporormiella* are morphologically distinct and the most useful to assess megafauna abundance (Davis and Shafer, 2006, Gill et al, 2009, Raczka et al, 2016). Spores of *Sporormiella* and other coprophilous fungi are well preserved in lakes sediments along with other proxies (charcoal and pollen). This combination of proxies that can be recovered from lake sediments allows the interpretation and understanding of ecosystem functioning. The use of *Sporormiella* to reconstruct megafauna abundance has been gaining prominence in recent years, after the relationship between megafauna dung and *Sporormiella* were established in Bechan Cave, Utah

(Davis et al, 1984). The proxy was tested in North America in 1977 and has since been used for this purpose (Davis et al, 1977). The validity of *Sporormiella* has been strengthened by modern calibration studies (Raczka et al, 2019, Raper and Bush, 2009).

These ascomycete spores develop on mammalian faeces (Bell, 1983). When herbivores feed on plants the spores are ingested, they endure digestion and later germinate on the dung of the animals (Figure 1.5). Dispersal is only over short distances (1-2 meters) due to the structure of the spore (Baker et al, 2013). The spores can concentrate around the shore, so the nearer the core is extracted to the shoreline the higher the spore concentration is likely to be (Raper and Bush, 2009). Additionally, the deposition and concentration of *Sporormiella* have also been shown to vary depending on a lake's bathymetry (Raczka et al 2018). Large animals produce more dung biomass and hence a relatively higher proportion of spores can germinate on their dung (Gill et al, 2013), making *Sporormiella* a reliable tool to estimate the abundance of large animals. Data from Gill et al, (2013) show that *Sporormiella* indicate the presence of megaherbivores and that it can be separated against mesofauna background levels. Therefore, the *Sporormiella* can be considered an appropriate tool to determine the presence and disappearance of megafauna.
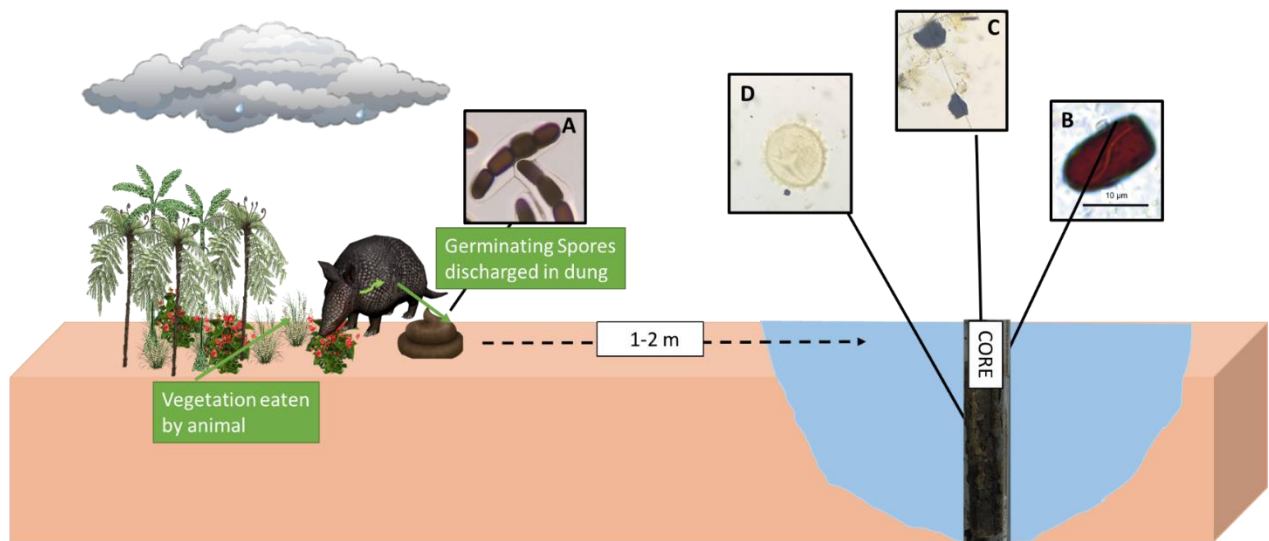
Figure 1. 5 Illustration of the process of the production of spores identified in a lake sediment core. After the animal digests the food the spores grow in the faeces (A) (Doveri, 2014). They are then transported across land 1-2m into water bodies and can accumulate in sediments. Through the use of sediment cores we can capture multiple environmental proxies. Including: Sporormiella (B)(Raczka et al., 2016), Charcoal (C) and pollen grains (D). (Camacho, 2015). Adapted from illustrations from (Bell, 1983).

To determine the period when the extinction event of megafauna from a sedimentary record occurs a threshold value is usually used. The value of this threshold varies in the literature as it is specific to the ecosystem, but generally it is stated to be around the 2% abundance level of *Sporormiella* (Burney et al, 2003, Davis and Shafer, 2006). A decline of spores under this level signifies a megafauna population collapse (Davis and Shafer, 2006).

1.6.B. Megafauna Extinctions

Globally, megafauna' extinction events occurred from the Late Pleistocene until the Early Holocene. By 10,000 cal yr BP at least 97 of the 150 (or more) genera that populated the continents had gone extinct (Barnosky et al, 2004a, Doughty et al, 2010). Within South America, the Pleistocene extinction events consisted of a loss of around 66 species (Barnosky et al, 2016). South America lost 83% of its megafauna genera, the largest loss out of all the continents (Koch and Barnosky, 2006). Thus, making it one of the most extreme turnover events in earth's history for this continent (Cione et al, 2009).

Although megafauna extinction events are highly acknowledged globally. The extinction of megafauna in tropical South America and the consequences of this

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event ecosystem functioning, are still poorly understood. Neither is the timing nor cause(s) of the event.

Although Eurasia only lost 36% of it megafauna genera research conducted in South America is more restricted than In Eurasia (Barnosky et al, 2004b). Barnosky and Lindsey (2010) demonstrated this data gap in the timing and cause of extinction in South America. They highlight that there are only a few dated studies on megafauna extinctions in the South American continent, with most data concentrated within the Southern tip of the continent. This is further emphasised by Lima-Ribeiro and Diniz-Filho (2013) review of data for extinct megafaunal taxa, in South America, that show that a total of 163 sites were appropriate, compared with the 298 in North America. In Amazonia, only a handful of records have recently become available and the data gap is especially prominent in the Western part of the basin (Lima-Ribeiro and Diniz-Filho, 2013) (Figure 1.6).
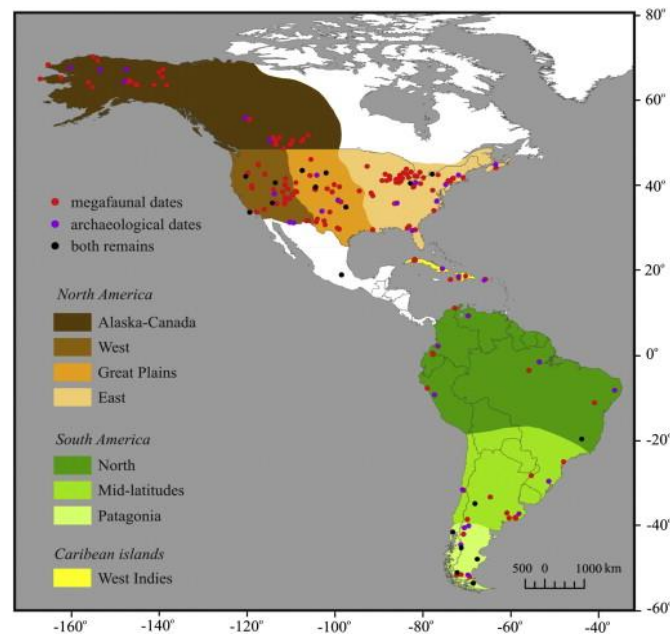
Figure 1. 6 Map from Lima-Ribeiro and Diniz-Filho (2013) study. Locations where reliable dated records were found and used in analysis. Map displays the difference in the amount of records conducted from North and South America. As the uneven distribution of studies in South America, higher concentration in the Southern Cone.

The megafauna extinction events are locally variable, and globally, it happened >50,000 years (Barnosky et al, 2004b). Not only did the number of extinct animals vary over time and space, but the duration of extinction events also appears to be significantly variable. The South America extinctions are thought

to be less concise than in other continents. For example, in North America extinction dates tend to cluster between 11,500 and 10,00 cal yr BP (MacPhee, 2018, Barnosky et al, 2004b). The last known occurrence dates are found to be over 40,0000 year in Northern South America (Barnosky and Lindsey, 2010). In Venezuela fossils of *Haplomastodon* dated back to ~48ka (Barnosky and Lindsey, 2010) whereas in the Argentina Pampas the fossil evidence show that some species had survived into the Early Holocene (Politis and Messineo, 2008).

In the wider Amazon region, the available data, although very scares, suggests that the extinction event occurred around the Pleistocene/Holocene transition. A later age for the functional extinction, approximately ~12,000 to 11,500 yr ago is also reported in South Eastern Brazil (Raczka, 2017). Data from Lake Pacucha in the Peruvian Andes suggests the decline was two-staged. The first decline occurring at 21,000 cal BP and the second and final extinction occurring at 15,800 cal yr BP (Rozas-Davila et al, 2016). Evidence from *Sporormiella* decline in Lake Llaviucu, in the high Ecuadorian Andes, shows a later extinction date around 12,800 years ago (Raczka et al, 2019). Other evidence from the Pacific coast of Ecuador suggests an initial extinction around 12,000 cal yr BP with final collapse occurring around 8000-6000 cal yr BP (Ficcarelli et al, 2003). Fossil evidence from Amazonia also suggests a similar trend of species extinction occurring at this period (Lima-Ribeiro and Diniz-Filho, 2013).

The available data suggests that megafauna extinction events in tropical South America were spread over several thousand years, from the Pleistocene into the early Holocene. The emerging picture is of megafauna persisting in certain areas for a much longer duration than in other locations. The factors and environmental conditions allowing for this longer survival are unknown.

Research questions that are hotly debatable are: How did the ecosystem respond and influence extinction events? Did changes in the ecosystem occur before or after these events? Over what period did the extinction occur? These questions need further examination to allow for a full understanding of megafauna extinctions in South America. Data from a range of localities must become available to provide the best possible understanding of these events

1.6.C. Megafauna and ecosystem function

Mega herbivores most likely played an important role in shaping ecosystems. The loss of such an important component of the ecosystem could have induced trophic cascade changes. Megafauna animals are considered to be keystone species because they consumed consumption of lower quality vegetation and long gut retention periods over large areas, creating a disproportionate effect on plant communities (Gill, 2014). Such large animals would have affected vegetation structure but also would have influenced nutrient cycling and fire activity by controlling fuel load (Rule et al, 2012). Megafauna also influenced species composition, forest structure and its dynamics through browsing and trampling on vegetation (Malhi et al, 2016). For example, large herbivores could suppress grass growth allowing other vegetation to increase (Crainel and McLauchlan, 2004). Moreover, palaeoecological analysis indicates they reduced below ground nutrient competition, favouring mature forest trees, impacting carbon dynamics in closed-canopy forests. Megafauna also compete with smaller herbivores for resources and their removal altered both the vegetation and fauna dynamics, impacting energy flows, and functioning of entire ecosystems (Malhi et al, 2016).

Finally, numerical modelling has highlighted megafauna's role in nutrient distribution on a continental scale. Doughty et al (2013) model demonstrates that these large animals acted as a nutrient pump, and even long after their extinction has created an ongoing legacy of uneven nutrient distribution (i.e. phosphorus) across Amazonia. The impact of megafaunal extirpation from ecosystems was extensive and acted at multiple levels within ecosystems.

1.6.D. Hypothesis of Megafauna extinction

Both globally and within South America, the cause of megafauna decline is a centre of controversy. A myriad of different theories and models have been suggested to explain their extinction (Hubbe et al, 2011). Generally, the cause of the extinctions are either related to humans, climatic changes or a synergy of the two, Figure 1.7 (Feranec et al, 2011). Alternate causes for extinction, such as extra-terrestrial impacts (Firestone et al, 2007) and diseases (Lyons et al., 2004) have been proposed, but these theories have insubstantial support.
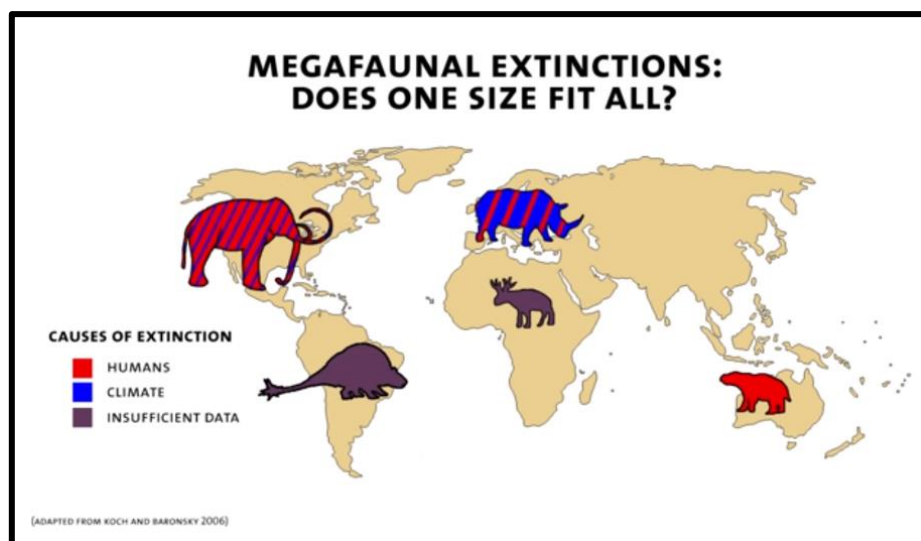
·   *Figure 1. 7 Image showing the global causes of extinction by continent. A simplified image by MacPhee (MacPhee, 2018) of Koch and Barnosky (2006) diagram. Highlighting the insufficient data in South America at present. Globally the cause of extinction events are due to multiple causes.*

Human's role in the megafaunal extinction was first proposed by Martin and Wright (1967) and since has grown in popularity. In North America, humans are thought to have played a large role in the collapse of megafauna populations. This has been termed the 'overkill hypothesis' and suggests that aboriginal populations (Clovis hunters) drove megafauna to extinction both directly via methods of hunting and indirectly through ecological disruption (AMNH, 2018). In North America, the first contact between early human populations and megafauna is implied as to the major cause of extinction. This is because the collapse of the megafauna quickly followed the timing of human arrival (MacPhee, 2018). Megafauna did not have time to adapt to human's actions. Conversely, in South America there was a longer overlap period, thus allowing

megafauna to have developed strategies to co-exist with humans and prolong the extinction window (Borrero, 2009). A primary problem of the overkill hypothesis to explain extinction in South America is the insufficient amount of direct evidence to support humans as the main factor behind the extinction. Links between humans and killing can be established via butchering marks on bones and/or human artefacts associated with hunting such as lithic tools and spear points (Ficcarelli et al, 1997). If causation of extinction was driven through mass killing evidence (e.g. bones) would be expected to occur in vast amounts, which they are not. However, new pieces of evidence suggest that humans hunted megafauna, at least in the southernmost tip of South America, in the Patagonia region (Politis et al, 2019). Although in tropical South America there is data suggesting an overlap between humans and megafauna, it does not directly support the overkill hypothesis. Charcoal and *Sporormiella* records from Lake Llaviucu (Ecuador) indicate human presence around the same time *Sporormiella* collapsed in the fossil record, which in turn suggest extinction (Raczka et al, 2019). However, megafauna and humans coexisted for 2000 years at Llaviucu region, thus the extinction may have been a prolonged process instead of an instant mass killing. Moreover, this interpretation of human's occupation at Llaviucu stems from the charcoal record, thus caution should be taken as there is not direct human evidence.

Climate is the second most prominent hypothesis for the cause behind the extinction of megafauna. Late-Pleistocene climate change is suggested to have caused changes to animal's habitats and resources resulting in their extirpation (Gallo et al, 2013). Climate change can act both directly and indirectly to alter species abundances. It is plausible that changes in fire activity, vegetation structures/composition and lake levels were driven by climatic changes. These changes decreased accessibility to vital resources for survival and altered the favourable conditions they were adapted to (Malhi et al, 2016). An alteration in vegetation before a decrease in megafauna indicates climate acted indirectly to cause megafauna collapse. In tropical South America studies by Rozas-Davila et al (2016) and Villavicencio and Werdelin (2018) support a climatic driver. These studies suggest that the climate forced habitats to change causing vegetation composition to alter consequently driving the decline in populations.

However, humans are proposed as a secondary causation in SE Brazil (Raczka et al, 2018). As humans actions increased pressures on the megafauna and so prevented recovery of the already deteriorated populations (Raczka et al, 2018). As this extra pressure did not allow populations to rebound and adapt to the changes caused by climate (Hubbe et al, 2011). In Peru, there is a possible coexistence between animals and humans. However, the interpretation that humans had an impact of megafaunal extinctions here depends on the confidence intervals used in the archaeological dates (Villavicencio and Werdelin, 2018).

This leads to the question: are the extinction of the megafauna a result of a synergy between humans and climate change? The combination of factors could have created a pressure over a prolonged period that megafauna could not withstand. For example, in Patagonia the amalgamation of causes is used to explain the collapse of megafauna populations at 12,300 cal yr BP. This extinction event was caused by rapid warming after the ACR causing forest dynamics to change, alongside human's occupation (Metcalf et al, 2016). Thus, due to a compilation of drivers rather than a single factor.

Alternative hypotheses have been constructed for the megafauna extinctions. One being an extra-terrestrial impact event (Firestone et al, 2007, Pino et al, 2019). This idea is parallel to the Chicxuclb impact event which has been linked to the killing 75% of species globally (MacPhee, 2018). The extra-terrestrial event is supported by Israde-Alcántara et al (2012) who used evidence from a range of sedimentary/mineral proxies to explain the link. However, the data is highly flawed and so generally disregarded. The primary problem being the poor and outdated chronology they based their research on, along with other data interpretation flaws (Blaauw et al, 2012). Another postulated cause of extinction is the hybrid disease hypothesis. This theory links megafauna extinctions to humans introducing novel hyper-diseases that attacked large animals and eventually caused their extinction (Lyons et al., 2004). However, again it is not sufficiently supported within the scientific community.

Large animals were more susceptible to extinction than small animals due to their physiology and reproductive strategies. Megafauna predominantly have K-strategies with long gestation periods, maturation time, life spans and have singular births (Malhi et al, 2016). Their rates of reproduction and adaptation

would be relatively slow compared to the rate of environmental and anthropogenic alterations (Cione et al, 2009) and would need a long time to respond and recover from climatic and anthropogenic stresses. Regardless of the final cause of extinction, it is likely that reduction of favourable habitats due to climate change at the end of the Pleistocene put megafauna species at an increased risk of human hunting (Hubbe et al, 2011).

1.7 Scientific Rationale

The Late Pleistocene-Holocene includes major global climatic upheaval, human's arrival into North and South America and the megafauna extinctions (Gill et al, 2013). This period is therefore critical for comprehending long-term ecosystem dynamics that can inform conservation and management. Earth is currently facing large environmental stresses created from increasing human population and their consequent impacts upon ecosystems (Armesto et al, 2010). Human population growth is rising environmental pressures beyond anything ecosystems have previously experienced. This is creating cumulative novel impacts that are already leaving a legacy of environmental implications (Maezumi et al, 2018). Ultimately, such stresses will have vast negative impacts on ecosystems and will change fire activity, vegetation structures and animal populations both directly and indirectly.

This study is the first attempt to investigate the changes in fire activity, vegetation composition and megafauna extinctions on ecosystem functioning from a strategic site in a Western Amazonia biodiversity hotspot. There is little research undertaken in South America and more specifically Western Amazonia looking at such changes. The void in data is partly due to the remoteness of Amazonian forests and the lack of long sedimentary archives that allow long temporal records of ecosystem changes (Burbridge et al, 2004). Lake Consuelo is one of a few sites with a long-temporal record of ecosystem dynamics in Western Amazonia spanning over 30,000 years (Urrego et al, 2010). Understanding the fire activity and megafauna extinction impacts and causes on biodiversity hotspots like Lake Consuelo, will allow addressing the resilience of these forests to fauna extirpation and can contribute to understanding potential future alterations under current global environmental changes. These include global temperatures increases, with temperatures predicted to rise by 1.5ºC in

the next 20 years (IPCC, 2018). Also, increasing drought frequency and intensity in the Amazonian regions, and increasing frequency and intensity ENSO events as well as an annual air temperature change of 2ºC by 2010 to 2040 (Marengo and Bernasconi, 2015).

Making overarching assumptions or extrapolating data, especially in an area as diverse as the Amazon could lead to skewed understandings (Barnosky et al., 2016). Thus, it is vital to study changes on a local ecosystem level as well as at regional scales to better understand ecosystem dynamics. Understanding the long-term ecology and the consequences of fire activity and megafaunal extinctions during the Quaternary is also of high interest for conservation and management of high-biodiversity ecosystems. Long-term ecological data can highlight vulnerable areas and inform conservation efforts and management (Gill, 2014). Thus, this study will not only help to understand the long-term ecosystem dynamics of biodiversity hotspots in Western Amazonia but will also provide long-term data which can aid ecosystem management during the Anthropocene (Emery-Wetherell et al, 2017).

1.8 Scientific Approach

The following section will discuss the scientific approach and sampling strategy designed to achieve the research aims. Three microfossil records will be used to achieve the objectives: sedimentary charcoal, fossil pollen and coprophilous fungi. The development stages involved in the production of charcoal records at local and regional scales will be discussed. Also, the quantification of *Sporormiella* spores and the sampling strategy for this analysis. The pollen record for the site of interest has been previously produced (Urrego et al, 2010). Here I describe how these published data will be used to evaluate correlations between vegetation change, fires activity and megafauna decline. A chronology will be produced for the sediment record using five pre-existing and unpublished radiocarbon dates to construct an age-depth model. Finally, the three proxies for fire activity, vegetation change and megafauna abundance will be linked together to examine ecosystem dynamics in Western Amazonia over the Late Pleistocene and Holocene periods.

1.8.A. Fire activity and charcoal record

Charcoal fractions will be analysed to create a fire activity record. Charcoal particles are not uniform in size, so are commonly divided into different size classes. By distinguishing between macro and micro-size particles, both signals from local and regional fires can be determined. For this study the two size boundaries chosen for local and regional signals were: >180 µm and 106-63µm.

These fractions were chosen for specific reasons.

1. The sizes are chosen in this study needed to be in a range allowing comparison of data to other studies, especially studies in close location proximity.
2. Keeping classes identical to the pilot study (Johnston, 2017), allowing all data to be combined to produce a high temporal resolution record of the fire activity in Lake Consuelo and the surrounding areas.
3. Charcoal particles <65µm are considered too small to identify to a high degree of accuracy.
4. Particles <65 µm are possibly broken pieces of charcoal particles from a larger piece. For examples broken in chemical preparation see Raczka et al, (2018).
5. Particles >100 µm travel far greater distances therefore the maximum boundary for 106 µm for micro-particles was chosen as can be deemed appropriate given the apparatuses available.
6. Quantification of two discrete size fractions circumvents problems with overlapping charcoal distributions and therefore allow teasing apart regional vs local fire activity changes.

Charcoal samples will be taken approximately every 5-10 cm down the core, in-between the places where samples were previously taken applying a systematic approach. This will allow a higher resolution record to be created giving a detailed history of the fire activity in Lake Consuelo across the last 28,000 years. The initial spores sampling locations will be at the same location as charcoal samples. This will allow a direct comparison between proxies that will be identified separately.

1.8.B. Vegetation and pollen record

To understand vegetation changes over time the pollen record from Lake
Consuelo will be used. Producing the raw data within the timeframe of a
Master's dissertation is not feasible due to the high concentration of biodiversity
and the steep learning curve associated with pollen analyses. Therefore,
secondary data will be used that have been previously published (Urrego et al,
2010). This pollen record was taken from another core which was extracted
from Lake Consuelo spanning back 43,000 years. Pollen sampling was
conducted every 5-10 cm giving intervals of ~400 years. At least 300 terrestrial
pollen grains were counted and distinguished in samples. Aquatic pollen grains
and spores were also counted but excluded from the total pollen sum. Over 150
different species of pollen were identified across the record.

The pollen record will be evaluated and summarized to analyse vegetation
changes concerning fire activity and megafauna decline. Species that show the
greatest amount of changes across the record will be selected. This will help to
determine if certain vegetation are controlled by fire activity, or if fires are
controlled through vegetation (Minckley and Shriver, 2011). Also, if megafauna
have any impacts on vegetation structure.

1.8.C. Megafauna abundance and dung spores

To investigate the presence/absence of megafauna at Lake Consuelo,
Sporormiella spores will be used to pinpoint when the spores declined in the
fossil record. The sampling strategy that will be employed will focus on taking
samples at even intervals across the entire length of the core. Following this
initial data collection, if the data analysed shows an interesting pattern/peak at
particular points more in-depth sampling will be carried out in these parts, to
produce a higher resolution record around the area of interest. Initially a
systematic sampling technique will be applied then a stratified sampling
approach will be taken for a more in-depth analysis. The spores will then be
identified by a range of different distinguishing features.
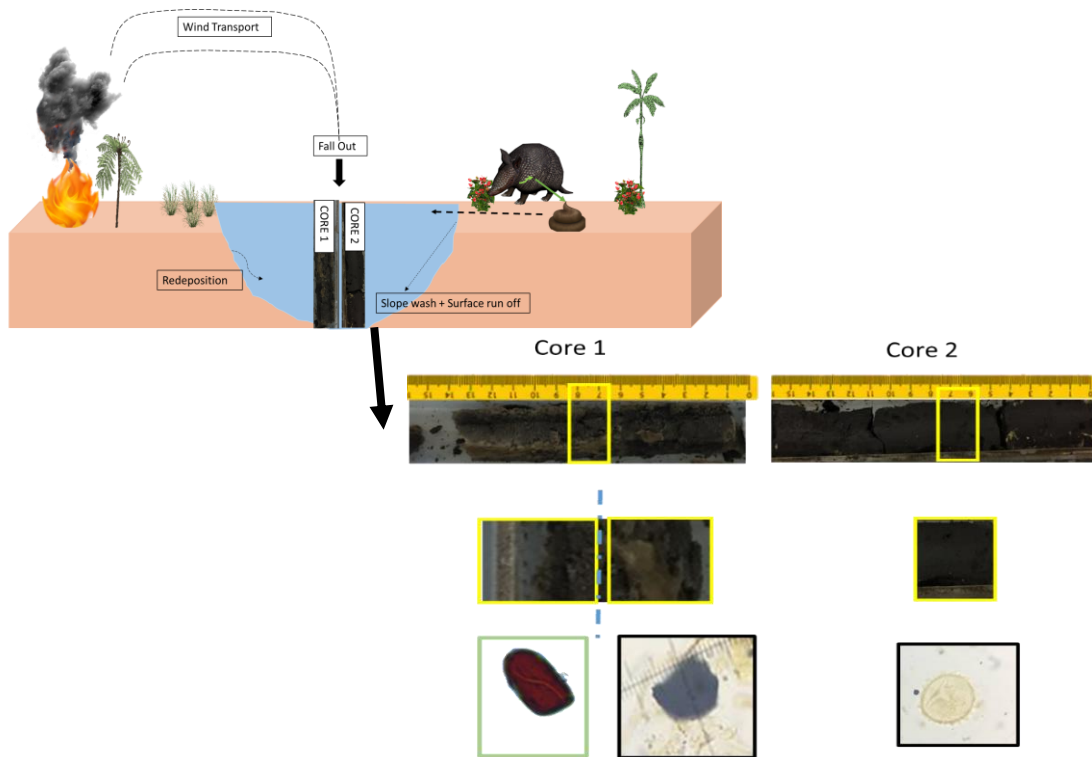
Figure 1. 8 Diagram illustrating the process from the initial source and production of each proxy. Use of two different cores to examine the three proxies used in the study. The location from the spores and charcoal taken from the same section in core 1. Pollen taken from a second core.

Chapter 2 Methodology

This chapter will provide details on the study area and the reasons why Lake Consuelo is appropriate for this study. Following this, details of how data was collected, processed, and analysed will be presented. Every method used has its own set of advantages and disadvantages. Thus, this chapter will explain each method chosen along with appropriate justification for the experimental design employed.

2.1 Regional Setting of Study Area

The focus of this research is Lake Consuelo in Western Amazonia (13°57.1'S, 68°59.45'W), Figure 2.1. Located in the Southeast of Peru near to the Bolivian border and the Eastern Andean Flank. The lake is situated 1360m Above Sea Level (ASL), in a humid region in a catchment dominated today by lower cloud forest. A forest cover has been present since the Late Pleistocene, however, the species composition has varied temporally (Urrego et al, 2010). Lake Consuelo is at the lower cloud forests limit and is currently dominated by the species: *Celtis, Trema, Acalypha, Cecropia and* Moraceae/Urticaceae (Mayle et al, 2009). Bioclimatic envelope modelling of Lake Consuelo's pollen record suggests that modern temperatures are 5-9°C warmer than in the LGM (Bush et al, 2004). The lake is located below Lake Titicaca (3810m ASL) and down-slope from the Bolivian Altiplano.

Other important sites where previous fire or megafauna extinction analysis has been conducted near Lake Consuelo are, Lake Titicaca (Paduano et al, 2003), Lake Refugio (Urrego et al, 2011), Lake Llaviucu (Raczka, 2017) and Lake Chochos (Bush et al, 2005), (Figure 2.2).

Figure 2. 1 Photograph of Lake Consuelo and surrounding cloud forest vegetation found at present (Urrego et al, 2010).

The present climate of Lake Consuelo is linked to South American Summer Monsoon (SASM), Amazonian Convection and South American Low-Level Jet (SALLJ) on both interannual and interannual timescales (Urrego et al, 2016). The moisture availability in this region is possibly mediated through cloud cover and considered the most important local factor influencing ecological changes. Four sediment cores were removed (Urrego et al, 2005, Urrego et al, 2010) using a Colinvaux-Vohnout piston corer (Colinvaux et al, 1997) in the two different field operations that were conducted in 2001 and 2008. The 2008 cores were collected from the centre of the lake reaching a depth of 7.7m and this core will be used in the study for primary data analysis. A pollen record from the 2001 cores has been previously published (Urrego et al, 2010) and will be used to help understand changes in the ecosystem related to changes in fire activity and megafauna abundance.

2.1.A. Location Justification

All samples were taken from sediment deposited in a Lake of a closed basin and surrounded by moderately steep slopes. These environmental factors help to preserve and limit the possibility of loss and contamination in the material. Meaning that the data collected are unlikely to be skewed from material that is

either foreign or not in situ. One main advantage of lake cores is that they allow a range of proxies to be preserved in situ. This is due to the anoxic conditions in a lake preventing movement and decay (Smol et al, 2002). Ultimately, this means that different proxies can be directly correlated, confidently knowing that they are from the same point in time. Thus, holistic ecosystem changes can be understood even when limitations in determining a precise chronology exist. The 2008 core was taken from the middle point in the lake thus, the deepest point below 10.5m water depth. Allowing the oldest possible data from Lake Consuelo to be examined covering back over the past 28,000 years.

Furthermore, Lake Consuelo contains material dating back to the Pleistocene and spans the transition period into the Holocene. Such long and complete records are very rare in Amazonia and tropical South America (Capriles et al, 2019). This is because the majority of lakes in the Andes formed in the last deglaciation period, meaning they are <14,000 years old (Seltzer et al, 2000). Hence, the Lake Consuelo record has a high study value in examining ecological changes in Western Amazonia. Moreover, Consuelo is located within a biodiversity hotspot near the Manu National Park, which is considered a world's top biodiversity hotspot (Tarabochia, 2016). Lake Consuelo is therefore important because the area's history contain important information regarding fauna and flora changes, but it is also important in terms of conservation in the future. Tropical montane cloud forests are highly threatened ecosystem (Myers et al, 2000). Therefore, these ecosystems are of high study importance to help understand their unique functioning's to help protect them (Malcolm et al, 2006).
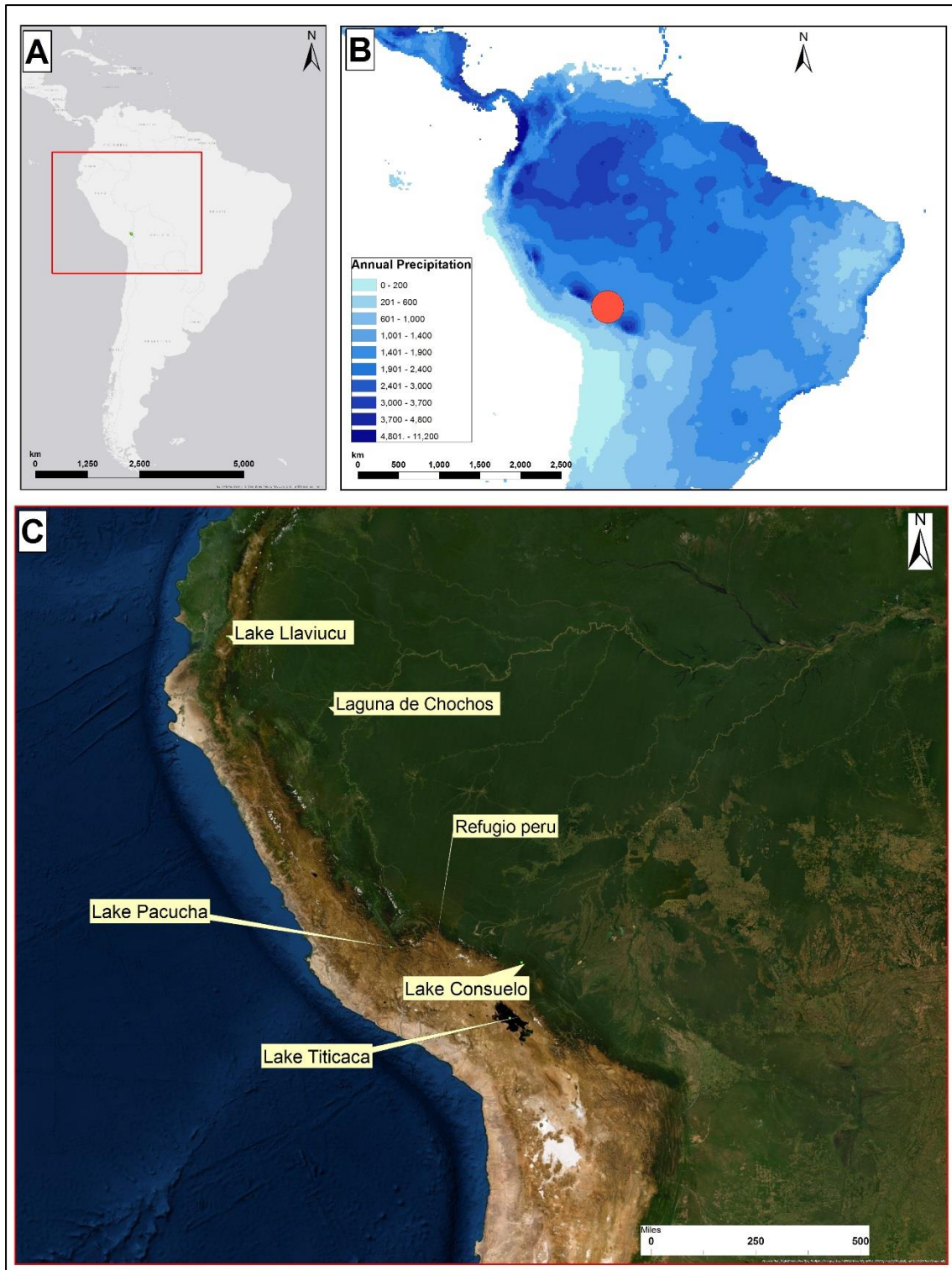
*Figure 2. 2 Location map **A**. Location of Lake Consuelo within South America. **B.**
Annual Precipitation data from WorldClim Data sets (Hijmans et al, 2005). Identifying
Lake Consuelo situation on the edge of a wetspot (red circle). **C.** Location of Lake
Consuelo and other sites where Megafauna extinction data are available through the
use of Sporormiella records. Or a fire record through use of charcoal.*

2.2 Preliminary Data

Previous work on the sediment core was conducted prior to this study. Former work includes the Radiocarbon dating in five places across the core's length (Urrego, unpublished). These radiocarbon ages identified that Lake Consuelo is older than 25,000 cal yr BP, and are of high importance as they allow a whole core chronology to be constructed to run the analysis proposed in this research (Libby et al, 1949). Moreover, radiocarbon dating is appropriate for the lake sediments and organic macro-remains, producing the most accurate dates for Consuelo's age range (Walker and Walker, 2005).

Other data formerly collected from the same sediment sequence used in this study includes two pilot studies, one on fire activity and the second on herbivore extinctions. These studies analysed charcoal particles (Johnston, 2017) and coprophilous spore abundance (Osmaston, 2017). This data highlighted a high potential to produce sturdy results on ecosystem changes with the application of further analysis. Having established the feasibility of the research, the present project was designed to provide a high-resolution environmental history for this area of Western Amazonia through more detailed analysis. Analysis of sediments, core descriptions and magnetic susceptibility were also taken previously to this study (Johnston, 2017, Osmaston, 2017). The core and previous samples were kept in the University cold store at 5ºC to ensure preservation of sediments.

2.3 Methodology

2.3.1. Sampling Strategy

The first stage of preparation consisted of subdividing the 7.7m core into 1cm sections. Artificial gaps were created in the core tubes due to transport and Styrofoam was used to prevent further shifting (Figure 2.3). Samples were taken at regular intervals to allow for both charcoal and *Sporormiella* analysis to be done at the same depth. This resulted in 43 samples of 1cm^3, where charcoal and *Sporormiella* analysis were integrated. Following this, 43 additional samples were taken to increase the resolution of the fire

reconstruction. In total, 86 samples were taken over the core on average every ~6cm. Therefore, the resolution for the fire record was higher than the resolution for the megafauna record. From the 1cm^3 samples two 0.5cm^3 subsections were taken using volumetric syringes. One subsection taken for charcoal and the other for *Sporormiella* preparation. (Appendix 2 and Appendix 4 lists all samples depths for charcoal analysis and *Sporormiella* analysis).

Prior to every stage in the preparation instruments were cleaned to ensure there was minimal cross contamination. All material in the core tubes were measured with a ruler and compared to previous measurements to make sure data was as accurate as possible. As the samples were taken from the same location it meant that even if the depths (cm) were out slightly from previous analysis due to shifting of the material the *Sporormiella* and charcoal sample data was known to be from the same age (i.e. from the same depth interval).
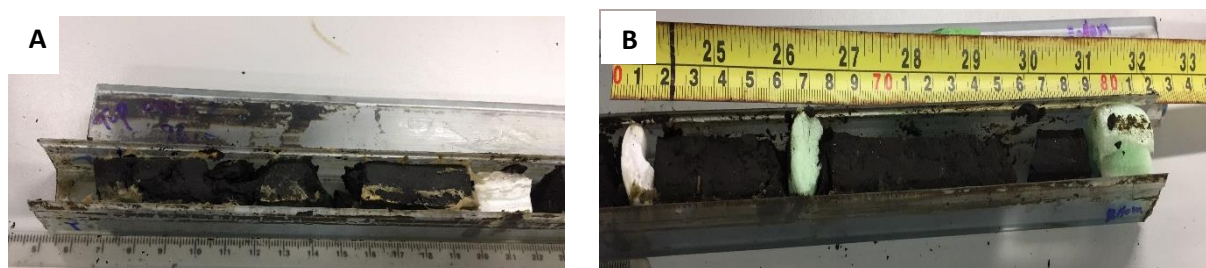
Figure 2. 3 A. and B. Photographs of the core before subsampling. Showing the gaps due to sediment moving during transport and how the sediment was fixed with Styrofoam to prevent shifting.

2.3.2 Charcoal Analysis

2.3.2.A. Preparation

The preparation followed the standard techniques (Whitlock and Larsen, 2002), fully detailed in Appendix 1. Distilled water was used to wash out the equipment to avoid contamination from local pollen sources in mains water. To ensure that final samples were clear for microscope identification chemical treatment processes were repeated depending on of the type of sample (Consult Appendix 1 for the precise treatments used). Samples that had high organics were also bleached to clear the samples from material that was not charcoal. To break up samples without breaking up individual charcoal fragments an ultrasonic bath was used so data was not skewed.

Sample residue was sieved into four different fractions: >180 µm, 180-106 µm, 106-63 µm and <63 µm. All samples were kept in the cold store for preservation until examined. Two fraction sizes were chosen for this study as explained in the scientific approach (Chapter 1). These were particles >180µm and between 106-63µm. Appendix 6 summarizes how different studies, including studies near to Lake Consuelo, use different size classes to distinguish macro and micro fractions. These studies along with prior charcoal analysis on the core were used to help to choose the size class appropriately for this study.

There is also a discrepancy in the type of method used to determine/count the charcoal particles. Some methods use pollen slides to examine the microscopic charcoal fractions. However, the method employed here was suitable as pollen slides were not examined and the chosen method isolates the charcoal making them clear and visible to count accurately (Whitlock and Larsen, 2002).

The potential loss of some sediment in preparation is possible, due to the transfer of material between sieves, tubes and other equipment used. However, this loss was minimised by washing out any material in the equipment with distilled water as best as possible. Moreover, there was potential charcoal breakage in the procedure, but this was limited by not touching the charcoal in the preparation and only breaking up sediment via chemical treatment and in the ultrasonic bath. These limitations would have been systematic errors therefore standard across all the data samples ensuing for a fair comparison between data.

Charcoal Quantification

Charcoal particles were examined under a Zeiss Stemi508 microscope at 10x magnification. The light shines down in this type of microscope making charcoal more distinguished and thus easier to count accurately. The samples were put into a pre-gridded petri dish and all pieces of charcoal were counted (up to a pin-point size) Figure 2.4. This gridded Petri dish allowed to count the charcoal systematically, so that there was no repeat counting.
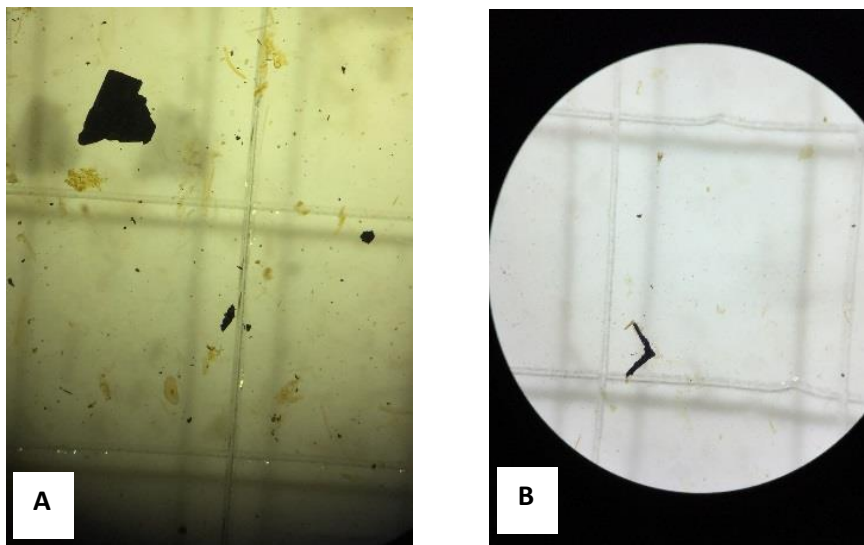
Figure 2. 4   A and B. Pictures of both macroscopic and microscopic charcoal taken down the microscope lens in the gridded Petri dish.

The charcoal particles were distinguished from other material by their angular edges, planar shape and jet black colouring (Whitlock and Larsen, 2002). When there was some degree of uncertainty on the fragment another test was conducted, for example, using a fine needle to break the fragment apart. If the material shattered into smaller angular fragments with the applied pressure, then it was defined as charcoal otherwise it was not quantified (Whitlock and Larsen, 2002).

2.3.3. *Sporormiella* Analysis

2.3.3.A. Preparation and Justification

Standard pollen and spore concentration techniques were used to concentrate *Sporormiella* spores (Faegri et al, 1989). This process is outlined in Appendix 3 and consists of three main steps: initial preparation, acetolysis and density separation. An exotic marker *(Lycopodium clavatum)* was added to each sample as a reference count and to calculate the concentration. Density separation was carried out using Sodium meta-tungstate, this stage was included to float off the *Sporormiella* spores. This is an imperative part of the process because *Sporormiella* spores are very light and small ~10µm (Burney et al, 2003). Density separation thus allowed spores and pollen to be separated from the rest of the sample without a sieve. The protocol use to concentrate the spores was already used and tested previously (Raczka et al, 2016).

After initial analysis, twelve more samples were prepared using the same methods as above. These were concentrated around the core depths where there was a clear peak in *Sporormiella*, 6cm either side of the peak. This resulted in an average 30-year resolution between samples around the largest peak. This was done to ensure that the peak event was not just one singular sample but rather an actual trend in the data set.

2.3.3.B. *Sporormiella* Microscopy

The Zeiss Axio imager A2 microscope was used to quantify *Sporormiella* spores at a 40x magnification. The sample was spread onto a microscope slide using glycerol to make the sample at an appropriate density level that allowed spores and pollen to be seen.

The spores were identified by:
- Their distinguishing features: dark brown colour, defined sigmoid germinal aperture, thick cell wall with no pores or gaps, and shape (Davis and Shafer, 2006). Figure 2.5 displays some of these features.
- Using the reference pictures and information from Aptroot and van Geel (2006), van Geel et al. (2011), Burney et al. (2003) and Davis and Shafer (2006).

- Taking photographs via the microscope camera and when unsure about a potential spore having them assessed by multiple experienced palynologists.

The *Sporormiella* raw counts from all 55 samples (from the two batches) were used to calculate both the concentration of the *Sporormiella* per cm^3 per samples and the relative abundance (%) equal to the total pollen sum. *Sporormiella* and pollen grains were quantified until reaching 600 pollen grains.

The relative abundance value is the value that will be used/discussed most frequently in this study, as these are the values expressed as percentages of the pollen sum. As data has shown that *Sporormiella* concentrations are seen as noisier than the abundance value (Parker and Williams, 2012) and abundance values are more commonly used in research.

The concentration values were worked out following the equation:

$$Sporomiella\ concentration = \frac{\left(\frac{Sporomiella\ count}{Lycopodium\ count}\right) \times Lyco\ spike\ added}{Sample\ volume\ or\ weight}$$

Where the sample volume was always 0.5cm^3 and the Lycopodium spike 20846.
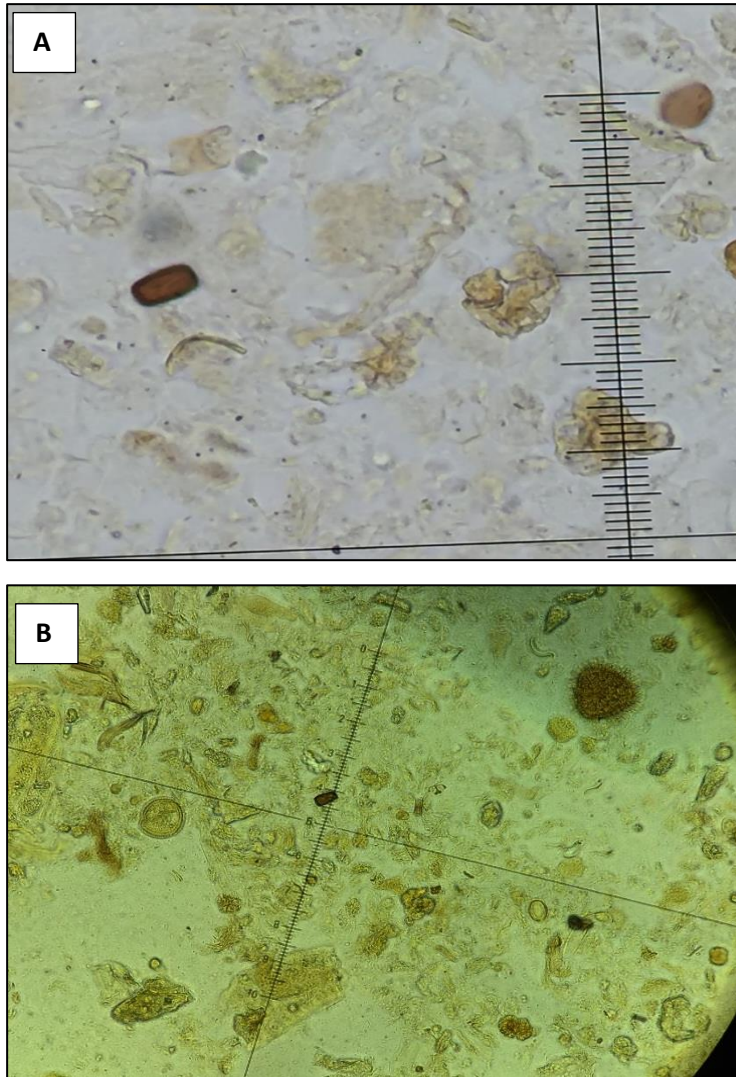
Figure 2. 5 A. Image showing one Sporormiella spore with its thick wall and S-shaped aperture. B. Image showing a different Sporormiella spore (middle of cross) and a lycopodium (exotic marker) grain (top right) as well as other pollen grains which were counted.

2.4 Chronology development

An age-depth model was produced to provide a chronology for the record. This model was based off five radiocarbon dates analysed previously at the [14]CHRONO Centre at Queens University Belfast. Table 3.1 shows all the radiocarbon dates and priori information used to develop the model. The age-depth model was produced using the Bacon Package on R Statistics program (Blaauw and Christen, 2011) and is based on Bayesian probabilities.

A Bayesian probability age model was used because unlike other methods, the model is based on prior knowledge of the sediment sequence (Blaauw and Christen, 2011). This is information such as, the accumulation rate, the variability and potential outlying dates. So that the model's outputs produced are the most likely possible. Also, Bayesian models tend to produce smaller model confidence intervals (Birks et al, 2012). This particular model type was chosen as allowed the most accurate model possible to be produced. Alternative methods, such as smooth-spline models in Clam are considered of lower accuracy (Blaauw and Christen, 2011) and thus not deemed appropriate for use.

Chapter 3 Results

Chapter 3 intends to outline and discuss all the data that was collected and analysed throughout the project. The age-depth model was produced through the software R. Graphs were formed using either C2 software (Juggins, 2014) or Grapher software (GrapherTM, 2018).

3.1 Age-Depth Model

A Bayesian age-depth model was generated using the R Statistics program with the additional Bacon Package (Figure 3.1). The age of the surface was taken to be the core extraction date (2010). The basal age of the sediment record obtained at 752cm was 25,287 ± 177 cal yr BP. The *acc.mean* value used, 31.5, was calculated so the value was specific for this core based on the difference in ages divided by the difference in depth. The *acc.shape* value 1.5 was used as this is the default value and most appropriate for this type of sediment deposit and shape.

Table 3. 1 Input in to R (bacon package) to produce the Bayesian Age-Depth model, assuming the top of the core is present (when core was taken, 2008) with a low error. Run with the corrected depths.

labID	Ages	Error ±	Depth	cc
surface	-58	1	0	0
con3	3903	40	73	3
con3	9812	57	325	3
con3	10758	61	385.5	3
con3	16720	68	591.2	3
con3	25287	177	752.2	3
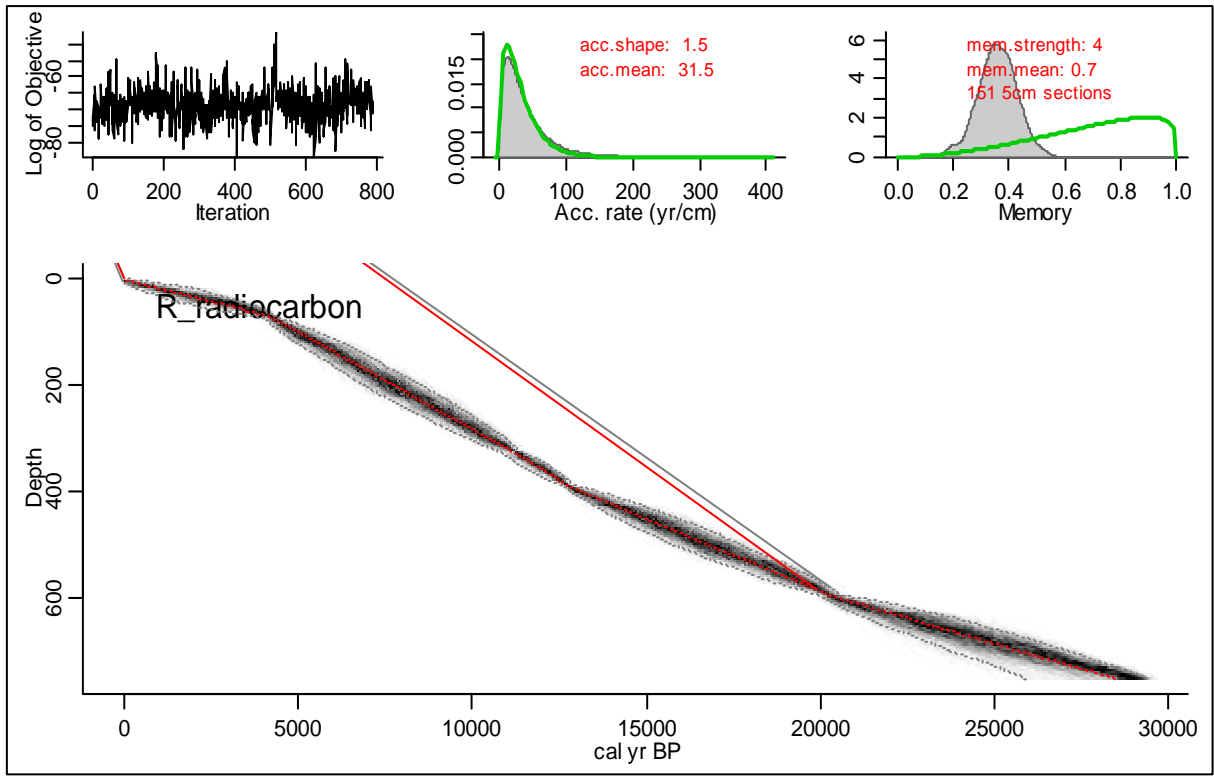
Figure 3. 1 Age-depth model. Produced in R statistic, Bayesian age model using Bacon. Using unpublished radiocarbon dates (Urrego et al, 2010), model run on the 5/2/19.

3.2 Charcoal Data

The sampling strategy employed allowed a resolution between samples of ~225 years, this allowed the interpretation of detailed changes in the fire frequency over the last 28,000 years. The local and regional fire activities showed both similarities especially in the earlier and later dates, however, there are also discrepancies between the two fraction sizes in concentration especially around the Mid-Holocene.

Late Pleistocene - Holocene

The general trend of the local charcoal record largely shadowed that of the regional record, especially between 28,000 to 12,000 cal yr BP (from 760cm to 360cm depth). Until 12,000 cal yr BP fire was continuously present but the concentrations of charcoal were low. Whitlock and Larsen (2002) state that a 'non-fire' event is represented by <50 particles of charcoal per cm^3. Based off this level there are a few 'non-fire' events dispersed across the record between

25,000 to 11,000 cal yr BP both locally and regionally, however concentration was never 0.

Holocene - Present

The shift in concentration occurs around the Pleistocene-Holocene boundary, with both record peaking at 12,300 cal yr BP ± 725. Followed by two local spikes of concentration at 11,800 cal yr BP ± 825 and 11,300 cal yr BP ± 660. The first substantial peak in regional charcoal concentration is at 10,300 cal yr BP ± 1200, not identified in local concentration. However, both fractions show a peak at 8860 cal yr BP ± 1500. From this point until around 6000 cal yr BP the two records largely match. At 5470 cal yr BP ± 1280 there is a large difference between the local and regional record, there is a peak of local charcoal but very small concentrations of charcoal in the regional record, again this is the case at 4770 cal yr BP ± 920. However, after this point until the end of the record there is great similarity between the two size fractions of charcoal concentration, apart from a larger regional peak at 3600 cal yr BP ± 1250 compared to smaller but still peak locally. There is only one 'non-fire' event after this 11,000 cal yr BP this a regional fire event recorded at 1300 cal yr BP.
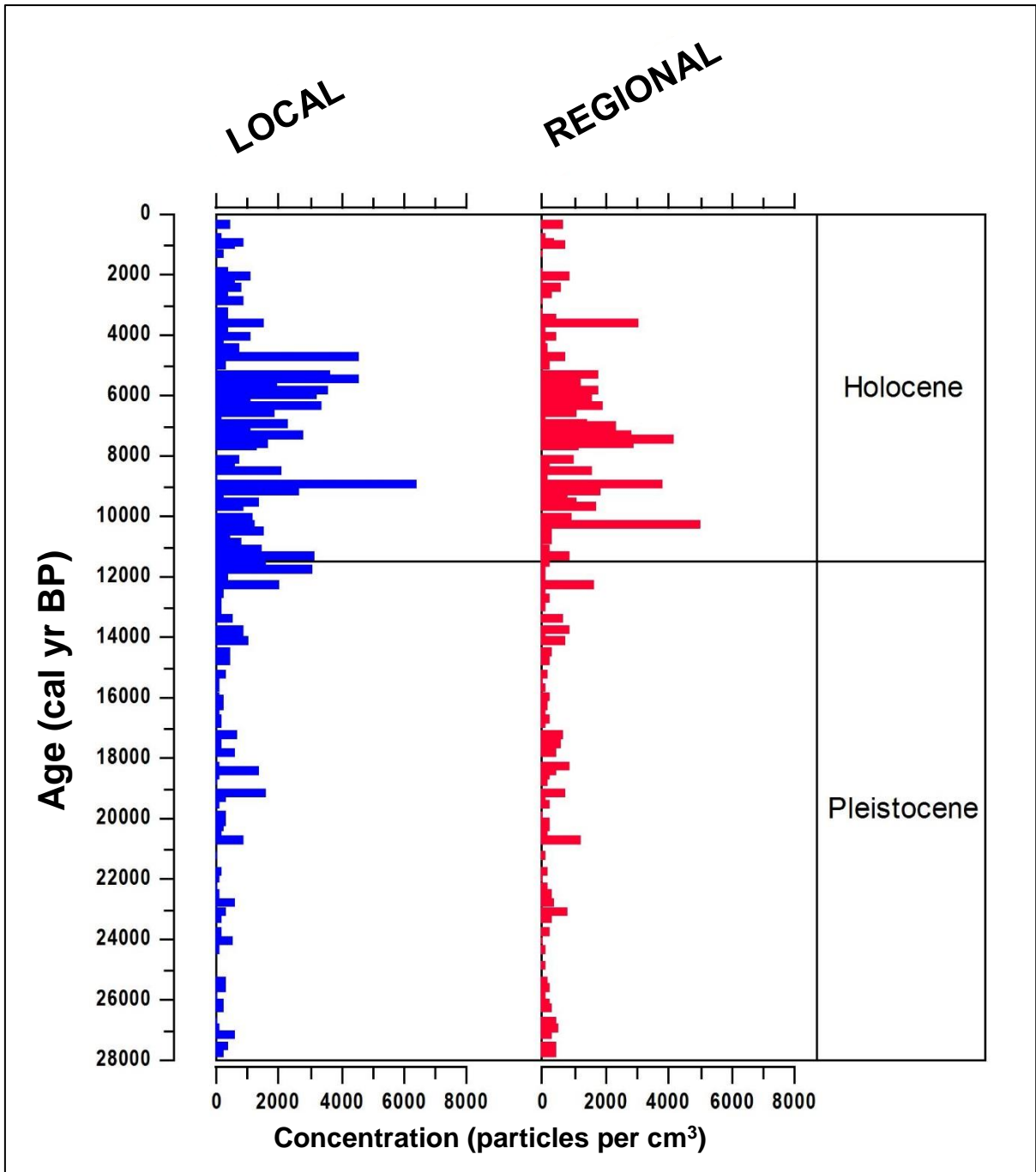
Figure 3. 2 Charcoal abundance in Lake Consuelo for two size fractions. Local (red) corresponds to charcoal particles >180 μm, and regional (blue) charcoal particles corresponds to charcoal particles > 63-106μm. The line separates the Pleistocene and the Holocene epochs at 11,500 cal yr BP. The graph is plotted against age (cal yr BP).

3.2.A. Statistical Analysis

T-tests were performed to identify statistical significance between the local and regional charcoal analysis. All tests were performed in Excel using the data analysis extension.

Firstly, a test between the local and regional charcoal concentration was run. The two-tailed T-test showed no significant difference at the 95% confidence level between the local and regional fire activity across the record ($t=1.97$, $p<0,05$). Suggesting that there are similarities between the macro and micro charcoal data. Thus, the activity is likely to be a result of the same influencing factor.

Table 3. 2 T-test results, two-tailed t test, the difference between local and regional charcoal concentrations.

	Variable 1	*Variable 2*
Mean	649.031	873.8295
Variance	717156.8	1187637
Observations	129	129
Hypothesized Mean Difference	0	
df	241	
t Stat	-1.84997	
P(T<=t) one-tail	0.032771	
t Critical one-tail	1.651201	
P(T<=t) two-tail	0.065542	
t Critical two-tail	1.969856	

The second T-test was run to compare the fire record in the Pleistocene against the fire record in the Holocene. To see if fire activity altered between the two epochs. The test was run separately for local and regional records. The boundary used for the transition was 11,500 cal yr BP. This value was chosen as it is very close to values used commonly in literature in South American records (Thompson et al, 1998, Borrero, 1996, Aldenderfer, 1999, Paduano et al, 2003, Urrego et al, 2016), as well as Urrego et al. (2010) study on Lake Consuelo and the NGRIP core date.

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Table 3. 3 T-test results between fire before and after 11,500 cal yr BP, for the local record (Charcoal particles >180µm)

	Variable 1	Variable 2
Mean	1334.25	420.4923
Variance	1726691	254849.8
Observations	64	65
Hypothesized Mean Difference	0	
df	81	
t Stat	5.198159	
P(T<=t) one-tail	7.38E-07	
t Critical one-tail	1.663884	
P(T<=t) two-tail	1.48E-06	
t Critical two-tail	1.989686	

Table 3. 4 T-test results between fire before and after 11,500 cal yr BP, for the regional record. (Charcoal particles >63 and <108 µm).

	Variable 1	Variable 2
Mean	960.8594	342
Variance	1167186	92387.25
Observations	64	65
Hypothesized Mean Difference	0	
df	73	
t Stat	4.413829	
P(T<=t) one-tail	1.72E-05	
t Critical one-tail	1.665996	
P(T<=t) two-tail	3.45E-05	
t Critical two-tail	1.992997	

The local fire record showed a statistically significant difference between fire in the Pleistocene and Holocene epochs, (Table 3.2) to the 95% confidence interval, (t=2.0, p<0.05).

The regional fire showed a statistically significant difference between fire in the Pleistocene and Holocene, (Table 3.3) to a 95% confidence interval, (t=2.0, p<0.5).

The local and regional fire activity records did not show a significant difference between them. However, there was a difference between fires activity from the Pleistocene and the Holocene.

3.3 Megafauna – *Sporormiella* record
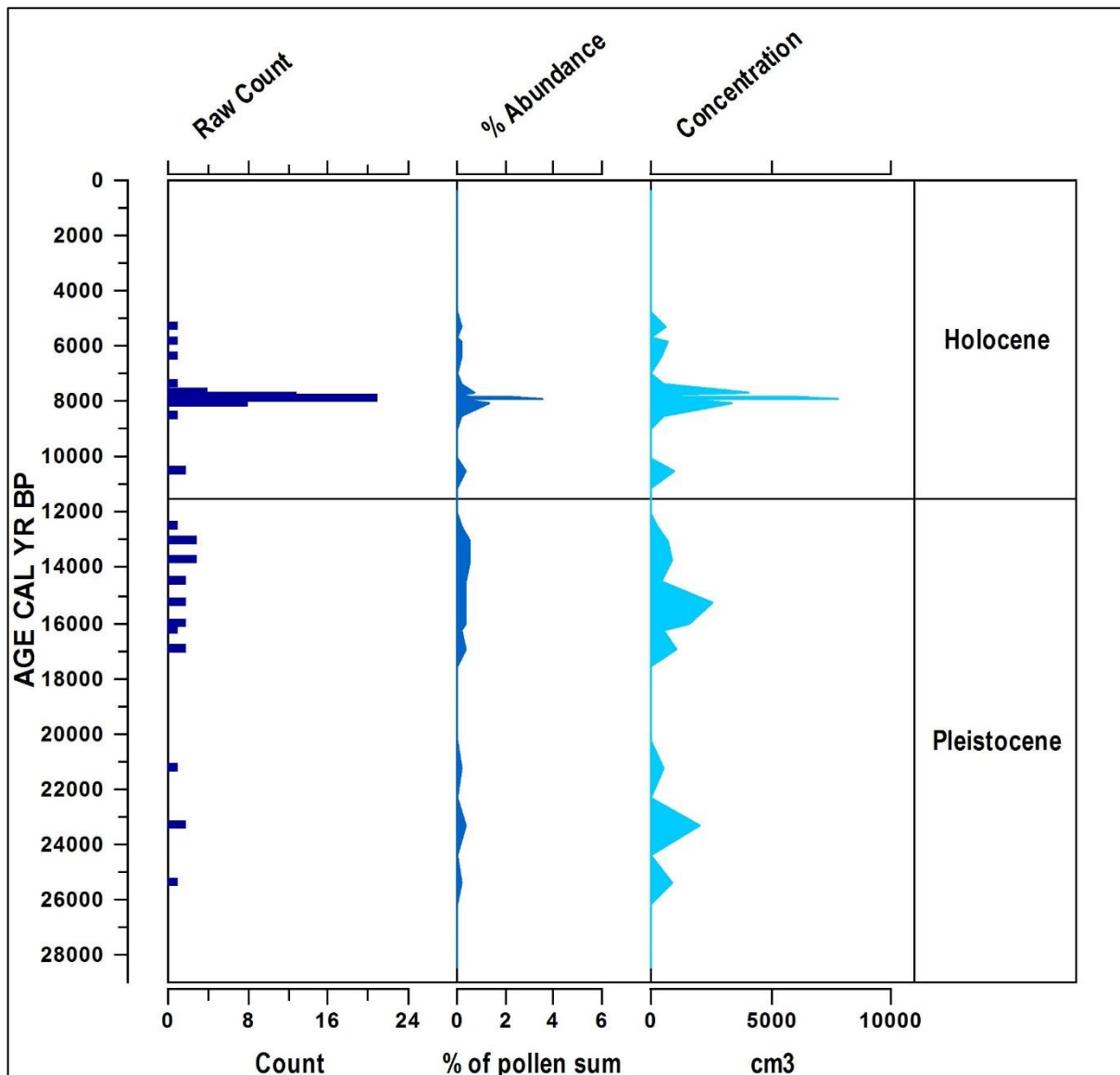
Figure 3. 3 Stratigraphic diagram of Sporormiella abundance data from Lake Consuelo. The graph shows from left to right on the x axis: raw data counts, Sporormiella percentages of the total pollen counting, and concentration of the spores per cm³ in each sample. The data was plotted against age on the y axis (cal yr BP). Two major zones were defined: Pleistocene and Holocene epochs, with a boundary set at 11,500 cal yr BP.

Sporormiella abundance was quantified in a total of 55 samples, giving an average resolution ~670 years between samples. The sample resolution, although lower than that of charcoal still allowed analysis on megafauna activity around Lake Consuelo and thus, allowing the research objectives to be achieved and research questions to be answered. As *Sporormiella* spores were identified in samples spanning the entire core, it is assumed that large herbivores were present at Lake Consuelo from the Late Pleistocene to the Early Holocene. The *Sporormiella* % abundance was very low throughout the entire core and the *Sporormiella* spores were not found in every sample analysed.

The differences between the raw counts, % abundance and concentration of *Sporormiella* abundance over the last 28,000 years is shown in Figure 3.3. All three data forms show great consistency, the only exception is around 15,200 cal yr BP when a peak in concentration values occurred, which was not present in the percentage abundance values.

Late Pleistocene – Holocene

The *Sporormiella* % abundance oscillated from ~25,400 cal yr BP until around 5000 cal yr BP. The first appearance of *Sporormiella* in the record occurred at 25,400 ± 3500 cal yr BP, no *Sporormiella* spores were identified from 28,500 cal yr BP until this point. From 25,400 ± 3500 cal yr BP until 21,300 ± 1840 cal yr BP, *Sporormiella* spores were present with values between 0.17 and 0.34%. Subsequently, *Sporormiella* decreased its abundance to 0%, for a sustained period of 4000 years. At ~17,000 cal yr BP the spores increased again and remains with values around 0.17 and 0.5 % until ~12,500 cal yr BP. This 4500 year period is the longest period in which *Sporormiella* was present in every sample.

Holocene – Modern

From 12,500 cal yr BP until 8500 cal yr BP *Sporormiella* was only present in one sample, at 10,500 ± 1040 cal yr BP. From 8500 cal yr BP to 5300 cal yr BP they are present again ranging from 0.2 to 3.5 % abundance in this period. After this period, they completely disappeared from the record. The final *Sporormiella* spores were found at 5300 cal yr BP at 0.6% abundance. In this final portion of the record, *Sporormiella* abundance reached its peak, which occurred around

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7900 ± 1800 cal yr BP with values ~3.5%. The higher resolution carried out around the peak showed the peak was not isolated or an anomalous data point, as *Sporormiella* was found in all samples surrounding this peak, however these were at a lower concentration varying between 0.17% and 2.17%.

3.3.A. Spores

Previous analysis where additional fungal spores were identified was carried out in 2017 (Osmaston, 2017). Including: *Splanchnonema foedans, Trichocladium asperum* and *Coniochaeta*, which are of significant importance concerning large herbivores (Van Geel et al, 2003; Baker et al, 2013). *Splanchnonema foedans* occurred in the samples from the late Holocene period whereas *Coniochaeta* types appeared from the Pleistocene around 25,000 cal yr BP until around 4000 cal yr BP. The largest spike in these spore's concentration occurs at 8740 ± 1530 cal yr BP (Figure 3.4). After this spike, the concentration of spores declines for the rest of the record.
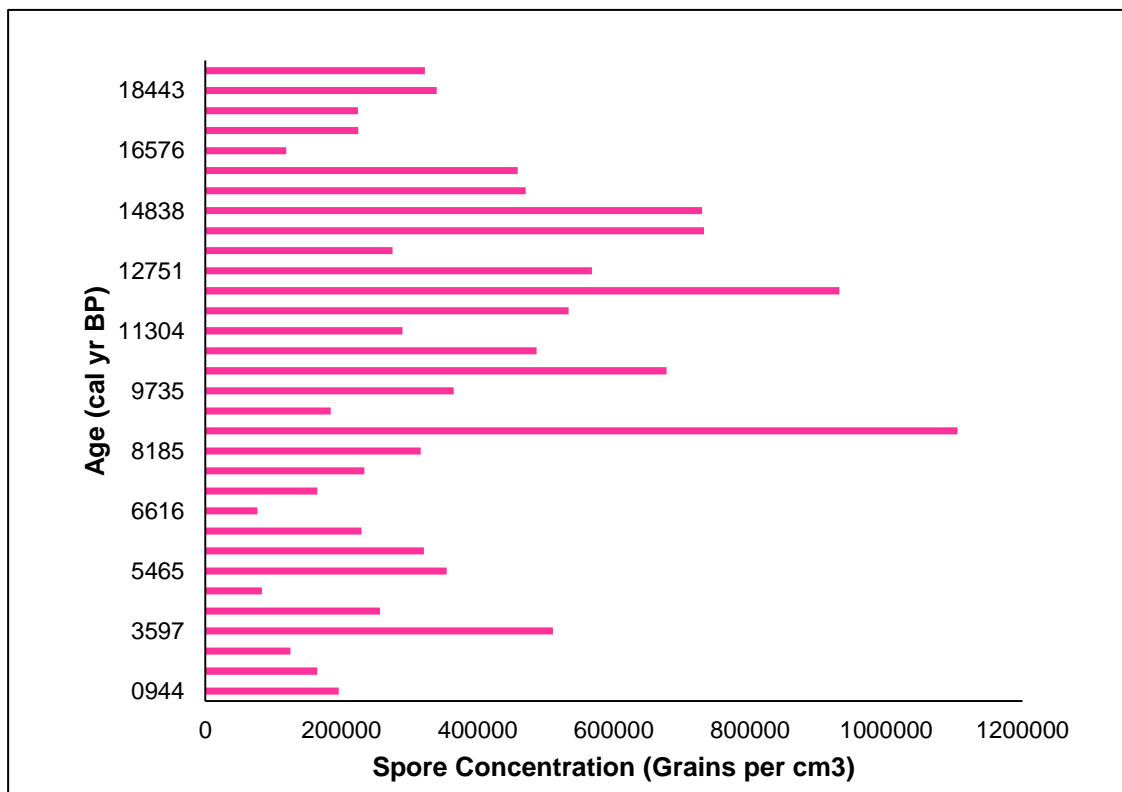
Figure 3. 4 Diagram of additional fungal spore's concentration (grains per cm^3) data from Lake Consuelo plotted against age cal yr BP. The concentration is a sum of all 'other' fungal spores identified from analysis in 2017 (Osmaston, 2017).

3.4. Pollen Record

The pollen data previously analysed (Urrego et al, 2010) was summarized by selecting the most important taxa from the original >260 taxa. The chosen taxa were ones that had the most significant changes and/or the highest abundance over the record (Figure 3.5). The large range of taxa reflects the high biodiversity in this area of Western Amazonia.

The pollen trend showed the internal forest composition to be different in the Pleistocene compared to the present. However, an overall forest structure largely remained throughout the record. Individual taxa altered across the record which caused the type of forest to change from upper montane to evergreen to a lower montane forest structure. These changes are generally gradual alterations over time, with a few abrupt alterations of individual species throughout the record (Figure 3.5).
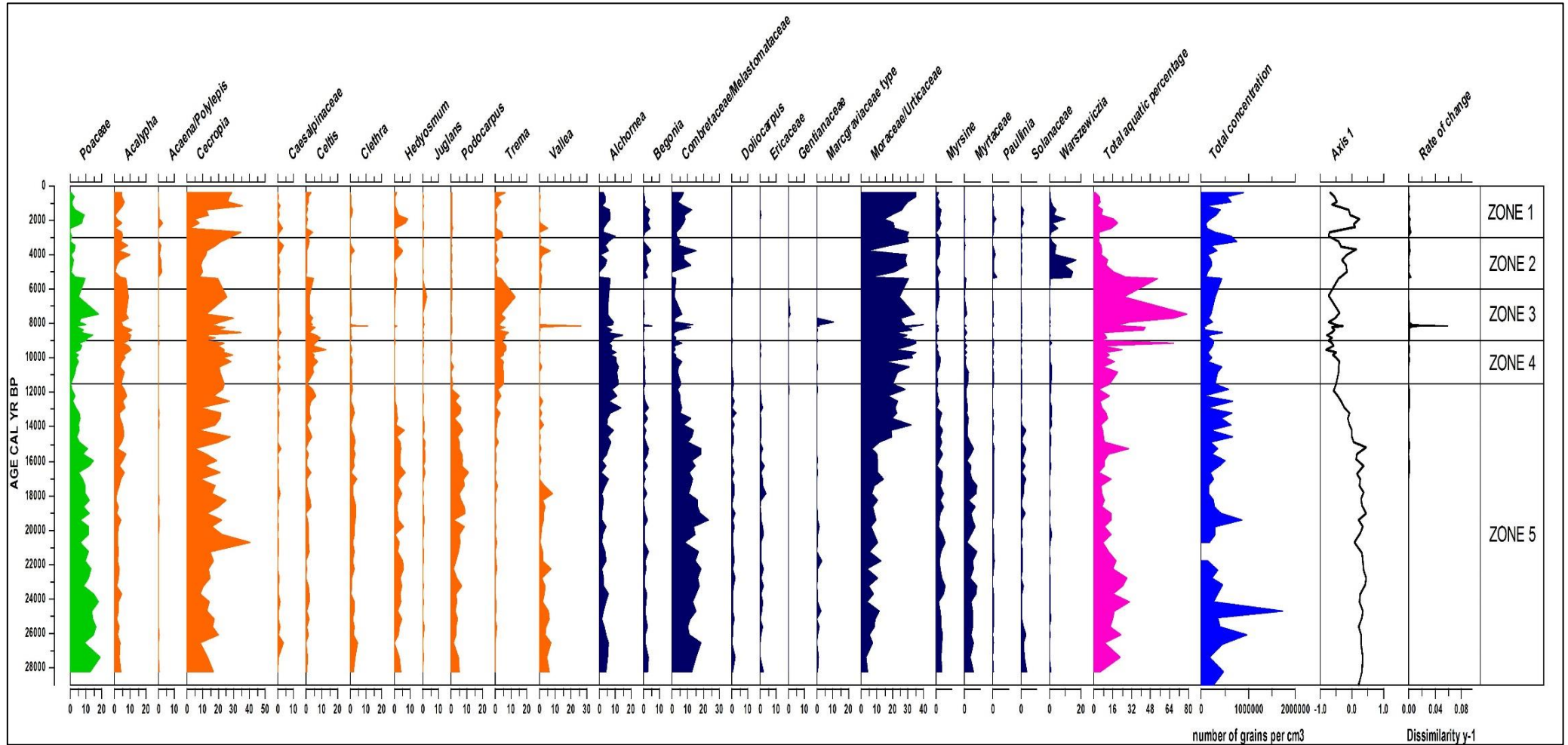
Figure 3. 5 Percentage pollen diagram identifying the vegetation changes over time using the most significant taxa from Lake Consuelo (Urrego et al, 2010). The rate of change is also added on the graph. Where green are the grasses, orange are trees and blue are shrubs. The graph has also been zoned visually, where there the most prominent changes in the record occur. The aquatics total percentage data is made up from species including Cyperaceae, Isöetes, Myriophyluim and Sagittaria (Urrego et al, 2010)

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The graphs were divided into 5 zones based on the major changes in the pollen record.

Zone 5 Pleistocene (30,000 – 11,500 cal yr BP)

This zone has limited major vegetation changes, until the end of the zone when the vegetation structure starts to change.

- The Axis one score (from the NMDS ordination analysis) is fairly constant, positive score until 15,000 cal yr BP. After this time the score gradually shifts to become negative.
- Total pollen concentration in this zone is the highest in the entire record. A peak of 17,262,26 grains per cm^3 was noted at ~24,000 cal yr BP. Total concentration after this peak fluctuates around a similar concentration.
- Aquatic % gradually increased from the start of the record until ~22,000 cal yr BP where it peaks and gradually declines. At ~15,000 cal yr BP there is a rapid increase and a peak which then drops back to levels before the peak until the end of the zone fluctuating around 10%.
- At ~22,000 cal yr BP pollen assemblage changes, the lower montane taxa start to assert dominance in the vegetation structure, while the upper montane forest taxa decrease significantly over the zone. Species that are not directly associated with a certain ecosystem, but had a prominent role in the past, decline through the zone. This includes Poaceae, which fluctuated and gradually decrease over the zone, reaching the lowest value at the end of the zone to <2%. Combretaceae/Melastomataceae, with values decreasing from around 15% to <5% by the end of the zone, *Vallea* follows the same pattern decreasing from 5% to <1%.
- At 15,000 cal yr BP Moraceae-Urticaceae abruptly increases from 7% to 19%. This level is then maintained over most of the Early/Mid-Holocene period. Other lowland and premontane taxa also show an increase here e.g. *Alchornea*.
- RoC is low and fundamentally constant, only starting to fluctuate slightly towards the end of the zone.

Zone 4 (11,500 cal yr BP – 9000 cal yr BP) Late Pleistocene/ Early Holocene

- NMDS1 in this zone stays fairly constant with negative values.
- Total concentration drops at ~10,000 cal yr BP remaining low.
- % aquatics are higher in Zone 4. As the zone ends there is a very abrupt and large increase reaching ~68% which drops sharply back to ~11%.
- Certain lowland/premontane taxa in this zone increase, while other upper montane taxa decline and fade completely, undergoing local extinctions, e.g. *Doliocarpus* and Ericaceae.
- Increases are identified in Poaceae which starts low at <1% gradually increasing to 10% by the end and Celtis which reaches its highest value, 12.6%.

Zone 3 (9000 cal yr BP – 6000 cal yr BP) Early to Mid-Holocene (MHDP)

- In this zone, there are the most dissimilar pollen assemblages in both NMDS axis, ~8600 cal yr BP.
- There is large variation in aquatics % and they are most abundant in this zone. They peak to ~80% at 7500 cal yr BP, the highest value reached in the record.
- RoC is not constant in this zone. At~8000 cal yr BP there is a large spike identifying an abrupt species turnover.
- Poaceae peaks ~7400 cal yr BP and is fairly high overall.
- *Cecropia*, fluctuates over the zone but mostly remains relatively high.
- Around 8000 cal yr BP many taxa have a noticeable sharp increase, including *Vallea*, which had otherwise virtually gone from 11,000 cal yr BP until this point. Combretaceae/ Melastomataceae also peaks along with Marcgraviaceae type and *Clethra*.

Zone 2 (6000 cal yr BP – 3000 cal yr BP)

- NMDS1 changes reaching positive values again until 3700 cal yr BP, where it sharply decreases back to negative values at 2900 cal yr BP.

- A sharp drop in total concentration is apparent at the start of this zone staying low and constant until ~3200 cal yr BP when concentration suddenly increase.
- Total aquatic sharply fall from 5400 cal yr BP reaching their lowest point, <5%, in the record by the end of the zone.
- Large shifts in taxa including: *Cecropia* which declines abruptly staying low then increasing by 20% finally peaking at the end of the zone. This is reflected in the total concentration value. Poaceae drops at the start of the zone and stays low nearly disappearing by the start of zone 1. *Celtis Trema* and Myrtaceae also reach very low levels. Species, such as *Warszewiczia*, that had been virtually absent before peak. Species such as *Hedyosmum* and *Begonia* which virtually vanished at the start of the Holocene reappear. Also, a small increase in tall palms although their overall abundance is low.

Zone 1 (3000 cal yr BP – 2008)

- There is a large shift in the NMDS axis 1 ordination values. Values start negative changing to positive in the middle, then end by sharply declining back to negative values.
- RoC fluctuates throughout the zone, decreasing towards the end of the zone. With the average value being higher than pre-Holocene values.
- Total concentration of pollen starts low around 120,000 grains per cm^3 but increases at the end to around 890,000 grains per cm^3.
- *Cecropia* follows the Roc trend and reached a peak value increasing from 8% to 35%.
- The total aquatic % decreases towards the end of the zone to ~5%.
- Poaceae peaks slightly at 1900 cal yr BP but then fades out along with special such as *Warszewicka, Hedyosmum, Clethra*. Moraceae/Urticaceae remains high in this zone dropping slightly from 30% to 18% but increases back up again.

3.5 Ecosystem Changes

By exploring the relationships between the three proxies more holistic ecosystem changes can be identified from the Late Pleistocene to present in Lake Consuelo and the surrounding regional environment. The highlighted zone 12,000-4000 cal yr BP (Figure 3.6) is where the largest ecosystem changes occur. Before 12,000 cal yr BP the vegetation remains relatively steady, however, just before the first large peak in the fire record there is a shift in the individual pollen % as well as the NMDS score. Aquatics reached its highest % abundance in this period. The same could be noticed in the *Sporormiella* % abundance and both local and regional charcoal concentrations. The concentration of 'other' spores' peaks slightly before the *Sporormiella* spores. Grasses fluctuated increasing from the Pleistocene/Holocene transition and then fluctuating again in the highlighted zone. Later, grasses decline at the same time *Sporormiella* peaks and then increases as fire increases and *Sporormiella* no longer become present in the record.
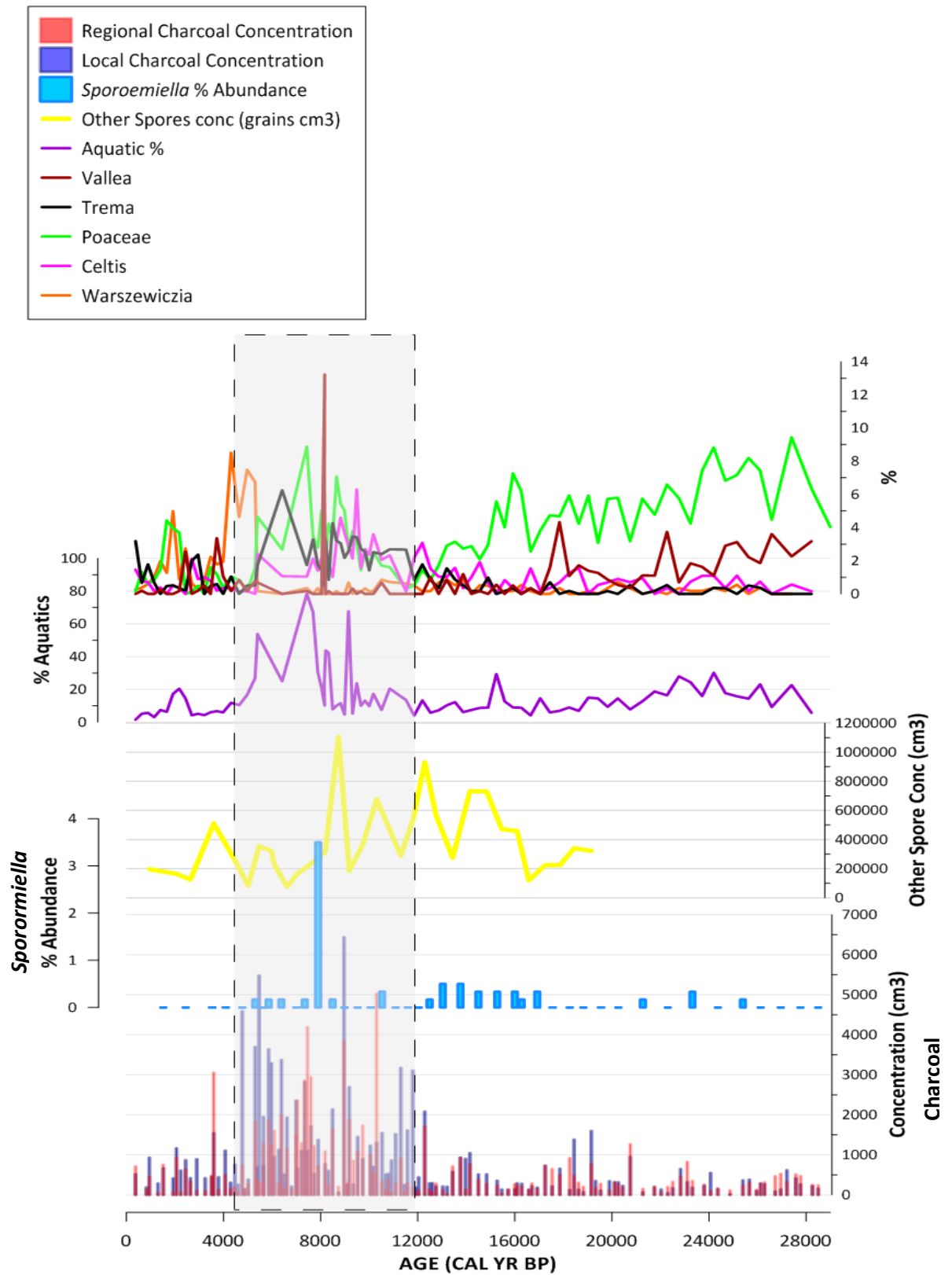
Figure 3. 6 Ecosystem changes in Lake Consuelo including data from, Sporormiella, 'other spores', charcoal (local and regional records), five pollen taxa and % aquatics.

3.6 Data on Human occupation

A recent study by Capriles et al (2019) analysed materials linked to anthropogenic activity in Llanos de Moxos, southwestern Amazonia. This is one of the closest sites to Lake Consuelo with unquestionable evidence of human occupation. Figure 3.7 summaries their data, they used a range of materials to assess human presence. The average ages for human presence fell between 4000-8000 cal yr BP, and maximum dates spanned from 15,000 cal yr BP.

There is an overlap between the evidence of humans in the study of Capriles et al (2019) and the fire and megafauna records data in this study. The first large peak representing a local fire was identified at Lake Consuelo around 10,000 cal yr BP, which is very close to the date of earliest human presence identified on the bases of shell midden at 10,600 cal yr BP by Capriles et al (2019). The second-largest peak of charcoal (local charcoal) around 5600 cal yr BP is within the period identified for increased human intensity. *Sporormiella* abundance peaks and falls within this period of occupation identified. The highest concentration of charcoal (macro and micro) also occur within this time frame.
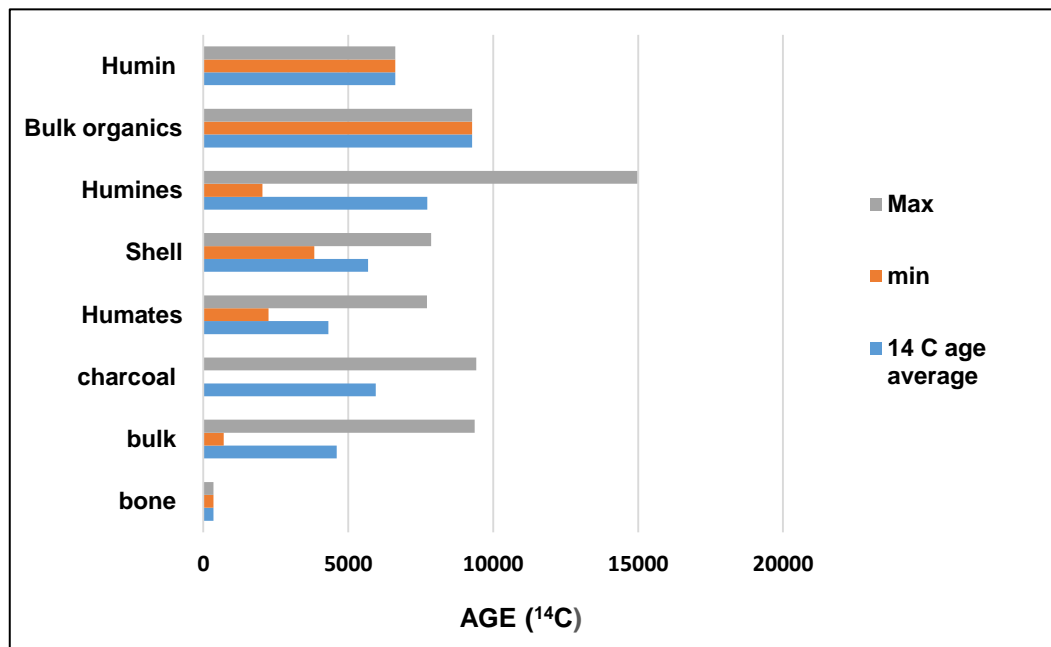
Figure 3. 7 The average, minimum and maximum ages ^{14}C of the material found at the Llanos de Moxos site, western Amazonia (Capriles et al, 2019). Data showing ages spanning up to 15000 cal yr BP.

Chapter 4 Discussion

The chapter will follow a chronological approach following Figure 4.1, examining how the environment around Lake Consuelo has changed over the past 28,000 years and the possible reason for these changes.
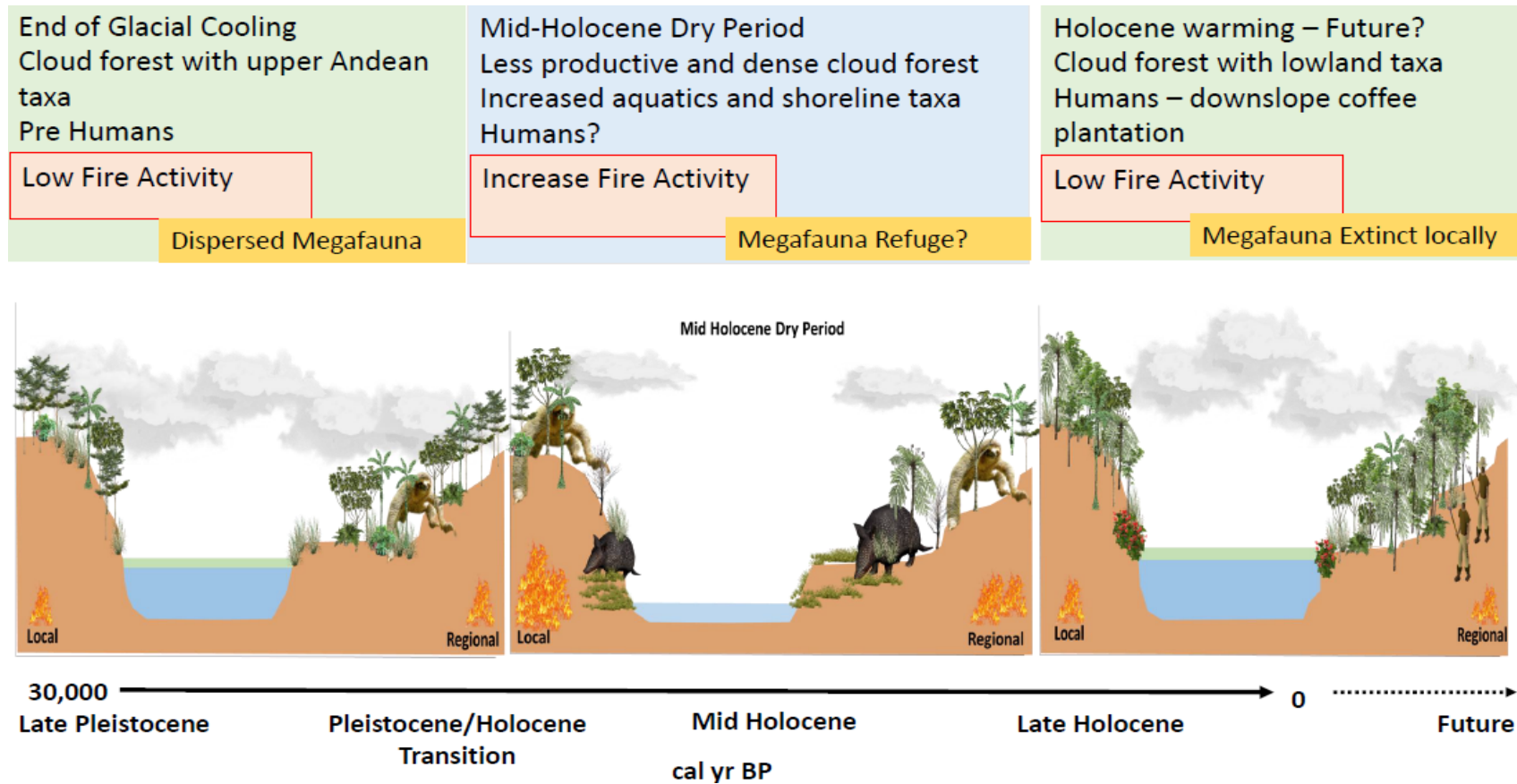
Figure 4. 1 Illustration of the ecosystem changes from 30,000 years ago at Lake Consuelo. Including the changes in fire, megafauna, vegetation, human occupation, and lake levels.

4.1 End of the Last Glacial Period and Pleistocene Holocene Transition (Figure 4.1 Left Panel)

A very significant finding was the presence of charcoal across the entire record (Figure 3.2). This indicates natural wildfires have occurred around Lake Consuelo for at least 28,000 years. The concentrations of charcoal are comparable to other fire records in South America in relation to the location and surrounding environmental conditions (refer to Appendix 8). There is no archaeological data nearby Lake Consuelo to suggest that fire events are human made, therefore, it is plausible to assume that the charcoal particles found during the Late Pleistocene portion of Lake Consuelo record are from naturally occurring fires. Previous research has produced the assumption that natural fires are very rare in cloud forests (Urrego et al, 2010). This is because: they retain moisture due to low lying cloud cover, have high humidity levels and canopy vegetation that is not favourable for fire ignition and development. Moreover, in the Late Pleistocene temperatures are estimated to be 5-9°C lower than today (Bush et al, 2004) further restricting fires ability to ignite and spread (Mayle et al, 2009). These conditions at Lake Consuelo during the Pleistocene would have thought to have suppressed fires. Therefore, the charcoal data presented in this research indicates that this is a novel finding. Other data shows fires can occur in a similar environment, such as Lake Siberia which is also situated in a cloud forest, and has a record of fire dating back 27,000 years (Mourguiart and Ledru, 2003). Consequently, this finding is not isolated but further highlights that cloud forests can have naturally occurring fires even in periods of cool temperatures.

During the Late Pleistocene, the concentrations of charcoal particles in the local-fire spectrum were low, and local fire charcoal particles had values generally lower than the regional fire concentrations (Figure 3.6/Figure3.2). Suggesting natural fires occurred but were suppressed, probably due to the climatic condition and limited fuel load. At Lake Titicaca, fire events have been recorded for the past 370k years (Hanselman et al, 2011), but during the Late Pleistocene, due to low fuel load concentrations, charcoal was also low (Paduano et al, 2003). Similarly, charcoal was recorded from 17,000 years ago

at Lake Chochos, even though conditions were humid (Bush et al, 2005). Vegetation cover in the Late Pleistocene was an upper montane forest, including species with greater resilience to colder temperatures (Mayle et al., 2009). This vegetation type largely restricts fires as there is a lower ignition source, in comparison to an open savanna ecosystem (Burbridge et al, 2004). Therefore, although fire has been an element of Western Amazonian ecosystems during the Pleistocene, it is not until the Late Pleistocene/Early Holocene that fire had a more significant role in this ecosystem (Figure 3.2). Altogether, the data suggest that fire activity in the Late Pleistocene around Lake Consuelo was controlled by both climate and vegetation.

During the Late Pleistocene *Sporormiella* spores were found and quantified, however in very low and sporadic concentrations. One possibility for this low concentration would be that only a few large animals visited the lake during this period. Probably, the dense vegetation and the steep slopes around Lake Consuelo being the limiting factor preventing large animal movement in the surrounding areas of the lake (Figure 4.1). Thus, their impact on fire activity and vegetation can be assumed as minimal. The concentration of *Sporormiella* found in Lake Consuelo is below the standard threshold used in other records (Raper and Bush, 2009). However, the results of spore concentration, may also be in relation to different environmental and methodological factors (consult Appendix 9). Overall, *Sporormiella* abundance data suggests that Megafauna may have been present, but largely dispersed around Lake Consuelo during the Late Pleistocene.

During the Late Pleistocene to the Early Holocene (around 12,000 cal yr BP) Lake Consuelo's charcoal record showed a clear shift in fire activity (Figure 3.2). There is a statistically significant increase in both local and regional charcoal concentrations. This increase is recognised across South America and is related to both climatic variations, human influences, and the vegetation composition (Power et al, 2008). Other lakes in Western Amazonia and Andean regions have also shown the change in charcoal/fire around this transition period. For example at Lake Caserococha this shift is dated to around 10,790 cal yr BP (Paduano, 2002) and at Lake Refugio to 12,000 cal yr BP (Urrego et al., 2011). During this transition phase, the climate followed a warming trend with intermittent phases of rain-storms and cooler episodes (Yacobaccio and

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Morales, 2005). These conditions are important to explain the increased fire activity, as they help vegetation to regrow and fuel load to accumulate, leading to a high probability of fire to ignite. At Lake Titicaca, the concentration of charcoal increased around 13,200 cal yr BP, probably as a consequence of fuel load accumulation concerning the shift in vegetation type (Paduano et al, 2003). During the Pleistocene-Holocene transition vegetation in Lake Consuelo shifted from a cloud forest dominated with upper-Andean taxa to a cloud forest with mid and low-elevation taxa (Figure 4.1). Until 12,000 cal yr BP charcoal was present in the record but in low concentrations, but at this phase concentration of charcoal, especially local charcoal, increased (Figure 3.2). At the time that vegetation also gradually altered composition type, reaching a new composition by 10,000 cal yr BP. Lake Consuelo is located at a lower altitude, making glacial impact weaker than higher elevation sites, such as Lake Caserococha, consequently making the occurrence of fires in this warming phase more probable. Therefore, the vegetation change as a consequence of the climate oscillations at the Pleistocene/Holocene transition was a likely driver for the enhanced fire activity around Lake Consuelo.

Fire activity due to human influences cannot be overlooked during the Pleistocene-Holocene transition. A peak in the local charcoal record during this transition is not reflected in the regional charcoal record (Figure, 3.2), suggesting a different or additional source of ignition. Armesto et al (2010) identified the increase in fire from 12,000-6000 cal yr BP in south-central Chile. They relate this not only to the changing climate and post-glacial warming, but also as a consequence of people using the land. Although no robust evidence is presented for humans to be present at Lake Consuelo around this time, it can be suggested that the local spikes in charcoal 12,000-11,000 cal yr BP could be related to human's arrival (Capriles et al 2019; Raczka et al, 2019). Therefore, during the Pleistocene-Holocene transition fire activity, although largely driven by the changes in climate and consequently the changes in vegetation, was also potentially influenced by humans.

4.2 The Mid Holocene Dry Period (Figure 4.1 middle panel)

In the Mid Holocene Dry Period (MHDP) climatic conditions were amplified causing extreme aridity in Amazonia with intensive storm events. Enhanced drought has been linked to, summer insolation changes resulting in drier atmospheric conditions (Yacobaccio and Morales, 2005). The signal of the MHDP in the fossil record varies amongst sites near Lake Consuelo. For example, Lake Titicaca faced a prolonged low stand 8500–3500 cal yr BP with the driest point at 5500 cal yr BP (Burbridge et al, 2004). At Lake Junin the event occurred at 10,000 cal yr BP and in the higher Sajama Mountains at 4000 cal yr BP. Moreover, data from speleothems in Amazonia show that $\delta^{18}O$ levels were high between 10,000-5000 cal yr BP indicating dry conditions (Cheng et al, 2013). Based on such records it can be expected that at Lake Consuelo this event would have occurred between 10,000 - 5500 cal year BP (Power et al, 2010). The MHDP also impacted the vegetation and environmental conditions around Lake Consuelo, but the drought was relatively mild compared to other regional records (Mayle and Power, 2008). The Mid Holocene Dry Event (MDHE) is evident in the paleorecord from Lake Consuelo from increases in aquatic and shoreline taxa indicating decreased lake levels (Urrego et al, 2010). Furthermore, the shift in vegetation seen in the NMDS analysis of the Lake Consuelo record (Urrego et al, 2010), as well as decreased pollen concentration, implies a change of forest composition to a less productive and less dense forest (Figure 3.6).

The concentrations of fire, both regionally and locally, during the MHDP are greater than identified in the rest of the record. The climate conditions during this phase can be related to this increase and fluctuation of fire activity. In the phases of aridity and humidity vegetation would have dried out, causing flora to lose their leaves. This would have triggered a feedback cycle, where the reduction in vegetation cover would have exposed the forest floor to sunlight, causing it to further dry out. This would have enhance the flammability of the forest, so that during the early wet thunderstorm season the area around Lake Consuelo would have been more likely to be ignited by lightning strikes (Urrego et al, 2013). A comparable fire behaviour is observed in Lakes Chalalán and

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Santa Rosa just downslope of Lake Consuelo (Urrego et al, 2013). The increase in CO_2 levels from 12,000 cal yr BP would also have enhanced fire activity, as it would have favoured plant growth, in turn increasing fuel load availability (Power et al, 2008). The wetter episodes that occurred in-between the drought period would have allowed the re-growth of vegetation, and for additional fuel to accumulate and fires to ignite and develop even in Lake Consuelo's humid cloud forest conditions. The peak of both local and regional charcoal around 8900 cal yr BP in Lake Consuelo's record, correlates to a regionally noted 9000 cal yr BP peak. This peak is identified in charcoal records in Lake Siberia (Mourguiart and Ledru, 2003), Lake Chalalán, Lake Santa Rosa and other Western Amazonian sites (Urrego et al., 2013). The regional coherence of this fire peak and the consistency between both regional and local charcoal records at Lake Consuelo, suggests that climate and fuel build up was the most probably cause of Mid-Holocene fires.

Although it is most likely that MHDP fires were driven by climate, human's role also needs to be considered. Naturally occurring fires in Western Amazonia are rare (Bush et al, 2016), as a consequence, the presence of charcoal and more so the high concentration of fractions >180μm during the Mid/Late Holocene in Lake Consuelo's fossil record may indicate human presence. It is plausible that due to the climate conditions, interspersed with wet/storm episodes, anthropogenic fires more commonly develop into wildfires. Although no direct archaeological data currently exists for early human occupation at Lake Consuelo, archaeological records from Bolivia (Coltorit et al, 2012) and Northern Peru date early human activities to the Early/Mid Holocene (Rademaker et al, 2014), Capriles et al (2019) also suggest humans arrived in Western Amazonia approximately around 10,600 cal yr BP. However, human activity is thought to have been limited to hunting and gathering until the late-Holocene (Lombardo and Prümers, 2010). Thus, while human's role cannot be disregarded as a factor driving small-scale fire activity, climate remains as the most likely driver of regional Mid-Holocene fires.

The charcoal spikes in the Late Holocene at Lake Consuelo are potentially a result of human migration and settlement. In Lake Siberia a similar pattern in charcoal is identified where fires are evidently anthropogenic, fire increased in the Late Holocene until ~4000 cal yr BP, peaking ~7000 cal yr BP (Mourguiart

and Ledru, 2003). During the drought period humans migrated to areas where moisture was greater, such as montane cloud forests, where humans probably used fire (Yacobaccio and Morales, 2005,Bush et al, 2007). The same explanation can be drawn for Lake Consuelo. Human induced fires commonly show a pattern of a peak, followed by a decline, and later another peak (Bush et al, 2015). This pattern is thought to happen because humans initially alter the environment, then their practices switch to lower intensive fire and land use. This could explain the decrease between the two largest local fire peaks (Figure 3.2). The timing of the peaks is also in line with the evidence of human occupation from Capriles et al (2019).

The most notable differences between the local and regional charcoal records are the events around 5400 to 4770 cal yr BP (Figure 3.2). There is a substantial increase in local charcoal fractions, but this is not evident in the regional charcoal fractions. This suggests an extra force acting at Lake Consuelo as well as the alternating dry and wet conditions to promote fire. This extra force is most likely to have been humans, starting fires for activities such as slash and burn during the Late Holocene (Bush et al, 2015). Then due to favourable environmental conditions, these fires may have expanded and become more extensive (Haberle and Ledru, 2001). However, humans alone would have been unlikely to cause the wildfires if the fuel state were not prone to fire. Thus, it here can be assumed that humans also had an important role influencing fires during the Late Holocene in Lake Consuelo, while local factors such as fuel availability and sensitivity of the lake to drought enhanced flammability.

In the Mid-Holocene, *Sporormiella* reaches peak abundance of 3.5% around 8000 cal yr BP, along with other coprophilous fungal spores, such as *Splanchnonema foedans* (see Appendix 10). High *Sporormiella* abundance during at Lake Consuelo could have resulted from changes in the distance of the coring site to the shoreline when lake levels were reduced. Available area for herbivores near the shore would have been closer to the location were the sediment core was collected. However, the Megafauna that are likely to have come to Lake Consuelo were probably alone or in small groups (a detailed discussion of this scenario can be consulted in Appendix 9). This suggests that despite lake level changes, it is reasonable that the increase in *Sporormiella*

abundance is indeed the result of increased Megafauna abundance at Lake Consuelo during the Mid-Holocene.

The timing of *Sporormiella* abundance peak is relatively late at Lake Consuelo in comparison with records in South America. The reason for a later survival here might be due to conditions around Lake Consuelo being more advantageous for large animals than elsewhere in the region. Although impacted by the MHDE, Lake Consuelo remained humid due to the moisture retention from cloud cover allowing a permanent body of water. Lake Consuelo likely became the main watering source for large animals from adjacent regional increasing the megafauna abundance. This is consistent with the evidence suggesting that favourable conditions in unique ecosystems might have resulted in localised refugia for megafauna (Graham et al, 2016, Ficcarelli et al, 2003) (see Appendix 11).

The late extinction of Megafauna in Lake Consuelo is consistent with other South American records. Megafauna extinctions globally occur before 10,000 cal yr BP (Barnosky et al, 2004, Barnosky and Lindsey, 2010). However, in South America dating of Megafauna remains and artefacts indicate megafauna survived until at least 8000 cal yr BP in various regions (Baffa et al, 2000, Cione et al, 2001, Coltorti et al, 2012, Barnosky and Lindsey, 2010, Borrero et al, 1998, Gutierrez and Martınez, 2008, Hubbe et al, 2007, Politis et al, 1995). Overall, it is therefore plausible that the persistence of a water body, cloud forest moisture and decline in vegetation density allowed the persistence of megafauna around Lake Consuelo until the Mid-Holocene.

Some connections can be made between fire activity, megafauna abundance and vegetation change at Lake Consuelo during the Mid-Holocene. Fire activity at Lake Consuelo acted to control megafauna both directly, by discouraging animals, and indirectly via habitat changes. But megafauna's presence also played a small influence on fire activity by preventing fuel build up and/or flammable species to grow. Megafauna potentially could have supressed fuel load via browsing and trampling which helps explain the decrease in fire and grasses when megafauna peak. Once megafauna decline fire increases along with grasses, the release of the herbivory pressure on vegetation possibly increased fuel load. The impacts of the animals on vegetation along with the warmer climate would have favoured fire development (Gill, 2014). The removal

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of species due to fire can promote grasses invasion further explaining the increase of grasses (Slivério et al, 2013). Bones of large animals have been identified in regions such as Bolivia and the Andean Cordillera and they are known to have grazed on grasses, tough leaves of trees and shrubs. *Trema,* a genus of short-lived, fast-growing pioneer trees and an indicator of disturbance events followed the same pattern as grasses (Yesson et al, 2004). It can be tentatively suggested that megafauna either used this species as a resource or trampled it, but it was able to quickly colonize the land after suppression. Moreover, *Trema* has generally greater coverage when fire activity is greater between 10,000 – 5000 cal yr BP. So, fires could have promoted growth of this taxon by creating forest gaps. Other relations between megafauna, fire and vegetation are seen but are not as direct. After *Sporormiella* peaks some species of trees increase, e.g. *Hedyosmum, Acaena/Polylepis and Warszeewiczia*. Also, the increases were seen in smaller shrubs, e.g. *Paulinia and Myrsine*. This could be a result of a release of trampling and browsing pressures from the animals (Bakker et al, 2016).

Therefore, fire acted to control megafauna both directly discouraging animals and indirectly via habitat changes. But megafauna's presence also played a small influence on fire activity by preventing; fuel to build up and/or flammable species to grow. However, overall vegetation changes are not strongly linked to the changes in animals across the record, only on an individual level. Hence, it can be suggested the relationship between megafauna with fire and vegetation in Lake Consuelo was minimal and that climate had the most influence in the alterations to fire activity, megafauna abundance and vegetation. Overall, the record of fire activity, megafauna abundance and vegetation change around Lake Consuelo during the Mid-Holocene suggests feedback mechanisms between vegetation, fauna and environmental change and seem initially triggered by and linked to climate change and regional drought.

4.3 The Late Holocene (Figure 4.1 Right Panel)

The charcoal record shows that both local and reginal charcoal concentrations decline from ~4000 cal yrs BP. This supports the pattern identified across South America where continental increases in fire are observed ~6000 cal yr BP and fire activity declines during the late Holocene (Power et al, 2008). The decline

from 4000 cal yrs BP in fire activity is related to the alterations in climate state, from the drought to wetter conditions. Despite the evidence that human's presence potentially increased and are still prevalent fire activity declined from the Mid to Late Holocene around Lake Consuelo (Figure 3.2). Therefore, it can be determined that regionally it is climate shifts that drive fire activity and that humans only play a secondary role.

The decrease and disappearance in megafauna from the record around the Mid-Late Holocene can be linked to both human and climatic influences. It is plausible that during the MHDP humans, in the form of hunter and gatherers who had developed hunting skills, were attracted to Lake Consuelo (Van der Hammen and Urrego, 1978). Therefore, humans could have played a role in the process of local extinction or driving the animals away from the area (Hester, 1966). However, it is more likely that due to the already low, isolated, and dispersed populations of megafauna around the Lake they could not recover and reproduce to levels needed for prolonged survival. Certain plant species peak as well as the total pollen concentration after fire activity declines around 4000 yr BP. The wetter conditions, reduced fire activity and the release of pressure from the megafauna could have allowed the growth and regeneration of vegetation, such as pioneer species like *Cecropia* and *Warszewiczia*. The combination of humans, the shift in climate, that affected vegetation composition and hence their habitat, as well as their low populations, can be used to explain the disappearance of megafauna locally.

4.4 Ecosystem functioning and resilience of Western Amazonian cloud forests

Lake Consuelo's palaeoecological data clearly shows that over the last 30,000 years there have been chances in fire activity, vegetation composition and megafauna' abundance. Documented changes have been shown to be related to a combination of both climatic variations as well as anthropogenic influences. But overall, it can be concluded that climate has had the greatest significance in driving ecosystem changes around Lake Consuelo during the last 28,000 years.

Lake Consuelo was densely vegetated with cloud forest with montane taxa (upper and lower) through the last glacial period and the Holocene. Although there is alteration between the types of vegetation found in the Pleistocene

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compared to those identified in the Holocene, the changes occurred gradually over time, and were not suddenly triggered by an abrupt climatic event. The pollen record indicates that plant species coped with external changes and adapted by migrating up/downslope. The persistence of cloud forest vegetation over the last 30,000 years suggests that vegetation localised around Lake Consuelo endured significant changes in fire activity, climate and the megafauna' extinctions.

Fire activity around Lake Consuelo generally paralleled major climate transitions, as climate influenced both fuel load and ignitability. The disparities identified between local and regional records, during the Mid-Holocene, suggests that humans were also likely contributors to fire activity. The paucity of archaeological data hinders further conclusions about human-landscape interactions around Lake Consuelo.

The prolonged existence of cloud forest around Lake Consuelo can also help explain the survival of megafauna until the Mid-Holocene in this region. The area surrounding Lake Consuelo would have provided a more suitable habitat to use as a refuge during a period of regional climate adversity: The Mid-Holocene dry period. Localised environmental conditions allowed for a reduced but constant body of water throughout the Holocene. Megafauna's activity potentially played a small role in the build-up of fuel load and thus fire activity during the MHDP and changes in species compositions. However, any influence these large herbivores may have had on the vegetation composition and fire activity seems to have been less substantial than those caused by the climate changes associated with the Last Glacial Maximum and Pleistocene-Holocene transition.

The findings from Lake Consuelo's can be used to guide management and conservation in Western Amazonia today. Long-term ecological data showing how localised ecosystems have responded to changes in fire activity, megafauna and humans is vital, especially with the increasing pressures placed on ecosystems by human population growth and climate change. The palaeoecological data from Lake Consuelo have shown the heterogeneity of environmental changes in a region like Western Amazonia. Lake Consuelo's vegetation across the last 28,000 years remained a cloud forest, thus this ecosystem has shown to have been resilient to fire activity, megafauna

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extinction and climate changes. These data highlight the importance and uniqueness of some localised ecosystems and how they should be prioritised for conservation in the future.

Chapter 5 Conclusions

This chapter intends to summarize the data and address the aims and objectives that were set out at the start of the project (Chapter 1). Also, it will explain the broad implications of the findings.

5.1 Summary of main findings

5.1.A. Fire Activity

Charcoal was identified over the entire record and therefore it can be stated that fires occurred in Lake Consuelo over the past 28,000 years. This is an important finding as the Late Pleistocene was a period devoid of humans in the American continent and thus render these fires as natural wildfires. It is somewhat unexpected to find wildfires here due to the presence of cloud forests and high moisture as well as the colder climate conditions of the glacial period. Therefore, cloud forests in Western Amazonia can burn naturally, and this finding should be recognised in plans for managing of this ecosystem.

Fire activity from the Late Pleistocene into the Holocene increased due to the climate conditions in the Pleistocene preventing the spread and ignition of large fires, due to limiting fuel load, flammability, and optimal climatic conditions. During the Holocene climate change (i.e. regional drought and extreme weather events) fire occurred more easily, due to drier and warmer climate interspersed with wet events and an increase in fuel load. During the Mid/Late Holocene, spikes in local fire activity and not in regional fire indicates that humans had an additional role in starting fires at Lake Consuelo. However, anthropogenic fires would been less likely to have occurred without the fuel state being conductive to fires. Thus, both humans and natural conditions worked in tandem at Lake Consuelo to influence fire activity during the Holocene. However, the climate has been the main driver of fire activity over the course of the last 28,000 years.

5.1.B. Megafauna

The peak of *Sporormiella* (and other coprophilous spores) occurred around 8000 cal yr BP, suggesting megafauna survived into the Mid-Holocene at Lake Consuelo. This suggests that Megafauna persisted longer around Lake Consuelo that in other South American sites. *Sporormiella* abundance was low suggesting that population sizes were also low. Potentially, Lake Consuelo

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acted as a refugium during the MHDP due to continuous supply of cloud moisture and a retained body of water making the area more favourable for animals. Humans potentially acted to drive away the animals directly through hunting or indirectly via starting fires altering habitats. However, due to their isolation and low reproduction rates megafauna were still susceptible to population collapse and became locally extinct. Humans potentially had an influence in preventing recovery of megafauna populations directly through hunting or indirectly via starting fires altering habitats and driving animals away from the Lake.

5.1.C. Ecosystem relationships

From the changes in all five variables considered in this study, it can be concluded that climate has been the main driver of change at Lake Consuelo over the past 28,000 years. Fire activity and vegetation composition responded to shifts in climate such as the transition into the Holocene and the MHDP, as climate altered forest fuel ignitability. Although, small alterations are seen to be a result of changes in fire activity, megafauna presence, vegetation alterations and human interactions. Megafauna had a small role in altering individual species composition e.g. grasses. They also had a potential role influencing the fuel load and thus fire activity, but changes were short lived and of low impact. Fires also had impacts on vegetation at a species level but again these were minimal. However, even though changes occurred the ecosystem has shown a strong degree of resilience to changes in fire activity, megafauna, climate and humans over time.

5.2 Wider implications of findings

Overall, the study contributes to the current evidence on fire activity and megafauna's extinctions in South America and more specifically Western Amazonia. The data suggests that the local environment and the functions of an individual ecosystem are of vital importance to the fauna and flora to persist. As no large impacts on the environment were caused by fire or megafauna, it suggests that climate, with a small role of humans, is the most important factor influencing alterations at Lake Consuelo.

These data can be used to update studies such as Mayle and Power (2008) who state there is no presence of charcoal in Lake Consuelo at the MHDE. This evidence was based on an initial search for charcoal within pollen slides

(Urrego et al, 2015). The greater precision and accuracy employed in this study allowed to produce a detailed charcoal record which has shown to disagree with this previous statement. Thus, allowing the conclusion that fires have been a natural part of the environment since the Late Pleistocene. Moreover, the data highlights that natural fires occur in cloud forests even when climate is not most favourable for fires to start. These results are important when looking at management and conservation strategies in the area and in similar environments.

Finally, the fossil record of Lake Consuelo has shown the importance of the area as a potential refugium for species, allowing prolonged survival. Evidence from coprophilous spores from 17,000 cal yr BP suggests that the area is suitable for animal survival. Moreover, the appearance of *Splanchnonema foedans* that dominated the Late Holocene, indicated recent fauna in the area, thus it to be a potential location for animal's survival in the future. This is largely due to the favourable environmental conditions here which are largely determined by the persistent cloud cover, allowing persistence of a water body even during the driest period of the Holocene.

These findings are important in the wider context of environmental management and conservation. Whereby measures should be taken in such hotspots to help preserve biodiversity in the face of future climate change and the increased pressures from anthropogenic influences that can potentially case further extinctions and increased fires. Important considerations should take place with this new data as the resilience of this ecosystem over the last 28,000 years could decline if pressure is exceeded beyond its threshold.

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Chapter 6 Research Potential

6.1 Future improvements

6.1.A. Charcoal analysis

- A counting method was employed to detect charcoal abundance. Other methods that could be considered in future to assess charcoal include:
    - Image analysis - where a threshold density is employed meaning other particles are not counted (Whitlock and Larsen, 2002).
    - NIH-image software – calculates charcoal area (Hanselman et al., 2011). This method has been in studies such as Paduano et al, (2003) where NIH software was used with a video system to measure precisely the surface area of irregular shapes and find the amount of pixels that a fragment had.
    - Image J software and photomicrography - used by Rozas-Davila et al, (2016).

6.1.B. Megafauna Analysis

The method employed to analyse megafauna is being increasingly tested and used. However, certain aspects of this technique (which were addressed in the study) have limitations and could be enhanced to help develop future research (Baker et al, 2013).

Common restraints and solutions employed in this study:

1. Spore Identification
    - Using experts and references to detect spores accurately. The training provided meant spores were identified accurately. Therefore, this was not a limit to this research.
2. Local hydrology
    - The core was taken from a closed basin with no external input from streams etc. Therefore, the input from the lake is from the local catchment and there is not a loss in sediments.

3. Limited understanding of taphonomy (environments of deposition and preservation)

   - This is an extension for future research as more studies surrounding this issue need to be conducted before this can be resolved. It is currently an unresolved factor in research.

4. Lack of quantitative reconstructions

   - Using Radiocarbon dating and Basyian age-depth models.

5. Presentation of *Sporormiella* data

   - Expressed as % of pollen sum to help data to be consistent with other research and reduce nose (relative abundance value).

   - Also include the raw count of the *Sporormiella* for each sample and concentration of *Sporormiella* using the lycopodium spike added, in case pollen input is not constant over the whole core.

None-the-less it is, to date, the best method that is available to study this megafauna extinctions, when fossil remains are unavailable.

- There is a possibility that the *Sporormiella* spores are not from mega-animals but rather from smaller mammals such as rabbits which need to be considered (Feranec et al, 2011). However, this factor cannot be controlled in this study and would require more studies into the production of *Sporormiella*. However, data has shown that megafauna records are generally distinguishable from the noise (Wood and Wilmshurst, 2013). Moreover, studies identifying use of them to detect megafauna in South America are published. Therefore, this limitation is of low concern in affecting the data.

- Future research into the impact and detection of animal type from *Sporormiella* spores would be advantageous to confirm this. Data such as this could help better understand the taxonomic preferences of the species. Also, the relation between spores and animal abundance/population.

- Take data from the shoreline of Lake Consuelo. To compare multiple cores from the different depositional areas in the basin to see the difference to get a more robust study, as cores collected for the use of pollen analysis are not always the more appropriate for that of megafauna analysis (Feranec et al, 2011).

6.1.C. Dating

- All age-depth models that are produced contain uncertainties. None-the-less knowing that the chronology produced was not completely accurate was accepted and considered in the interpretation of the study's results and data analysis.

- Another limitation in age-depth models is the errors associated with Radiocarbon dates. All dates have associated uncertainties and errors (Blaauw et al, 2007). Again, errors were factored in when analysing data, acknowledging the date provided from the model was not a precise date but had a range of dates in which it could fall depending on the model run and parameters.

- To increase the age-depth relationship models the two most important factors are, the amount and quality of the data and information. However, more Radiocarbon dates could not be taken due to their expense (Birks et al., 2012). There could have been possible sedimentation changes between the five radiocarbon dates. However, more radiocarbon dates were taken from another one of the Lake Consuelo cores. These dates produced were very similar to the core used in this study and the sedimentation rates were also very similar. Thus, the five dates used were satisfactory for the production of a chronology.

6.1.D. Human evidence

- There is no known history of human occupation around Lake Consuelo (Bush et al, 2004, Urrego et al, 2010). No archaeological studies have been conducted directly in this area. As more information (archaeological data) becomes available to show the potential occupation of the site, it will help place the palaeoecological data in context. As the information currently on humans is indirect (charcoal) but more direct data would allow greater confirmation.

Appendices

Appendix 1
Charcoal Preparation Work Protocol (adapted from the Laboratory Manual, 2015).

1. Samples measuring 1cm^3 were taken approximately every 6cm down the whole length of the core
2. Each sample was syringed into a test tube to extract half of the material (measuring 0.5cm^3)
3. 10ml of Sodium Hexometaphosphate (5%) was added to the sample (see below)
4. Samples were vortexed
5. Samples were put into the ultrasonic bath at 75°C for 15 minutes
6. Samples were vortexed
7. The samples were then sieved at 180µm to separate into two fractions (>180µm and <180µm)
8. Samples were put into the centrifuge at 1200rpm for 5 minutes
9. The excess liquid in the test tube was decanted
10. 10ml of distilled water was then added
11. Samples were vortexed
12. The <180µm fraction was sieved into smaller fractions (<63µm and 63-106µm)
13. All samples were put into the centrifuge
14. The excess liquid in the test tube was decanted
15. Add 15ml of KOH (Potassium Hydroxide) (10%) to samples (See below)
16. Samples were placed in the ultrasonic bath at 60°C for 20 minutes
17. Samples were put into the centrifuge
18. The excess liquid in the test tube was decanted
19. 10ml of distilled water added
20. Samples were vortexed
21. Samples were put back into the centrifuge
22. The excess liquid in the test tube was decanted
23. 10ml of distilled water was added

Additional steps applied in the protocol:

Step 3: this step was used to help aid with the breaking/disaggregation of the sediment. This chemical treatment is especially necessary in older samples as these samples contained clay particles and were silt rich.

Step 15: This step also aids sample cleaning. This is vital to ensure the solution is clear to allow for charcoal to be easily identified under the microscope. KOH treatment was most affective on the organic material.

Ultrasonic bath use: this step is to help break down sample whilst avoiding breaking up individual charcoal fragments so not to skew data. As breaking up As breaking up sediment through touching in any way could have caused particles to fragment which would have increased particle counts and thus giving an incorrect reconstruction of fire activty.

Bleaching of the samples using Hydrogen peroxide around 6% was carried out when there was a high amount of organics in the sample which could be mistaken for charcoal.

Appendix 2

Depths (cm) where samples were taken, the converted depth, including previous samples (Johnston 2017).

Sample	Depth converted	Sample	Depth Converted
1	8.5	66	355.5
2	15.5	67	360.5
3	17.5	68	370
4	23.5	69	378
5	27.5	70	383
6	32.5	71	388
7	34.5	72	397
8	38	73	402
9	42	74	408
10	45	75	417
11	50	76	423
12	56	77	428
13	60	78	437
14	61.5	79	446.5
15	64.5	80	458
16	69.5	81	463
17	74.5	82	470
18	81.5	83	477
19	86.5	84	480.2
20	92.5	85	485.2
21	96.5	86	493.2
22	101.5	87	496.4
23	112.5	88	501.4
24	115.5	89	510.4
25	118.5	90	517.9
26	125.5	91	526.9
27	125.5	92	537.7
28	132.5	93	542.7
29	137	94	547.7
30	141.5	95	553.7
31	148.5	96	562.7
32	152.5	97	567.7
33	156.5	98	573.7
34	160.5	99	583.7
35	167.5	100	589.7
36	173.5	101	593.7
37	175.5	102	597.7
38	181.5	103	603.7
39	186.5	104	613.7
40	190.5	105	623.2
41	195.5	106	628.2
42	200.5	107	633.2
43	200.5	108	637.2
44	216.5	109	643.2
45	221.5	110	648.2
46	227.5	111	652.2
47	236.5	112	661.2
48	246	113	666.2
49	250	114	672.2
50	253.5	115	681.2
51	259.5	116	691.2
52	266	117	696.2
53	273.5	118	701.2
54	284.5	119	704.2

55	288.5	120	706.7
56	293.5	121	715.4
57	301.5	122	718.7
58	306.5	123	723.7
59	310.5	124	730.7
60	315.5	125	734.7
61	321.5	126	742.7
62	330.5	127	746.7
63	336.5	128	756.7
64	341.5	129	762.7

Appendix 3

Acetolysis and density separation of Sporormiella
Prepared by: Dunia H. Urrego & Angela Elliot – 22nd May 2018

Pollen preparations need great care. Cleanliness and good technique are essential for accurate preparations with no contamination. Even more importantly hazardous chemicals are used and so advice must be sought on handling. Protective clothing gloves and goggles / facemasks must be worn.

An essential part of the preparation is the use of clean equipment. Therefore after use, all tubes, stirrers, funnels, sieves etc. must be thoroughly washed and then soaked overnight in Hydrogen Peroxide before rinsing with distilled water and stored separately from general laboratory equipment.

Turn on waterbath first thing in morning at 90°C.

1. Set apart 2 sets of centrifuge plastic tubes: 12 x 15ml plastic tubes and 12 x 2ml eppendorf tubes.
2. Label all tubes with sample reference, using a permanent marker pen.
3. Place $0.5cm^3$ subsample in corresponding centrifuge tube (according to labels)
4. Add one lycopodium tablet to each sample, using forceps.
5. Add 10% Hydrochloric Acid from the wash bottle dropwise until tablets have dissolved (approx. 3ml)
6. Add approximately 10 ml of distilled water to each tube
7. Centrifuge at 2500 rpm for 5 minutes and decant (repeat water, centrifuge, decant)
   NOTE: Discard supernatant taking care as the pellet is often not very firm when in water.
8. Add approximately 3 ml of KOH to each sample and place in hot water bath for 10 minutes
9. Centrifuge at 2500 rpm for 5 minutes and decant in appropriate container
10. Add approximately 10 ml of distilled water to each tube, centrifuge at 2500 rpm for 5 minutes and decant
11. Repeat step 10.
12. Proceed to Acetolysis

Acetolysis
The Acetolysis mixture reacts VIOLENTLY with water and so great care must be exercised, again using a fume cupboard and full personal protection. Acetolysis Mixture can self-oxidise (explosively) on standing so must never be made in advance, only make sufficient for each batch and dispose of excess immediately.

The Acetolysis Mixture should be prepared by a **Technician using a fume cupboard.**

The Acetolysis solution is 9 parts Acetic Anhydride + 1 part conc. Sulphuric Acid.
- For 12 samples: pour 54 ml acetic anhydride and slowly add 6 ml sulfuric acid. This will allow for 5 ml per sample and there should be no excess.
- For 16 samples: pour 72ml acetic anhydride and slowly add 8 ml sulfuric acid. This will allow for 5 ml per sample and there should be no excess.

1. Add approx. 2 ml of 100% Glacial Acetic Acid (red wash bottle) to the residue. Centrifuge at 2500 rpm for 5 minutes and the supernatant is discarded into a tub of water.
2. Stage 1 is then repeated to ensure that all water is removed
3. Pipette 5 ml Acetolysis mixture into each tube slowly and stir with stick
4. Put all 12 samples into the hot water bath at 90°C for 5 minutes. Note: Leave the glass stir rods in the test tubes. Stir sample after 5 minutes. Remove samples from bath.
5. Add 1 ml of glacial acetic acid (red wash bottle) to each tube to stop the reaction.
6. Centrifuge at 2500 rpm for 5 minutes and decant. Note: The supernatant is discarded into a DRY beaker and disposed of by the Technician.
7. Add approximately 10 ml of distilled water to each tube. Centrifuge and decant supernatant.
8. Repeat stage 7 with water, taking care to get rid of as much water as possible
9. Proceed to density separation

Density separation
1. First make up separation liquid of required density between 1.9 and 2.0 g/l (sodium meta-tungstate in distilled water)
2. Add approx. 3ml of spt solution to each sample, make sure centrifuge tube is tightly lidded and vortex to ensure through mixing
3. Centrifuge for 5 minutes at 2500 rpm
4. Label a second set of 15ml centrifuge tubes
5. Using a clean pipette for each sample transfer the top layer of the density separation to the micro eppendorf centrifuge tube
6. Once all floating material is transferred to the microtubes, fill up microtubes with distilled water. Cap tubes and centrifuge for 5 minutes at 2500 rpm. Decanting off the water.
7. Save washings to reclaim spt
8. Repeat step 6
9. Remove last trace of water and add a few (2 or 3) drops of glycerol taking care not to dissolve the sample too much.
10. Place samples overnight in the over at 60°C to evaporate remaining water.
11. Save all SPT washings, filter and reclaim SPT

Appendix 4 *Table of depths where samples were taken for Sporormiella analysis*

number sample	converted depth	Batch
1	8.5	1
2	27.5	1
3	42	1
4	60	1
5	69.5	1
6	92.5	1
7	112.5	1
8	129.5	1
9	136	1
10	152.5	1
11	173.5	1
12	186.5	1
1.a	198.5	2
1.b	200.5	2
1.c	201.5	2
1.d	202.5	2
1.e	203.5	2
1.f	204.5	2
13	205.5	1
1.g	206.5	2
1.h	207.5	2
1.i	208.5	2
1.j	209.5	2
1.k	210.5	2

1.l	211.5	2
14	227.5	1
15	246	1
16	266	1
17	284.5	1
18	301.5	1
19	321.5	1
20	341.5	1
21	360.5	1
22	378	1
23	397	1
24	417	1
25	437	1
26	458	1
27	477	1
28	485.2	1
29	501.4	1
30	517.9	1
31	537.7	1
32	553.7	1
33	573.7	1
34	593.7	1
35	613.7	1
36	633.2	1
37	652.2	1
38	672.2	1
39	691.2	1
40	704.2	1
41	718.7	1
42	734.7	1
43	746.7	1

Appendix 5

Input in to R (bacon package) to produce the Basyian Age-Depth model, assuming the top of the core is present (when core taken, 2008) with a low error. Run with the corrected depths

labID	ages	error	depth	cc
Surface	-58	1	0	0
con3	3903	40	73	3
con3	9812	57	325	3
con3	10758	61	385.5	3
con3	16720	68	591.2	3
con3	25287	177	752.2	3

Appendix 6

Table identifying previous charcoal analysis near to Lake Consuelo. This data were used to help to define the class boundary sizes for charcoal analysis.

Reference	Location	Size charcoal µm	Notes
(Hanselman et al., 2011)	Lake Titicaca	>180	Lake very close to study site and similar time period
(Paduano et al., 2003)	Lake Titicaca	≥180 (local) and 179–65 (regional)	Lake very close to study site and similar time period
(Rozas-Davila et al., 2016)	Lake Pacucha (Peru)	>180	Close lake to study site also consider Megafauna
(Johnston, 2017)	Lake Consuelo	>180 (local) and 106-63 (regional)	Pilot study
(Urrego et al., 2011)	Lake Refugio (Peru)	>180	Close lake to study site, compare to vegetation changes
(Bush et al., 2005)	Laguna de Chochos, Peru	>100 (local) <100 (Regional)	Studies local and regional charcoal. Their classes differ from other literature.
(Burbridge et al., 2004)	Bolivian Amazon	Particles were sorted into categories of 54–180, 181– 250, 251– 500, and >500. (separate regional and local)	Bolivian border
(Raczka et al., 2019)	Lake Llaviucu	>180 (local)	Poorly dispersed – paper looking at proxies studies here in area near.

Appendix 7

Table of sedimentation rates across the whole core length

depth	median	depth interval	time interval	sedimentation rate cm/year
0	-58.2			
1	-13.5	1	44.7	0.022371
2	32.3	1	45.8	0.021834
3	79	1	46.7	0.021413
4	125.7	1	46.7	0.021413
5	171.2	1	45.5	0.021978
6	221.6	1	50.4	0.019841
7	284.1	1	62.5	0.016
8	345	1	60.9	0.01642
8.5	373.3	0.5	28.3	0.017668
9	401.6	0.5	28.3	0.017668
10	454.8	1	53.2	0.018797
11	532.4	1	77.6	0.012887
12	614.1	1	81.7	0.01224
13	682.3	1	68.2	0.014663
14	738.5	1	56.2	0.017794
15	791.1	1	52.6	0.019011
15.5	822.7	0.5	31.6	0.015823
16	854.3	0.5	31.6	0.015823
17	916.3	1	62	0.016129
17.5	943.6	0.5	27.3	0.018315
18	970.9	0.5	27.3	0.018315

19	1032.8	1	61.9	0.016155
20	1090.2	1	57.4	0.017422
21	1153.8	1	63.6	0.015723
22	1213.5	1	59.7	0.01675
23	1272.7	1	59.2	0.016892
23.5	1301.95	0.5	29.25	0.017094
24	1331.2	0.5	29.25	0.017094
25	1395.1	1	63.9	0.015649
26	1456.7	1	61.6	0.016234
27	1515.7	1	59	0.016949
27.5	1554.2	0.5	38.5	0.012987
28	1592.7	0.5	38.5	0.012987
29	1688.5	1	95.8	0.010438
30	1762.5	1	74	0.013514
31	1823.8	1	61.3	0.016313
32	1887.3	1	63.5	0.015748
32.5	1924.05	0.5	36.75	0.013605
33	1960.8	0.5	36.75	0.013605
33.5	1993.5	0.5	32.7	0.015291
34	2026.2	0.5	32.7	0.015291
34.5	2058.85	0.5	32.65	0.015314
35	2091.5	0.5	32.65	0.015314
36	2135.3	1	43.8	0.022831
37	2184.6	1	49.3	0.020284
38	2237.2	1	52.6	0.019011
39	2286.4	1	49.2	0.020325
40	2331.1	1	44.7	0.022371
41	2382.1	1	51	0.019608
42	2439.7	1	57.6	0.017361
43	2506.5	1	66.8	0.01497
44	2572.1	1	65.6	0.015244
45	2633.9	1	61.8	0.016181
46	2684.3	1	50.4	0.019841
47	2739.2	1	54.9	0.018215
48	2789.2	1	50	0.02
49	2840.1	1	50.9	0.019646
50	2896.9	1	56.8	0.017606
51	2953.9	1	57	0.017544
52	3010.2	1	56.3	0.017762
53	3064.2	1	54	0.018519
54	3121.7	1	57.5	0.017391
55	3187.7	1	66	0.015152
56	3245.3	1	57.6	0.017361
57	3310.2	1	64.9	0.015408
58	3376	1	65.8	0.015198
59	3449.7	1	73.7	0.013569
60	3509	1	59.3	0.016863
61	3567.7	1	58.7	0.017036
61.5	3597	0.5	29.3	0.017065
62	3626.3	0.5	29.3	0.017065
63	3684.7	1	58.4	0.017123
64	3756.7	1	72	0.013889

64.5	3790.8	0.5	34.1	0.014663
65	3824.9	0.5	34.1	0.014663
66	3877	1	52.1	0.019194
67	3927.2	1	50.2	0.01992
68	3981.2	1	54	0.018519
69	4036.7	1	55.5	0.018018
69.5	4068.85	0.5	32.15	0.015552
70	4101	0.5	32.15	0.015552
71	4137.9	1	36.9	0.0271
72	4175.4	1	37.5	0.026667
73	4222.3	1	46.9	0.021322
74	4268	1	45.7	0.021882
74.5	4288.6	0.5	20.6	0.024272
75	4309.2	0.5	20.6	0.024272
76	4334.9	1	25.7	0.038911
77	4363	1	28.1	0.035587
78	4390.7	1	27.7	0.036101
79	4415	1	24.3	0.041152
80	4435.8	1	20.8	0.048077
81	4460.7	1	24.9	0.040161
81.5	4474.7	0.5	14	0.035714
82	4488.7	0.5	14	0.035714
83	4513.5	1	24.8	0.040323
84	4537.2	1	23.7	0.042194
85	4562.4	1	25.2	0.039683
86	4589.3	1	26.9	0.037175
86.5	4604.65	0.5	15.35	0.032573
87	4620	0.5	15.35	0.032573
88	4647.4	1	27.4	0.036496
89	4672.2	1	24.8	0.040323
90	4694.7	1	22.5	0.044444
91	4724.9	1	30.2	0.033113
92	4758.9	1	34	0.029412
92.5	4770.85	0.5	11.95	0.041841
93	4782.8	0.5	11.95	0.041841
94	4808.8	1	26	0.038462
95	4832.4	1	23.6	0.042373
96	4857.5	1	25.1	0.039841
96.5	4873.35	0.5	15.85	0.031546
97	4889.2	0.5	15.85	0.031546
98	4918.7	1	29.5	0.033898
99	4949.6	1	30.9	0.032362
100	4971.7	1	22.1	0.045249
101	5000.3	1	28.6	0.034965
101.5	5015.8	0.5	15.5	0.032258
102	5031.3	0.5	15.5	0.032258
103	5063.6	1	32.3	0.03096
104	5086.8	1	23.2	0.043103
105	5106.3	1	19.5	0.051282
106	5134.2	1	27.9	0.035842
107	5161.5	1	27.3	0.03663
108	5190.5	1	29	0.034483

109	5214.3	1	23.8	0.042017
110	5235.7	1	21.4	0.046729
111	5266.7	1	31	0.032258
112	5292.4	1	25.7	0.038911
112.5	5307	0.5	14.6	0.034247
113	5321.6	0.5	14.6	0.034247
114	5345	1	23.4	0.042735
115	5369.8	1	24.8	0.040323
115.5	5383.05	0.5	13.25	0.037736
116	5396.3	0.5	13.25	0.037736
117	5423.6	1	27.3	0.03663
118	5451.5	1	27.9	0.035842
118.5	5465	0.5	13.5	0.037037
119	5478.5	0.5	13.5	0.037037
120	5510.6	1	32.1	0.031153
121	5534.7	1	24.1	0.041494
122	5556.8	1	22.1	0.045249
123	5578.5	1	21.7	0.046083
124	5601.6	1	23.1	0.04329
125	5628.3	1	26.7	0.037453
125.5	5643.3	0.5	15	0.033333
126	5658.3	0.5	15	0.033333
127	5686.8	1	28.5	0.035088
128	5719.7	1	32.9	0.030395
129	5752.4	1	32.7	0.030581
129.5	5768.3	0.5	15.9	0.031447
130	5784.2	0.5	15.9	0.031447
131	5815.3	1	31.1	0.032154
132	5846.9	1	31.6	0.031646
132.5	5858	0.5	11.1	0.045045
133	5869.1	0.5	11.1	0.045045
134	5893.3	1	24.2	0.041322
135	5917.8	1	24.5	0.040816
136	5941.6	1	23.8	0.042017
137	5972.7	1	31.1	0.032154
138	6002.5	1	29.8	0.033557
139	6026.4	1	23.9	0.041841
140	6056.5	1	30.1	0.033223
141	6078.9	1	22.4	0.044643
141.5	6089.55	0.5	10.65	0.046948
142	6100.2	0.5	10.65	0.046948
143	6125.6	1	25.4	0.03937
144	6154.1	1	28.5	0.035088
145	6182.1	1	28	0.035714
146	6208.3	1	26.2	0.038168
147	6236	1	27.7	0.036101
148	6264.6	1	28.6	0.034965
148.5	6276.3	0.5	11.7	0.042735
149	6288	0.5	11.7	0.042735
150	6314.2	1	26.2	0.038168
151	6340.9	1	26.7	0.037453
152	6366.2	1	25.3	0.039526

152.5	6383.2	0.5	17	0.029412
153	6400.2	0.5	17	0.029412
154	6430.6	1	30.4	0.032895
155	6455	1	24.4	0.040984
156	6483.1	1	28.1	0.035587
156.5	6497.85	0.5	14.75	0.033898
157	6512.6	0.5	14.75	0.033898
158	6538.7	1	26.1	0.038314
159	6574.4	1	35.7	0.028011
160	6599.5	1	25.1	0.039841
160.5	6616	0.5	16.5	0.030303
161	6632.5	0.5	16.5	0.030303
162	6659.5	1	27	0.037037
163	6688.6	1	29.1	0.034364
164	6715	1	26.4	0.037879
165	6747.1	1	32.1	0.031153
166	6768.9	1	21.8	0.045872
167	6792.2	1	23.3	0.042918
167.5	6806.4	0.5	14.2	0.035211
168	6820.6	0.5	14.2	0.035211
169	6843.8	1	23.2	0.043103
170	6873.2	1	29.4	0.034014
171	6901.7	1	28.5	0.035088
172	6937.4	1	35.7	0.028011
173	6972.7	1	35.3	0.028329
173.5	6986.1	0.5	13.4	0.037313
174	6999.5	0.5	13.4	0.037313
175	7025.3	1	25.8	0.03876
175.5	7039.65	0.5	14.35	0.034843
176	7054	0.5	14.35	0.034843
177	7082.6	1	28.6	0.034965
178	7115.4	1	32.8	0.030488
179	7144.6	1	29.2	0.034247
180	7170.6	1	26	0.038462
181	7198.1	1	27.5	0.036364
181.5	7211.75	0.5	13.65	0.03663
182	7225.4	0.5	13.65	0.03663
183	7254.3	1	28.9	0.034602
184	7279.1	1	24.8	0.040323
185	7308	1	28.9	0.034602
186	7330.5	1	22.5	0.044444
186.5	7346	0.5	15.5	0.032258
187	7361.5	0.5	15.5	0.032258
188	7389.6	1	28.1	0.035587
198.5	7401.6	10.5	12	0.875
189	7413.6	-9.5	12	-0.79167
190	7444.3	1	30.7	0.032573
190.5	7457.8	0.5	13.5	0.037037
191	7471.3	0.5	13.5	0.037037
192	7503.4	1	32.1	0.031153
193	7534.4	1	31	0.032258
194	7558.8	1	24.4	0.040984

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195	7589.6	1	30.8	0.032468
195.5	7601.75	0.5	12.15	0.041152
196	7613.9	0.5	12.15	0.041152
197	7643.4	1	29.5	0.033898
198	7670.2	1	26.8	0.037313
198.5	7682.35	0.5	12.15	0.041152
199	7694.5	0.5	12.15	0.041152
200	7723.6	1	29.1	0.034364
200.5	7736.35	0.5	12.75	0.039216
201	7749.1	0.5	12.75	0.039216
201.5	7764.5	0.5	15.4	0.032468
202	7779.9	0.5	15.4	0.032468
202.5	7792.05	0.5	12.15	0.041152
203	7804.2	0.5	12.15	0.041152
203.5	7818.05	0.5	13.85	0.036101
204	7831.9	0.5	13.85	0.036101
204.5	7844.3	0.5	12.4	0.040323
205	7856.7	0.5	12.4	0.040323
205.5	7870.9	0.5	14.2	0.035211
206	7885.1	0.5	14.2	0.035211
206.5	7898.3	0.5	13.2	0.037879
207	7911.5	0.5	13.2	0.037879
207.5	7925.1	0.5	13.6	0.036765
208	7938.7	0.5	13.6	0.036765
208.5	7950.65	0.5	11.95	0.041841
209	7962.6	0.5	11.95	0.041841
209.5	7976	0.5	13.4	0.037313
210	7989.4	0.5	13.4	0.037313
210.5	8004.9	0.5	15.5	0.032258
211	8020.4	0.5	15.5	0.032258
211.5	8033.3	0.5	12.9	0.03876
212	8046.2	0.5	12.9	0.03876
213	8078.6	1	32.4	0.030864
214	8109.3	1	30.7	0.032573
215	8137.2	1	27.9	0.035842
216	8169.1	1	31.9	0.031348
216.5	8184.85	0.5	15.75	0.031746
217	8200.6	0.5	15.75	0.031746
218	8225.1	1	24.5	0.040816
219	8252.6	1	27.5	0.036364
220	8281.7	1	29.1	0.034364
221	8309.7	1	28	0.035714
221.5	8324.6	0.5	14.9	0.033557
222	8339.5	0.5	14.9	0.033557
223	8366.9	1	27.4	0.036496
224	8396.2	1	29.3	0.03413
225	8430.4	1	34.2	0.02924
226	8451.5	1	21.1	0.047393
227	8475.3	1	23.8	0.042017
227.5	8490.35	0.5	15.05	0.033223
228	8505.4	0.5	15.05	0.033223
229	8533.6	1	28.2	0.035461

230	8559	1	25.4	0.03937
231	8585.5	1	26.5	0.037736
232	8621.2	1	35.7	0.028011
233	8645.1	1	23.9	0.041841
234	8669.6	1	24.5	0.040816
235	8697.5	1	27.9	0.035842
236	8724.6	1	27.1	0.0369
236.5	8736.6	0.5	12	0.041667
237	8748.6	0.5	12	0.041667
238	8778.4	1	29.8	0.033557
239	8804.1	1	25.7	0.038911
240	8825.8	1	21.7	0.046083
241	8848.2	1	22.4	0.044643
242	8870.6	1	22.4	0.044643
243	8894.9	1	24.3	0.041152
244	8915	1	20.1	0.049751
245	8940	1	25	0.04
246	8963	1	23	0.043478
247	8990.3	1	27.3	0.03663
248	9024.6	1	34.3	0.029155
249	9058.7	1	34.1	0.029326
250	9087.1	1	28.4	0.035211
251	9112.7	1	25.6	0.039062
252	9138.6	1	25.9	0.03861
253	9164.3	1	25.7	0.038911
253.5	9180	0.5	15.7	0.031847
254	9195.7	0.5	15.7	0.031847
255	9225.9	1	30.2	0.033113
256	9255.8	1	29.9	0.033445
257	9282.6	1	26.8	0.037313
258	9311.6	1	29	0.034483
259	9335.8	1	24.2	0.041322
259.5	9350.25	0.5	14.45	0.034602
260	9364.7	0.5	14.45	0.034602
261	9388.2	1	23.5	0.042553
262	9412.5	1	24.3	0.041152
263	9443.5	1	31	0.032258
264	9474.4	1	30.9	0.032362
265	9498.5	1	24.1	0.041494
266	9526.4	1	27.9	0.035842
267	9555.1	1	28.7	0.034843
268	9588.6	1	33.5	0.029851
269	9618.3	1	29.7	0.03367
270	9643.3	1	25	0.04
271	9670.3	1	27	0.037037
272	9692.3	1	22	0.045455
273	9718.1	1	25.8	0.03876
273.5	9734.55	0.5	16.45	0.030395
274	9751	0.5	16.45	0.030395
275	9780.8	1	29.8	0.033557
276	9811.3	1	30.5	0.032787
277	9840.9	1	29.6	0.033784

278	9866.2	1	25.3	0.039526
279	9893	1	26.8	0.037313
280	9917	1	24	0.041667
281	9945.3	1	28.3	0.035336
282	9978.4	1	33.1	0.030211
283	10007.9	1	29.5	0.033898
284	10034	1	26.1	0.038314
284.5	10048	0.5	14	0.035714
285	10062	0.5	14	0.035714
286	10091	1	29	0.034483
287	10119.8	1	28.8	0.034722
288	10150.8	1	31	0.032258
288.5	10165.65	0.5	14.85	0.03367
289	10180.5	0.5	14.85	0.03367
290	10209.5	1	29	0.034483
291	10234.9	1	25.4	0.03937
292	10263.6	1	28.7	0.034843
293	10294.1	1	30.5	0.032787
293.5	10306.45	0.5	12.35	0.040486
294	10318.8	0.5	12.35	0.040486
295	10345	1	26.2	0.038168
296	10371.3	1	26.3	0.038023
297	10402.3	1	31	0.032258
298	10432.6	1	30.3	0.033003
299	10460.8	1	28.2	0.035461
300	10489.7	1	28.9	0.034602
301	10516.7	1	27	0.037037
301.5	10532.6	0.5	15.9	0.031447
302	10548.5	0.5	15.9	0.031447
303	10577.4	1	28.9	0.034602
304	10609.8	1	32.4	0.030864
305	10642.5	1	32.7	0.030581
306	10666	1	23.5	0.042553
306.5	10681.7	0.5	15.7	0.031847
307	10697.4	0.5	15.7	0.031847
308	10725.8	1	28.4	0.035211
309	10756.7	1	30.9	0.032362
310	10783.7	1	27	0.037037
310.5	10795.2	0.5	11.5	0.043478
311	10806.7	0.5	11.5	0.043478
312	10832.1	1	25.4	0.03937
313	10850.2	1	18.1	0.055249
314	10878.4	1	28.2	0.035461
315	10905.6	1	27.2	0.036765
315.5	10918.35	0.5	12.75	0.039216
316	10931.1	0.5	12.75	0.039216
317	10958.7	1	27.6	0.036232
318	10989.9	1	31.2	0.032051
319	11022.2	1	32.3	0.03096
320	11051	1	28.8	0.034722
321	11078.1	1	27.1	0.0369
321.5	11090.55	0.5	12.45	0.040161

322	11103	0.5	12.45	0.040161
323	11130.1	1	27.1	0.0369
324	11156.1	1	26	0.038462
325	11183	1	26.9	0.037175
326	11213	1	30	0.033333
327	11236.3	1	23.3	0.042918
328	11256.1	1	19.8	0.050505
329	11274.4	1	18.3	0.054645
330	11290.9	1	16.5	0.060606
330.5	11303.9	0.5	13	0.038462
331	11316.9	0.5	13	0.038462
332	11338.8	1	21.9	0.045662
333	11362.4	1	23.6	0.042373
334	11386	1	23.6	0.042373
335	11405.7	1	19.7	0.050761
336	11434.1	1	28.4	0.035211
336.5	11447.95	0.5	13.85	0.036101
337	11461.8	0.5	13.85	0.036101
338	11488.6	1	26.8	0.037313
339	11512.9	1	24.3	0.041152
340	11537.8	1	24.9	0.040161
341	11562.8	1	25	0.04
341.5	11576.05	0.5	13.25	0.037736
342	11589.3	0.5	13.25	0.037736
343	11614.4	1	25.1	0.039841
344	11636.4	1	22	0.045455
345	11659	1	22.6	0.044248
346	11685	1	26	0.038462
347	11709.5	1	24.5	0.040816
348	11733.7	1	24.2	0.041322
349	11756.6	1	22.9	0.043668
350	11782.4	1	25.8	0.03876
350.5	11795.3	0.5	12.9	0.03876
351	11808.2	0.5	12.9	0.03876
352	11833.6	1	25.4	0.03937
353	11858.8	1	25.2	0.039683
354	11883.2	1	24.4	0.040984
355	11909.9	1	26.7	0.037453
355.5	11919.9	0.5	10	0.05
356	11929.9	0.5	10	0.05
357	11954.6	1	24.7	0.040486
358	11979.7	1	25.1	0.039841
359	12004.8	1	25.1	0.039841
360	12026.6	1	21.8	0.045872
360.5	12039.65	0.5	13.05	0.038314
361	12052.7	0.5	13.05	0.038314
362	12075.4	1	22.7	0.044053
363	12103.7	1	28.3	0.035336
364	12128.5	1	24.8	0.040323
365	12152.8	1	24.3	0.041152
366	12173.9	1	21.1	0.047393
367	12204.2	1	30.3	0.033003

368	12231.1	1	26.9	0.037175
369	12262.3	1	31.2	0.032051
370	12290	1	27.7	0.036101
371	12313.4	1	23.4	0.042735
372	12339.1	1	25.7	0.038911
373	12366.3	1	27.2	0.036765
374	12393.7	1	27.4	0.036496
375	12418.4	1	24.7	0.040486
376	12444.1	1	25.7	0.038911
377	12467.5	1	23.4	0.042735
378	12489.5	1	22	0.045455
379	12515	1	25.5	0.039216
380	12536.8	1	21.8	0.045872
381	12557.7	1	20.9	0.047847
382	12579.5	1	21.8	0.045872
383	12602.3	1	22.8	0.04386
384	12631.9	1	29.6	0.033784
385	12660.5	1	28.6	0.034965
386	12690.4	1	29.9	0.033445
387	12722.6	1	32.2	0.031056
388	12751.4	1	28.8	0.034722
389	12776.9	1	25.5	0.039216
390	12802.3	1	25.4	0.03937
391	12837.3	1	35	0.028571
392	12870.5	1	33.2	0.03012
393	12901	1	30.5	0.032787
394	12933.8	1	32.8	0.030488
395	12961.9	1	28.1	0.035587
396	12997.2	1	35.3	0.028329
397	13033.4	1	36.2	0.027624
398	13064.4	1	31	0.032258
399	13098.4	1	34	0.029412
400	13129	1	30.6	0.03268
401	13169.1	1	40.1	0.024938
402	13210.5	1	41.4	0.024155
403	13248.1	1	37.6	0.026596
404	13281.5	1	33.4	0.02994
405	13315.5	1	34	0.029412
406	13356.3	1	40.8	0.02451
407	13395.8	1	39.5	0.025316
408	13439.4	1	43.6	0.022936
409	13478.5	1	39.1	0.025575
410	13512.5	1	34	0.029412
411	13547.4	1	34.9	0.028653
412	13586.7	1	39.3	0.025445
413	13621.6	1	34.9	0.028653
414	13658.4	1	36.8	0.027174
415	13697.5	1	39.1	0.025575
416	13723.9	1	26.4	0.037879
417	13761	1	37.1	0.026954
418	13796.6	1	35.6	0.02809
419	13839.4	1	42.8	0.023364

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420	13868.1	1	28.7	0.034843
421	13908.5	1	40.4	0.024752
422	13944.4	1	35.9	0.027855
423	13974.8	1	30.4	0.032895
424	14011.2	1	36.4	0.027473
425	14043.5	1	32.3	0.03096
426	14079.1	1	35.6	0.02809
427	14116.3	1	37.2	0.026882
428	14151.4	1	35.1	0.02849
429	14193.5	1	42.1	0.023753
430	14231.6	1	38.1	0.026247
431	14268	1	36.4	0.027473
432	14304.8	1	36.8	0.027174
433	14345.6	1	40.8	0.02451
434	14386.8	1	41.2	0.024272
435	14425	1	38.2	0.026178
436	14461.2	1	36.2	0.027624
437	14500.1	1	38.9	0.025707
438	14538	1	37.9	0.026385
439	14573.6	1	35.6	0.02809
440	14612	1	38.4	0.026042
441	14646.3	1	34.3	0.029155
442	14683	1	36.7	0.027248
443	14717.5	1	34.5	0.028986
444	14755.4	1	37.9	0.026385
445	14793.4	1	38	0.026316
446	14822.3	1	28.9	0.034602
446.5	14837.5	0.5	15.2	0.032895
447	14852.7	0.5	15.2	0.032895
448	14890.1	1	37.4	0.026738
449	14916.7	1	26.6	0.037594
450	14956.2	1	39.5	0.025316
451	14991.5	1	35.3	0.028329
452	15039	1	47.5	0.021053
453	15075.3	1	36.3	0.027548
454	15122	1	46.7	0.021413
455	15153.4	1	31.4	0.031847
456	15200.7	1	47.3	0.021142
457	15233.8	1	33.1	0.030211
458	15273	1	39.2	0.02551
459	15312.1	1	39.1	0.025575
460	15343.8	1	31.7	0.031546
461	15381.7	1	37.9	0.026385
462	15425.7	1	44	0.022727
463	15463.2	1	37.5	0.026667
464	15504.9	1	41.7	0.023981
465	15542.1	1	37.2	0.026882
466	15575.9	1	33.8	0.029586
467	15620.4	1	44.5	0.022472
468	15662.5	1	42.1	0.023753
469	15697.3	1	34.8	0.028736
470	15726.2	1	28.9	0.034602

471	15772.9	1	46.7	0.021413
472	15812.7	1	39.8	0.025126
473	15848.5	1	35.8	0.027933
474	15887.5	1	39	0.025641
475	15933.3	1	45.8	0.021834
476	15965.6	1	32.3	0.03096
477	15999.6	1	34	0.029412
478	16028.4	1	28.8	0.034722
479	16060.1	1	31.7	0.031546
480	16093.1	1	33	0.030303
481	16130.9	1	37.8	0.026455
482	16168.1	1	37.2	0.026882
483	16207.9	1	39.8	0.025126
484	16245.7	1	37.8	0.026455
485	16283.3	1	37.6	0.026596
486	16326.4	1	43.1	0.023202
487	16363.4	1	37	0.027027
488	16407.3	1	43.9	0.022779
489	16443.7	1	36.4	0.027473
490	16476.6	1	32.9	0.030395
491	16506	1	29.4	0.034014
492	16540.7	1	34.7	0.028818
493	16576.1	1	35.4	0.028249
494	16620.3	1	44.2	0.022624
495	16650.7	1	30.4	0.032895
496	16684.5	1	33.8	0.029586
496.5	16705.45	0.5	20.95	0.023866
497	16726.4	0.5	20.95	0.023866
498	16771.5	1	45.1	0.022173
499	16817.2	1	45.7	0.021882
500	16865.5	1	48.3	0.020704
501	16905.3	1	39.8	0.025126
501.5	16924.1	0.5	18.8	0.026596
502	16942.9	0.5	18.8	0.026596
503	16973.1	1	30.2	0.033113
504	17006.7	1	33.6	0.029762
505	17043.8	1	37.1	0.026954
506	17076.8	1	33	0.030303
507	17112.5	1	35.7	0.028011
508	17155.6	1	43.1	0.023202
509	17187.2	1	31.6	0.031646
510	17232.3	1	45.1	0.022173
510.5	17251.1	0.5	18.8	0.026596
511	17269.9	0.5	18.8	0.026596
512	17315.7	1	45.8	0.021834
513	17346.2	1	30.5	0.032787
514	17393.2	1	47	0.021277
515	17434.9	1	41.7	0.023981
516	17457.8	1	22.9	0.043668
517	17496.2	1	38.4	0.026042
518	17537.7	1	41.5	0.024096
519	17569.2	1	31.5	0.031746

520	17605.6	1	36.4	0.027473
521	17647.5	1	41.9	0.023866
522	17686	1	38.5	0.025974
523	17718.5	1	32.5	0.030769
524	17756.2	1	37.7	0.026525
525	17789.7	1	33.5	0.029851
526	17825	1	35.3	0.028329
527	17856.6	1	31.6	0.031646
528	17889.5	1	32.9	0.030395
529	17931.6	1	42.1	0.023753
530	17964.7	1	33.1	0.030211
531	18001.7	1	37	0.027027
532	18038.9	1	37.2	0.026882
533	18076.5	1	37.6	0.026596
534	18116.3	1	39.8	0.025126
535	18148.6	1	32.3	0.03096
536	18184.4	1	35.8	0.027933
537	18217.9	1	33.5	0.029851
538	18261.8	1	43.9	0.022779
539	18300.1	1	38.3	0.02611
540	18335.3	1	35.2	0.028409
541	18369.5	1	34.2	0.02924
542	18405.8	1	36.3	0.027548
543	18443.1	1	37.3	0.02681
544	18481.4	1	38.3	0.02611
545	18524.5	1	43.1	0.023202
546	18556.9	1	32.4	0.030864
547	18588.7	1	31.8	0.031447
548	18623.5	1	34.8	0.028736
549	18653.7	1	30.2	0.033113
550	18685.2	1	31.5	0.031746
551	18720.8	1	35.6	0.02809
552	18754.5	1	33.7	0.029674
553	18790.2	1	35.7	0.028011
554	18824.9	1	34.7	0.028818
555	18869.8	1	44.9	0.022272
556	18900.9	1	31.1	0.032154
557	18940	1	39.1	0.025575
558	18968.8	1	28.8	0.034722
559	19007.5	1	38.7	0.02584
560	19044.9	1	37.4	0.026738
561	19081.2	1	36.3	0.027548
562	19120	1	38.8	0.025773
563	19152.1	1	32.1	0.031153
564	19179.2	1	27.1	0.0369
565	19214	1	34.8	0.028736
566	19250.2	1	36.2	0.027624
567	19290.9	1	40.7	0.02457
568	19325.7	1	34.8	0.028736
569	19362.8	1	37.1	0.026954
570	19403.6	1	40.8	0.02451
571	19432.9	1	29.3	0.03413

572	19465.7	1	32.8	0.030488
573	19496.6	1	30.9	0.032362
574	19532.6	1	36	0.027778
575	19564.4	1	31.8	0.031447
576	19600.9	1	36.5	0.027397
577	19640.1	1	39.2	0.02551
578	19677.9	1	37.8	0.026455
579	19715.3	1	37.4	0.026738
580	19756.4	1	41.1	0.024331
581	19788.2	1	31.8	0.031447
582	19817.2	1	29	0.034483
583	19856.7	1	39.5	0.025316
584	19896.8	1	40.1	0.024938
585	19937	1	40.2	0.024876
586	19965.8	1	28.8	0.034722
587	19999.4	1	33.6	0.029762
588	20034.3	1	34.9	0.028653
589	20073.8	1	39.5	0.025316
590	20115.7	1	41.9	0.023866
591	20147.2	1	31.5	0.031746
592	20183.4	1	36.2	0.027624
593	20220.1	1	36.7	0.027248
594	20264.2	1	44.1	0.022676
595	20306.1	1	41.9	0.023866
596	20353	1	46.9	0.021322
597	20400.9	1	47.9	0.020877
598	20447.2	1	46.3	0.021598
599	20490	1	42.8	0.023364
600	20531.5	1	41.5	0.024096
601	20582.8	1	51.3	0.019493
602	20648.7	1	65.9	0.015175
603	20705.9	1	57.2	0.017483
604	20757.7	1	51.8	0.019305
605	20812.1	1	54.4	0.018382
606	20863.8	1	51.7	0.019342
607	20913.1	1	49.3	0.020284
608	20967.2	1	54.1	0.018484
609	21019.6	1	52.4	0.019084
610	21071.2	1	51.6	0.01938
611	21128.7	1	57.5	0.017391
612	21184.9	1	56.2	0.017794
613	21231.2	1	46.3	0.021598
614	21275.2	1	44	0.022727
615	21318.5	1	43.3	0.023095
616	21386.3	1	67.8	0.014749
617	21450.7	1	64.4	0.015528
618	21501	1	50.3	0.019881
619	21549.7	1	48.7	0.020534
620	21598.9	1	49.2	0.020325
621	21652.5	1	53.6	0.018657
622	21708.7	1	56.2	0.017794
623	21751.9	1	43.2	0.023148

624	21799.1	1	47.2	0.021186
625	21851.9	1	52.8	0.018939
626	21909.5	1	57.6	0.017361
627	21963.1	1	53.6	0.018657
628	22027	1	63.9	0.015649
629	22087.2	1	60.2	0.016611
630	22134.2	1	47	0.021277
631	22189.5	1	55.3	0.018083
632	22255.6	1	66.1	0.015129
633	22301.6	1	46	0.021739
634	22352.1	1	50.5	0.019802
635	22400.8	1	48.7	0.020534
636	22448.9	1	48.1	0.02079
637	22505.3	1	56.4	0.01773
638	22559.2	1	53.9	0.018553
639	22619	1	59.8	0.016722
640	22665.9	1	46.9	0.021322
641	22725.7	1	59.8	0.016722
642	22778	1	52.3	0.01912
643	22829	1	51	0.019608
644	22889.7	1	60.7	0.016474
645	22935.8	1	46.1	0.021692
646	22989	1	53.2	0.018797
647	23050.4	1	61.4	0.016287
648	23105.7	1	55.3	0.018083
649	23168.4	1	62.7	0.015949
650	23212.3	1	43.9	0.022779
651	23264.2	1	51.9	0.019268
652	23317.5	1	53.3	0.018762
653	23372.9	1	55.4	0.018051
654	23430.6	1	57.7	0.017331
655	23472.2	1	41.6	0.024038
656	23538.6	1	66.4	0.01506
657	23594	1	55.4	0.018051
658	23643.4	1	49.4	0.020243
659	23693.4	1	50	0.02
660	23740.3	1	46.9	0.021322
661	23801.2	1	60.9	0.01642
662	23852.5	1	51.3	0.019493
663	23909.5	1	57	0.017544
664	23968.7	1	59.2	0.016892
665	24030.3	1	61.6	0.016234
666	24064.1	1	33.8	0.029586
667	24115.2	1	51.1	0.019569
668	24157.7	1	42.5	0.023529
669	24201.7	1	44	0.022727
670	24243.4	1	41.7	0.023981
671	24301.6	1	58.2	0.017182
672	24364.2	1	62.6	0.015974
673	24426.5	1	62.3	0.016051
674	24491.9	1	65.4	0.015291
675	24545.2	1	53.3	0.018762

676	24600.3	1	55.1	0.018149
677	24654.3	1	54	0.018519
678	24707.2	1	52.9	0.018904
679	24763.4	1	56.2	0.017794
680	24812.8	1	49.4	0.020243
681	24867.9	1	55.1	0.018149
682	24915.6	1	47.7	0.020964
683	24978.8	1	63.2	0.015823
684	25050.2	1	71.4	0.014006
685	25097.6	1	47.4	0.021097
686	25137.3	1	39.7	0.025189
687	25196.2	1	58.9	0.016978
688	25245.1	1	48.9	0.02045
689	25293.8	1	48.7	0.020534
690	25338.8	1	45	0.022222
691	25397	1	58.2	0.017182
692	25451.8	1	54.8	0.018248
693	25508.7	1	56.9	0.017575
694	25555.1	1	46.4	0.021552
695	25610.5	1	55.4	0.018051
696	25663	1	52.5	0.019048
697	25717	1	54	0.018519
698	25779.5	1	62.5	0.016
699	25841.1	1	61.6	0.016234
700	25905.4	1	64.3	0.015552
701	25962	1	56.6	0.017668
702	26021.6	1	59.6	0.016779
703	26068.9	1	47.3	0.021142
704	26126.7	1	57.8	0.017301
705	26174.2	1	47.5	0.021053
706	26228.5	1	54.3	0.018416
707	26286.8	1	58.3	0.017153
708	26346.9	1	60.1	0.016639
709	26400.9	1	54	0.018519
710	26453.2	1	52.3	0.01912
711	26513.4	1	60.2	0.016611
712	26569	1	55.6	0.017986
713	26621.1	1	52.1	0.019194
714	26681.2	1	60.1	0.016639
715	26728.2	1	47	0.021277
715.5	26756.95	0.5	28.75	0.017391
716	26785.7	0.5	28.75	0.017391
717	26838.8	1	53.1	0.018832
718	26896.3	1	57.5	0.017391
719	26956.6	1	60.3	0.016584
720	27006.8	1	50.2	0.01992
721	27051.5	1	44.7	0.022371
722	27105	1	53.5	0.018692
723	27155	1	50	0.02
724	27211.5	1	56.5	0.017699
725	27260.6	1	49.1	0.020367
726	27314.8	1	54.2	0.01845

727	27369.6	1	54.8	0.018248
728	27425.8	1	56.2	0.017794
729	27473.5	1	47.7	0.020964
730	27524.1	1	50.6	0.019763
731	27579.2	1	55.1	0.018149
732	27624.1	1	44.9	0.022272
733	27665.6	1	41.5	0.024096
734	27720.3	1	54.7	0.018282
735	27770.8	1	50.5	0.019802
736	27829.1	1	58.3	0.017153
737	27884.8	1	55.7	0.017953
738	27959	1	74.2	0.013477
739	28013.6	1	54.6	0.018315
740	28073.3	1	59.7	0.01675
741	28127.9	1	54.6	0.018315
742	28203.3	1	75.4	0.013263
743	28262.5	1	59.2	0.016892
744	28324.3	1	61.8	0.016181
745	28389	1	64.7	0.015456
746	28436.6	1	47.6	0.021008
747	28500.1	1	63.5	0.015748
748	28565.1	1	65	0.015385
749	28624.6	1	59.5	0.016807
750	28681.1	1	56.5	0.017699
751	28739.1	1	58	0.017241
752	28798.8	1	59.7	0.01675

This section of the Appendices provides future support for points raised in the discussion chapter (Chapter 4).

Appendix 8 – Charcoal Concentration Analysis

Concentration of charcoal at Lake Consuelo fluctuated between 0 to 6438 particles per cm^3. This concentration level is a lot lower than levels identified in other areas of South America. In upland savanna areas of Guayana charcoal concentration are recorded to reach levels up to 300,000 particles/cm^3 (Leal et al, 2016). This could be due to recurrent fires coming from other savannas nearby and reaching former forests creating large wildfires. Again, in Southern Patagonia data shows that concentrations of charcoal are a lot higher (Heusser, 1995) as well as in lower elevations in dry areas of Amazonia (Lake Sauce) (Bush et al, 2016). Both these records suggest a human causation for fire, in an optimal climate for spreading. Moreover, generally there is a link between areas with low forest cover and elevated fire activity (Loughlin, 2008). Whereas, Consuelo is surrounded by wetter regions and thus fires are largely supressed, unless conditions were optimal such as in the MHDE. Although humans caused fires are likely around Lake Consuelo and explain the larger peaks, the distance fires could have spread would have been more restricted due to moisture levels in the environment and denser vegetation. However, in other areas such as the Ecuadorian Andes, e.g. Lake Surucucho and the El Tiro Pass, charcoal concentration is found in lower concentrations than at Lake Consuelo. At Lake Surucucho concentration stayed below 100 particles per cm^3 (Colinvaux et al, 1997). The increase in concentration of charcoal at El Tiro Pass is related to only humans rather than

natural causes (Niemann and Behling, 2007). These areas are situated at a higher elevation than Lake Consuelo and thus fires were limited naturally by available biomass and climate, so largely supressed (Bush et al, 2005).

Appendix 9 – Discussion for the concentration/abundance levels of *Sporormiella* found at Lake Consuelo.

The *Sporormiella* % abundance never exceeded 3.5% abundance. Generally, studies implement a 2% threshold level to determine extinction events (Davis, 1987). However, this threshold is not spatially unanimous, thus needs to be considered in terms of the location and pollen sum (Raczka et al, 2016). In a study from Raczka et al, (2019) this value is shown inappropriate and a higher level is used. In their study area (Andes) there was a high number of low-density mammals (deer) who survived for longer, this contributed to a background level of *Sporormiella.* Thus, they appropriately factored this into the threshold value used. A similar case can be made for Lake Consuelo, however a lower threshold % is required. Hence, the 2% level may not always be the most meaningful indicator of the megafauna extinctions in a particular environment (Feranec et al, 2011).

The low *Sporormiella* value might also reflect the actual number of animals which visited Lake Consuelo. The overall population of animals might have been small and therefore there is only a very small amount of *Sporormiella* spores being deposited in the lake sediments (Raczka et al, 2016). The environmental conditions could be responsible for this. The steepness of the slopes and the dense vegetation could have restricted animal's movement to/around the lake making it a less favourable habitat.

Another reason to explain the low *Sporormiella* % abundance, could be linked to the basin's high productivity. Lake Consuelo has a highly productive pollen system, this high pollen concentration could have dampened the *Sporormiella* signal, so a low % abundance could be representative of a large signal of megafauna. Whereas, in areas of lower productivity the *Sporormiella* abundance might show up at a higher % in the record, without necessarily there having been more megafauna. This is demonstrated via the comparison of the extinction and peak spores in SE Brazil compared to the levels in the forests in North East USA. In the Lagoa Santa region there is a much lower productivity (lower pollen concentration) than in US and Lake Consuelo data sets, *Sporormiella* values reached nearly 20% (Raczka et al, 2018). However, in North East USA a system of higher productivity, *Sporormiella* was never >9% abundance (Gill et al, 2009). This illustrates the regionally variability and implications of pollen productivity in a given site. Overall, the extreme productivity around Lake Consuelo and dissolving effect of large pollen concentrations are the two factors that most likely explain the low concentration of *Sporormiella* spores in the record.

Another factor that is known to influence *Sporormiella* concentration in lake records is the relationship between lake size or the distance between the coring point and shoreline (Raczka et al, 2018). The core was taken from the centre of the lake (i.e. the deepest point), so that the oldest record possible was collected. However, this also could have had implications for the megafauna record because, as the distance from the shoreline increases *Sporormiella* abundance decreases (Raper and Bush, 2009). This is because the spores are deposited close to the ground and their gelatinous sheath structure makes their travel distance limited (Raper and Bush, 2009). Consequently, accumulating around shorelines and decreasing in abundance towards

the middle of a lake (Raczka et al 2016, Raper and Bush, 2009). Other factors are lake morphology and bathymetry, these can impact *Sporormiella* distribution within a lake. Thus, where there are no spores or low % of spores found in a sample this might not mean that the megafauna were not present. But due to external factors they were not always detected in samples (Davis and Shafer, 2006).

The timing of the *Sporormiella* peak/decline occurred in the regionally recognised MHDE. The MHDE could have also altered the local ecosystem productivity. If pollen concentrations were lowered it could have potentially caused a relative increase in *Sporormiella* values. Moreover, if the lake underwent substantial shrinking the core site would have been closer to the shoreline, in-turn increasing *Sporormiella* values. Therefore, it is plausible that the peak is due to external/climatic conditions altering spore concentration. Megafauna change could consequently be due to change in taphonomic signal rather than related to megafauna abundance or population size itself.

Although, these factors do alter *Sporormiella* concentration levels and thus need consideration, they are not exclusively the only plausible explanations for the observed trends. Sedimentation rates did not greatly alter in this period and throughout the record, meaning sediment entering the lake (via lake erosion, land erosion/runoff) was fairly constant (Appendix 7). Thus, *Sporormiella* concentration values should not have necessary increased. The LOI also shows constant organic carbon values around this time and for that reason sedimentation and accumulation seem not to be factors causing *Sporormiella* % change (Urrego et al, 2010).

Appendix 10 - Coprophilous spores and their relation to Megafauna

Other coprophilous fungal spores were analysed along with *Sporormiella* as there spores also can be used to identify the presence of herbivores (Burney et al, 2003, Davis and Shafter, 2006, Gill et al, 2009). A similar pattern in these spores was found to that of the *Sporormiella*. Such coprophilous spores have been recognized to appear together with *Sporormiella* in other locations, such as in the Galapagos (Froyd et al, 2013) to indicate herbivore presence. Across the record there is a change in the type of species for examples *Coniochaeta* were more abundant in the Pleistocene, whereas species such as *Splanchnonema foedans* were greater in the Holocene. Indicating a change in species with the fluctuations in vegetation and climate. The maximum peak of these spores occurred very closely to the *Sporormiella* peak (samples were analysed from slightly different depths, which can explain the offset) and declines after also. Thus, these can support the evidence of megafauna occurring later around Lake Consuelo than other regions.

Appendix 11 – Supporting data for Lake Consuelo acting as a refuge area for Megafauna

The idea of an area acting as a refuge from extinction has been previously discussed for other regions. Research conducted on St. Paul Island, Alaska showed a longer survival of megafauna as the area did not go through the same changes as elsewhere. The woolly mammoth populations have been dated until 5,600 ± 100 yr ago, which is nearly 8000 years after their vanishing from mainland North America 13,200 yr ago

(Graham et al, 2016). Ficcarelli et al (2003) findings of mammal fragments further support this theory. Their research found mammals survived on the coastal Ecuadorian areas until their final extinction between 8000-6000 cal yr BP. The animals migrated due to climate changes from Cordillera areas around 12,000 cal yr BP to an area where more suitable conditions existed. The subsequent shift of vegetation structures forced megafauna to become isolated in these contracted areas where conditions were favourable. Finally causing a final extinction when the vegetation altered back to dense formations. The data at Lake Consuelo follows a similar trend, as there is an initial appearance and then a decline just prior to 12,000 cal yr BP, followed by the main peak and disappearance at 7700 cal yr BP. Thus, the changes in climate that caused shifts in vegetation ultimately lead to the migration of animals to the lake as the conditions at the time offered a suboptimal habitat (Raczka et al, 2017). However, due to their isolation and increase in biological stress as vegetation composition, vegetation density increased and consequently megafauna decreased (Figure 3.6).

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