Chapter 4

Vegetation and Fire at the Last Glacial Maximum in Tropical South America

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Abstract This chapter aims to review current knowledge of the key vegetation types, and their composition, structure, distribution, and fire regime across the South American tropics during the global Last Glacial Maximum ca. 21,000 cal yr BP (calendar years before present). We do this by synthesising previously published Last Glacial Maximum fossil pollen and charcoal data as well as Last Glacial Maximum vegetation model simulations, in comparison with ecoregion/biome maps of present day vegetation. Both model simulations and empirical data suggest that there were no large-scale differences in major biome distributions between the Last Glacial Maximum and present (notwithstanding the Atlantic forests of SE Brazil), with biome shifts largely associated with ecotonal areas – downslope expansion of montane grasslands in the Andes at the expense of montane forest, and savanna expansion at the expense of rainforest and gallery forest at the Amazon basin margins. However, species composition and structure of these Last Glacial Maximum forests was quite different from those of today. At the Last Glacial Maximum, pollen data show that montane Andean taxa descended into the lowlands to form novel non-analogue forest communities with lowland Amazonian taxa, whilst vegetation model simulations show that carbon limitation caused by low atmospheric CO_2 likely produced forest communities with reduced canopy density and hence lower biomass than present-day forests. These pollen data-model comparisons show that although Amazonia was probably still dominated by closed forest at the Last Glacial Maximum, its carbon store may have been only 50% of present. Most charcoal records show reduced burning during the Last Glacial Maximum compared with today, most likely due to the significantly colder temperatures.

Keywords Charcoal · Last Glacial Maximum · pollen · Quaternary · tropical South America

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F. Vimeux et al. (eds.), *Past Climate Variability in South America and Surrounding Regions*, Developments in Paleoenvironmental Research 14,
DOI 10.1007/978-90-481-2672-9_4,

4.1 Introduction

The vegetation in tropical South America during the Last Glacial Maximum ca. 21 cal ka BP (21,000 calendar years before present), has been a topic of great interest and debate for several decades, particularly in Amazonia, concerning the spatial extent of forest versus savanna (Haffer 1969; Haffer and Prance 2001; Colinvaux et al. 2000), and the structural (Cowling et al. 2001) and floristic (Colinvaux et al. 2000) composition of those forests. This focus on the Last Glacial Maximum period in particular stems from interest in how ecosystems responded to the radically different global boundary conditions at the time compared with present; namely, maximum global expansion of ice-sheets, CO_2 concentrations half those of today, lowered temperatures (by 5°C in the tropical lowlands), and differing precipitation regimes (in some areas higher (e.g. Bolivian Altiplano, Baker et al. 2001), and others lower than present (e.g. lowland Bolivia, Mayle et al. 2000)).

The purpose of this chapter is to describe the vegetation and fire regime of tropical South America at the Last Glacial Maximum and how it differed from that of today. This is done by synthesising previously published fossil pollen and charcoal data, together with vegetation model simulations. We then consider the palaeoecological, palaeoclimatic, and carbon cycling implications of these data-model comparisons, and also explore the limitations to our current understanding of Last Glacial Maximum ecosystems, and potential avenues for overcoming these limitations in the future.

4.2 Methods and Approach

We collated previously published pollen data from sites across tropical South America (above 30°S) (Table 4.1), either by obtaining pollen percentage values from the published paper, or from the pollen data spreadsheet from the site analyst (D. Urrego, Consuelo). We retrieved charcoal data from the publicly available Global Fossil Charcoal Database (GCD v. 1) (Power et al. 2008). We stress that the focus here is on the *global* Last Glacial Maximum, when global ice-volume was at its maximum and global sea-levels and atmospheric CO_2 concentrations were at a minimum (120 m below present and 190–200 ppm, respectively). This time period does not equate with the time of maximum glacial expansion in South America, and in fact approximates the onset of deglaciation in the Andes (Seltzer et al. 2002; Smith et al. 2005; Van der Hammen et al. 1980).

Since most fossil pollen and charcoal records have low temporal resolution through the last glacial period, as a result of low sedimentation rates in most lakes during the Pleistocene, we consider a broad temporal window of 6 ka, centred on the Last Glacial Maximum, i.e. 18–24 cal ka BP. This ensures a sufficiently large number of pollen/charcoal samples to obtain as robust and reliable a reconstruction of Last Glacial Maximum vegetation as possible. To obtain insights into the climatic

Table 4.1 Site metadata

Site name	Latitude	Longitude	Elevation (m)	Country	Ecoregion/Regional veg	Investigator
Last Glacial Maximum charcoal records						
Chaplin	−14.4667	−61.0667	200	Bolivia	Madeira-Tapajos moist forest	Burbridge et al. 2004
Titicaca	−16.1344	−69.1553	3810	Bolivia/Peru	Central Andean wet puna	Baker et al. 2001
Siberia 93–1	−17.83333	−64.718889	2920	Bolivia	Cloud forest, open forest, & Puna	Mourguiart and Ledru 2003
Morro de Itapeva	−22.78333	−45.57333	1850	Brazil	Mixture of grassland, Araucaria forest, and Atlantic rainforest	Behling 1997
Catas Altas	−20.083333	−43.36667	755	Brazil	Semi-deciduous tropical forest	Behling and Lichte 1997
Cambara do Sul	−29.0525	−50.101111	1040	Brazil	Prior to settlement: mosaic of Araucaria forest and grassland	Behling et al. 2004
Sao Francisco de Assis	−29.586667	−55.217222	100	Brazil	Lowland campos or grassland	Behling et al. 2005
Lagoa do Caco	−2.970219	−43.267808	120	Brazil	Restinga, cerrado, rainforest	Ledru et al. 2002
Pata	0.2667	−66.0667	300	Brazil	Negro-Branco moist forests	Bush et al. 2002, 2004b
Last Glacial Maximum pollen records						
Salar de Uyuni	−20	−68	3653	Bolivia	Central Andean wet puna	Chepstow-Lusty et al. 2005
Consuelo	−13.95	−68.983333	1360	Peru	Cloud forest	Urrego et al. 2005
Titicaca	−16.1344	−69.1553	3810	Bolivia/Peru	Central Andean wet puna	Baker et al. 2001
Siberia	−17.83333	−64.718889	2920	Bolivia	Cloud forest, open forest, & Puna	Mourguiart and Ledru 2003
Fuquene-3	5.45	−73.766667	2580	Colombia	Eastern Cordillera moist forest	Van der Hammen and Hooghiemstra 2003
Timbio	2.4	−76.6	1750	Colombia	Cauca Valley montane forests	Wille et al. 2000
Amazon Fan	5.201944	−47.018889	0	N/A	Atlantic Ocean	Haberle and Maslin 1999
Lake Pata	0.2667	−66.0667	300	Brazil	Negro-Branco moist forests	Bush et al. 2002, 2004b
Chaplin	−14.4667	−61.0667	200	Bolivia	Madeira-Tapajos moist forest	Burbridge et al. 2004
El Pinal	4.133333	−70.38333	180	Colombia	Llanos	Behling and Hooghiemstra 1999

Table 4.1 (continued)

Site name	Latitude	Longitude	Elevation (m)	Country	Ecoregion/Regional veg	Investigator
Marine Core GeoB 3104–1	−3.666667	−37.716667	0	N/A	Atlantic Ocean	Behling et al. 2000
Volta Velha	−26.066667	−48.633333	5	Brazil	Serra do Mar coastal forests	Behling and Negrelle 2001
Catas Altas	−20.083333	−43.36667	755	Brazil	Semi-deciduous tropical forest	Behling and Lichte 1997
Morro de Itapeva	−22.78333	−45.57333	1850	Brazil	Mixture of grassland, Araucaria forest, and Atlantic rainforest	Behling 1997
Sao Francisco de Assis	−29.586667	−55.217222	100	Brazil	Lowland campos or grassland	Behling et al. 2005
Dragoa	0.270261	−66.687805	300	Brazil	Negro-Branco moist forests	Bush et al. 2004b
Verde	0.292314	−66.678423	300	Brazil	Negro-Branco moist forests	Bush et al. 2004b
Cambara du Sol	−29.0525	−50.101111	1040	Brazil	Prior to settlement: mosaic of Araucaria forest and grassland	Behling et al. 2004
Lagoa do Caco	−2.970219	−43.267808	120	Brazil	Restinga, cerrado, rainforest	Ledru et al. 2002
Last Glacial Maximum sites with Hiatus						
Salitre	−19	−46.766667	970	Brazil	Cerrado savanna	Ledru et al. 1993
Carajas	−6.5	−49.5	800	Brazil	Mato Grosso seasonal forests	Absy et al. 1991; Sifeddine et al. 1994
Serra Negra	−19	−46.75	1170	Brazil	Cerrado savanna	Oliveira 1992
Aguas Emendadas	−15	−47.58	1040	Brazil	Cerrado savanna	Barberi 1994
Itapeva	−22.78333	−45.57333	1850	Brazil	Mixture of grassland, Araucaria forest, and Atlantic rainforest	Behling 1997
Bella Vista	−13.6167	−61.5500	190	Bolivia	Madeira-Tapajos moist forest	Burbridge et al. 2004; Mayle et al. 2000

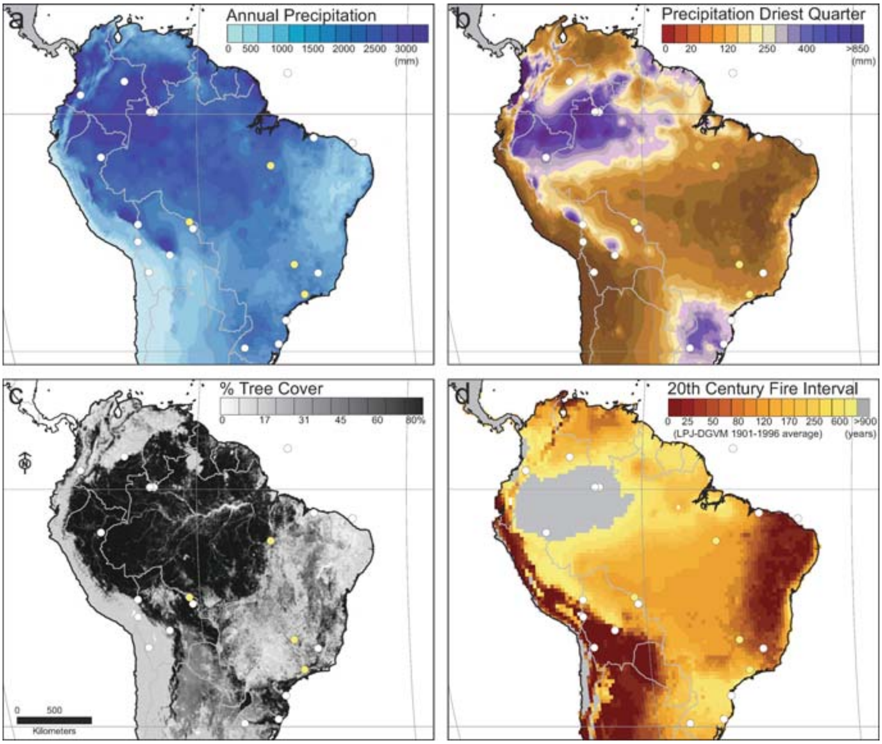

Fig. 4.1 Map showing site locations in relation to present-day rainfall, tree-cover, and fire regime. WorldClim bioclimatic variables (Hijmans et al. 2005) of (**a**) annual precipitation, and (**b**) precipitation of the driest quarter (driest 3 months), characterise present-day climatic variability across the South American tropics. The percent tree cover map (De Fries et al. 2000) (**c**) illustrates the relative forest cover (available biomass). Simulated variations in historical fire-return-intervals using the LPJ-DGVM (Lund–Potsdam–Jena Dynamic Global Vegetation Model) (Thonicke et al. 2001) are shown in panel (**d**). Pollen and charcoal sites are shown by *white circles*. Yellow circles denote sites with a sedimentary hiatus spanning the Last Glacial Maximum

and atmospheric controls upon these Last Glacial Maximum tropical ecosystems, we also consider these empirical data in the light of previously published vegetation model simulations under differing Last Glacial Maximum climatic and CO_2 scenarios.

The locations of the study sites are shown in Figs. 4.1, 4.2, and 4.3, superimposed upon maps of annual and seasonal precipitation (Hijmans et al. 2005), tree cover (De Fries et al. 2000), fire regime (Thonicke et al. 2001), and biomes/ecoregions (Olson et al. 2001), enabling comparisons between modern ecosystems and their environmental setting versus Last Glacial Maximum ecosystem reconstructions. The relative proportions of the most abundant pollen taxa for each site within the 18–24 cal ka BP Last Glacial Maximum window are depicted as colour-coded pie-charts (Fig. 4.2), whilst the inferred Last Glacial Maximum vegetation type is shown

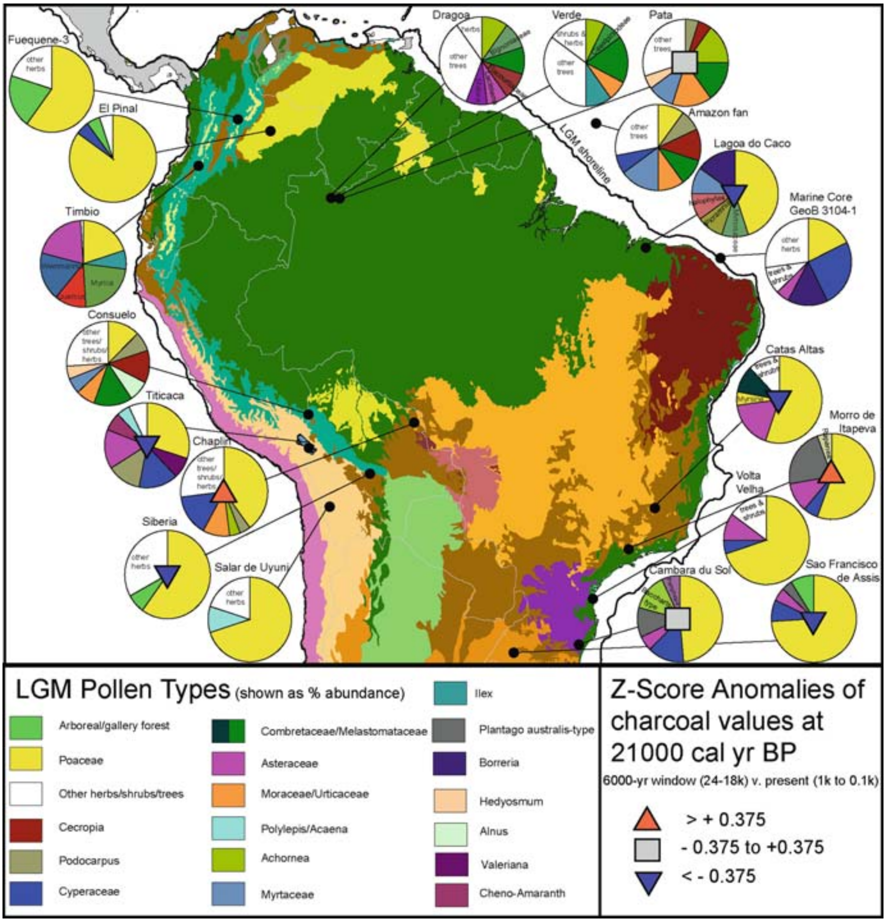

Fig. 4.2 Map showing percentages of most abundant pollen types in Last Glacial Maximum pollen assemblages of sites discussed in the text, depicted as colour-coded pie-charts. Accompanying site meta-data and references are shown in Table 4.1. Last Glacial Maximum charcoal anomalies are shown as *colour-coded triangles* or *squares* in the centre of the pie-charts (see Power et al. 2008 for full details). Last Glacial Maximum pollen and charcoal data are shown in relation to present-day distributions of modern biomes/ecoregions, following Olson et al. (2001), which are colour-coded according to the key in Fig. 4.3. The *black outline* of the map shows the Last Glacial Maximum shoreline of South America, when global sea-level was 120 m below present

as a colour-coded circle at the site location (Fig. 4.3). To obtain an indication of differences in fire regime between the Last Glacial Maximum and present, Z-score charcoal anomalies (showing whether there is more, or less, charcoal in the 24–18 cal ka BP window versus present (1–0.1 cal ka BP)) are depicted as red and blue triangles, respectively, in the centre of the pie-charts, whilst negligible anomalies (or charcoal absence) are shown as grey squares. For full details of how these charcoal anomalies were calculated, see Power et al. (2008).

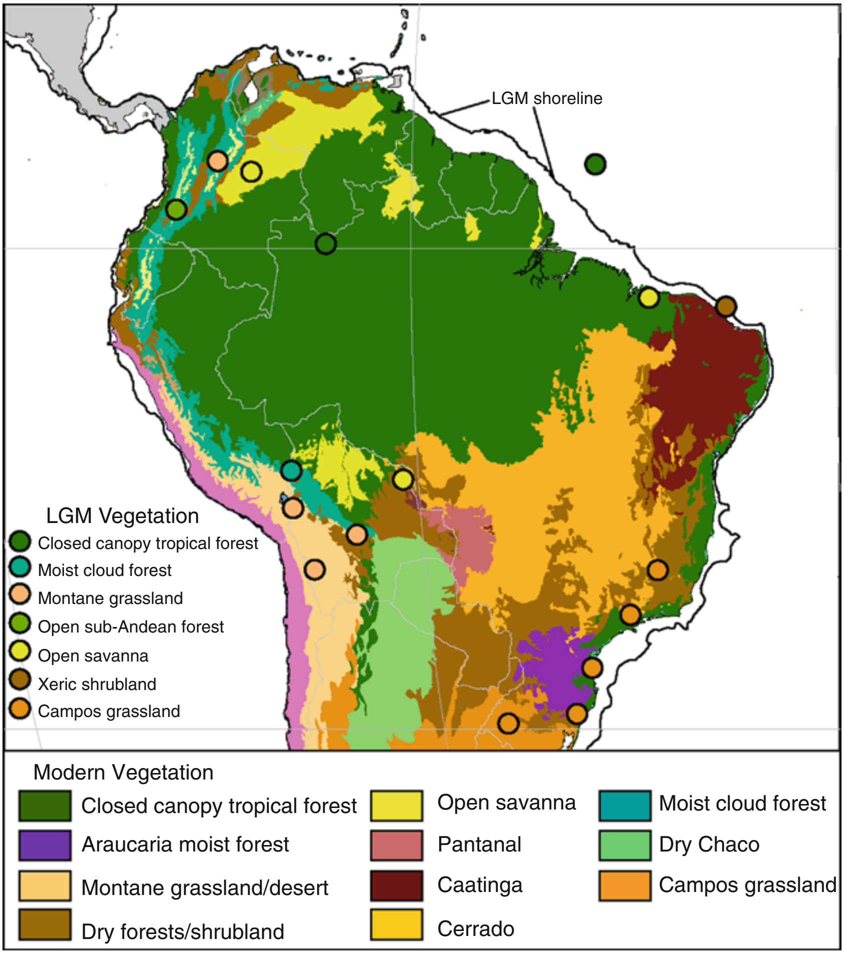

Fig. 4.3 Map showing the pollen-based Last Glacial Maximum vegetation reconstructions for each site, depicted as colour-coded circles at the site locations, in relation to present-day distributions of modern biomes/ecoregions, following Olson et al. (2001). The *black outline* of the map shows the Last Glacial Maximum shoreline of South America, when global sea-level was 120 m below present

4.3 Last Glacial Maximum Pollen-Based Vegetation Reconstructions

Site metadata are shown in Table 4.1, Last Glacial Maximum pollen percentages for each site are shown in Fig. 4.2, and pollen-based Last Glacial Maximum vegetation inferences are shown in Fig. 4.3. Modern ecoregions/biomes are shown in Figs. 4.2 and 4.3.

4.3.1 Andean Records

4.3.1.1 Bolivian Altiplano

The highest elevation pollen sites in the South American tropics are Lake Titicaca and the Salar de Uyuni salt flat in the high Andean Bolivian Altiplano. These sites are well above modern forest-line, surrounded by open, herbaceous puna vegetation. However, surface sample pollen spectra from Titicaca (Paduano et al. 2003) contain a mix of puna, sub-puna, and Andean forest elements, showing that interpretation of pollen records from these sites is complicated by a large wind-blown component of pollen originating from updraft from different vegetation communities of lower elevations of the eastern Andean flank. Other proxy data from both these sites show that Last Glacial Maximum precipitation was greater than present on the Altiplano, causing Titicaca to overflow and turn the Salar de Uyuni into a 130 m deep lake (Baker et al. 2001). The Last Glacial Maximum pollen assemblages (Paduano et al. 2003) are generally similar to those of today (dominated by herbaceous puna elements, especially Poaceae and Cyperaceae), demonstrating that temperatures were too low to support trees. Pollen concentrations of all taxa are extremely low in Last Glacial Maximum assemblages, consistent with an open puna landscape, indicating that occasional increases in *Podocarpus* (40%) and Moraceae (10%) pollen are likely percentage artefacts and due to long-distance dispersal from populations at much lower elevations. However, Chepstow-Lusty et al. (2005) argue that 10% *Polylepis/Acaena* pollen in Last Glacial Maximum sediments of the Salar de Uyuni are indicative of small *P. tarapacana* trees or shrubs growing locally and/or regionally on the Altiplano, rather than long-distance transport from lower elevations. This inference is based on observations of scattered individuals of this tree/shrub (up to 3 m high) growing among the puna on the western slope of Sajama mountain at 4,400 m.

4.3.1.2 Bolivian/Peruvian Cloud Forests

Lake Consuelo and Siberia both occur in the cloud forest on the eastern flank of the Andes, below Titicaca and the Salar de Uyuni, respectively. Siberia is located toward the present upper cloud forest limit, ecotonal with open forest and puna, whilst Consuelo is located toward the present lower cloud forest limit. The modern pollen spectra of Siberia are dominated by arboreal pollen (25–75%), reflecting its cloud forest location (Mourguiart and Ledru 2003). During the Last Glacial Maximum, the low proportion of arboreal pollen at this site (4–10%) and high grass abundance (60%) points to an open herbaceous landscape, with *Alnus* (25%) growing in lower elevation valleys. Although the authors, Mourguiart and Ledru (2003), interpret this open glacial vegetation as indicative of climatic aridity, we agree with Baker et al. (2003) that a more parsimonious explanation is that forest was excluded because of low temperatures, rather than low precipitation. This explanation seems more consistent with well documented high precipitation on the neighbouring Altiplano during the Last Glacial Maximum (Baker et al. 2001) and pollen data from Lake

Consuelo, a lower elevation cloud forest site (Bush et al. 2004a; Urrego et al. 2005). Vegetation modelling studies by Marchant et al. (2002), albeit for the Colombian Andes, corroborate this hypothesis that temperature, rather than precipitation, was the primary control in determining high altitude forest versus grassland.

At Lake Consuelo, the present-day cloud forest is reflected in surface pollen spectra dominated by Moraceae/Urticaceae, *Acalypha*, *Alchornea*, *Celtis*, *Trema*, and *Cecropia*. Although Last Glacial Maximum pollen assemblages also contain these taxa, they differ crucially in the additional presence of higher altitude Andean taxa such as *Alnus, Bocconia, Hedyosmum,* and *Podocarpus*, forming a unique Last Glacial Maximum forest community without modern analogue. Using purpose-designed temperature transfer functions for modern distributional ranges derived from herbarium collections, Bush et al. (2004a) showed that this non-analogue forest assemblage signifies a humid climate that was 5–9°C cooler than present during the Last Glacial Maximum. Furthermore, this pollen record is consistent, not only with evidence from Titicaca and the Salar de Uyuni, but also other glaciological records from the Andes (Seltzer et al. 2002; Smith et al. 2005) which show that the Last Glacial Maximum in tropical South America marks the end of the last glacial stage, with rising temperatures commencing 22 cal ka BP. This transition is marked by the loss of the high-Andean taxa from the Consuelo pollen record.

4.3.1.3 Colombian Montane Forests

The two Colombian sites, Timbio and Fuquene-3, are located in the lower montane and upper montane Andean forest zones, respectively, although the catchments of both sites have long been deforested over recent centuries (Fuquene) and millennia (Timbio). Furthermore, much of the Holocene pollen record of Timbio is missing, making comparisons between Last Glacial Maximum and “natural” vegetation under present climatic conditions problematic for this site. Last Glacial Maximum pollen assemblages at Timbio are dominated by *Ilex*, *Myrica*, *Quercus*, *Weinmannia*, Poaceae, and Asteraceae, pointing to a diverse and open forest with tree species that are today typical of Upper sub-Andean forests. The authors (Wille et al. 2000) argue that the relatively open character of these forests (Poaceae 20%, Asteraceae 20%), together with peaks in *Quercus* and low values of *Podocarpus* pollen, point to relatively dry conditions, whilst presence of taxa such as *Bocconia*, which are today confined to the upper forest limit, are indicative of Last Glacial Maximum temperatures significantly less than present.

The complete Holocene record at Fuquene-3, and its shorter history of human impact, allows for clearer Last Glacial Maximum versus modern vegetation comparisons than at Timbio. Last Glacial Maximum pollen assemblages at Fuquene-3 are characterised by high Poaceae abundance relative to the arboreal taxa *Polylepis/Acaena*, *Alnus*, *Quercus*, and *Weinmannia*, indicative of grass-paramo, especially the peaks in characteristic herbs such as Cruciferae, Caryophyllaceae, and *Jamesonia*. The authors, van der Hammen and Hooghiemstra (2003), infer from these pollen data that the upper forest line was located at ca. 2000 m elevation during the Last Glacial Maximum (ca. 580 m below the lake), signifying a temperature depression of 7–8°C at the site compared with present. Furthermore, peak abundance of aquatic taxa (e.g. Cyperaceae, *Myriophyllum*, *Ludwigia*) are suggestive of lower lake-levels, and hence drier conditions, compared with present (Van der Hammen and Hooghiemstra 2003).

4.3.2 Lowland Records

4.3.2.1 Amazon Rainforests

Laguna Chaplin (Mayle et al. 2000; Burbridge et al. 2004) and the "Hill of Six Lakes" (Bush et al. 2004b) are the only two localities within the present-day lowland humid evergreen Amazonian forests that have records which span the Last Glacial Maximum. Carajas (Absy et al. 1991) and Bella Vista (Burbridge et al. 2004) also have Amazonian Pleistocene records but have major sedimentary hiatuses spanning the Last Glacial Maximum (Table 4.1).

The three closely neighbouring sites atop the Hill of Six Lakes (Pata, Dragao, and Verde) have Last Glacial Maximum pollen assemblages dominated by forest taxa, with a mix of lowland Amazonian (e.g. *Alchornea*, Combretaceae/Melastomataceae, Moraceae/Urticaceae, Myrtaceae, Caesalpinioideae, Bignoniaceae) and Andean (e.g. *Podocarpus*, *Ilex*, *Weinmannia*) elements. Negligible percentages of herb pollen (< 5% Poaceae) shows that these forests must have had closed canopies. This mix of lowland Amazonian and Andean tree taxa shows that these Last Glacial Maximum forests were without modern analogue and suggests that temperatures were ca. 5ºC below present (Colinvaux et al. 1996). Publication of these Last Glacial Maximum pollen data from Pata over a decade ago (Colinvaux et al. 1996) provided the first convincing evidence to challenge the then widely accepted glacial rainforest refugium hypothesis (Haffer 1969; Haffer and Prance 2001) which proposed that Amazonia was dominated by savanna, instead of forest, during the Last Glacial Maximum under an arid climate. However, Colinvaux himself acknowledged that data from a single locality in an area the size of Europe by no means constituted a sufficiently rigorous test of this refugium hypothesis.

Three years later Haberle and Maslin (1999) published a 40,000-yr Pleistocene history of Amazonian vegetation from a fossil pollen record taken from the Amazon Fan core ODP-932. The Last Glacial Maximum pollen assemblage from this off-shore core is remarkably similar to that of Pata, dominated by a mixture of lowland and Andean forest taxa, indicative of a colder Last Glacial Maximum climate in the lowland basin than present. Since the Amazon Fan collects sediment from the entire Amazon basin, this core potentially provides a much more rigorous test of Haffer's refugium hypothesis. Notwithstanding the peaks in Andean taxa (e.g. *Podocarpus*), the Last Glacial Maximum Fan pollen assemblage is remarkably similar to that of modern samples taken throughout the length of the Amazon river, leading Haberle and Maslin (1999) to infer that the spatial extent of Amazon forest at the Last Glacial Maximum was similar to present and that Haffer's rainforest refugium hypothesis must therefore be unsupported. These results from ODP-932 are corroborated by pollen data from three other Amazon Fan cores (ODP-940A, 944A, and 946A) which also show little palynological difference between glacial and interglacial sediments (Hoorn 1997).

It is clear though, that rainforest cover was at least slightly reduced at the Last Glacial Maximum compared with present, at least at the southern rainforest-savanna ecotone of the basin, as revealed by pollen data from Laguna Chaplin in NE Bolivia (Mayle et al. 2000; Burbridge et al. 2004). This site is presently surrounded by largely undisturbed humid evergreen rainforest, but only 30 km from the ecotone with semi-deciduous dry forests and savannas to the south. Modern surface pollen spectra are characterised by 45% Moraceae and only 3% Poaceae and 6% Cyperaceae, whereas Last Glacial Maximum sediments are dominated by 40% Poaceae, 15% Cyperaceae, and only 10% Moraceae, consistent with open herbaceous savanna. Punyasena et al. (2008) applied a newly developed climate-vegetation model (based on the modern abundance distributions of 154 Neotropical plant families, Punyasena 2008) to the Chaplin and Bella Vista pollen datasets. Their model results strengthen the earlier qualitative climate reconstructions by Mayle et al. (2000), showing that this Last Glacial Maximum savanna community of NE Bolivia was a function of both lower precipitation and lower temperatures, compared with present.

Although there are no pollen data to support a savanna-dominated Amazon basin during the Last Glacial Maximum (or any other period during the Quaternary), the paucity of Last Glacial Maximum records, combined with uncertainty over the palaeoecological significance of these few records, means that our knowledge of Amazonia's ecosystems during the Last Glacial Maximum remains extremely imprecise and a topic of continued debate and speculation. For example, Pennington et al. (2000) cogently argued that Last Glacial Maximum pollen spectra from Pata, interpreted by Colinvaux et al. (2000) and Bush et al. (2004b) as a rainforest signal, albeit with Andean elements, could equally well be interpreted as a predominantly semi-deciduous dry forest signal owing to the fact that most dry forest families are a subset of rainforest families and because most pollen types cannot be identified to species level, thus frustrating attempts to distinguish these ecosystems. The fact that semi-deciduous dry forests grow under similarly dry and seasonal climates as Brazilian *cerrado* savannas means that distinguishing between these two types of tropical forest has important palaeoclimatic (Mayle 2004, 2006; Mayle et al. 2004) implications for Amazonia at the Last Glacial Maximum. Also, the markedly different carbon storage values between rainforest (320 tons C ha^{-1}) and dry forest (260 tons C ha^{-1}) (Adams and Faure 1998) means that determining which of these two forest types dominated the Amazon basin would shed light on the magnitude of its carbon store, with implications for understanding global carbon cycling at the Last Glacial Maximum (Mayle and Beerling 2004; Beerling and Mayle 2006).

Furthermore, the palaeoecological significance of the Amazon Fan pollen record is also controversial, with some (e.g. H. Hooghiemstra, personal communication 2003; Berrio et al. 2000), arguing that rather than reflecting basin-wide vegetation, it may instead be a riparian signal of seasonally-flooded *varzea/igapo* forest lining the Amazonian rivers. If true, the Last Glacial Maximum pollen assemblage from the

Fan would reveal little about the vegetation occupying *terra firme* areas beyond the ribbon of forest lining the rivers, and therefore unsuitable for testing the rainforest refugium hypothesis. Fortunately, recent studies of pollen rain signatures of different kinds of rainforest and dry forest (Gosling et al. 2009, Burn 2008) and advances in Amazon pollen taxonomy have the potential to resolve these uncertainties of interpretation of fossil pollen assemblages. In particular, Burn and Mayle (2008) have shown that, not only can Moraceae and Urticaceae families be palynologically differentiated from one another, but the key tropical forest family Moraceae can also be palynologically separated into its constituent genera, providing the potential for distinguishing between riparian, seasonally flooded evergreen forest versus *terra firme* evergreen forests beyond the rivers.

4.3.2.2 Savanna/Woodland/Thorn-Scrub

El Pinal, Caco, and Marine core GeoB 3104-1 presently have catchments within highly seasonal, dry vegetation types beyond the limits of humid Amazonian forests. Laguna El Pinal (Behling and Hooghiemstra 1999) is located in the centre of the open, grass-dominated *Llanos Orientales* savannas of Colombia, where trees (predominantly *Mauritia* palm) are largely restricted to the lake shore and gallery forests lining rivers. Surface pollen spectra of this site are therefore dominated by Poaceae (65%) and Cyperaceae (12%), gallery forest taxa accounting for only 17% of the pollen sum. During the Last Glacial Maximum the *Llanos* was even more open than today (Poaceae 85%, Cyperaceae 5%, gallery forest 5%), indicative of a drier climate than present.

Lagoa do Caco (Ledru et al. 2002) is located just beyond the present eastern limit of Amazon rainforest, surrounded by an ecotonal mix of *restinga* (coastal steppe vegetation), *cerrado* (woody savanna), and gallery (riparian) forest. The open character of this vegetation is reflected in the high percentages of herbaceous pollen in the surface sample (*Borreria* 5%, Poaceae 30%, halophytes 2%). During the Last Glacial Maximum, vegetation was even more open (*Borreria* 15%, Poaceae 45%, halophytes 10%), pointing to drier conditions than present.

Last Glacial Maximum pollen assemblages from marine core GeoB 3104-1, dominated by the herbs Poaceae, Cyperaceae, *Borreria*, and Asteraceae (Behling et al. 2000), are similar to those from modern surface samples collected from rivers, lakes, and soils across the *caatinga* thorn-scrub dominated landscape of NE Brazil, demonstrating that this xeric vegetation, and its arid climate, also predominated during the Last Glacial Maximum.

4.3.2.3 Atlantic Forests and Campos Grasslands of SE Brazil

Behling and his collaborators have produced pollen-based Quaternary vegetation histories of numerous sites from a range of ecosystems and altitudes across SE Brazil – Volta Velha (Behling and Negrelle 2001): Atlantic evergreen rainforest, 5 m elevation; Catas Altas (Behling and Lichte 1997): semi-deciduous dry forest, 755 m elevation; Morro de Itapeva (Behling 1997): ecotone between cloud forest, rainforest, dry forest, and *Araucaria forest*, 1850 m elevation; Sao Francisco de Assis (Behling et al. 2005): lowland grassland *Campos*, with riverine gallery forest, 100 m elevation; Cambara do Sul (Behling et al. 2004): *Araucaria* forest with patches of *Campos* grassland, 1040 m elevation.

What is particularly interesting about these pollen records is that, despite the diversity of ecosystems that these sites encompass today (rainforest, dry forest, *Araucaria* forest, grassland *Campos*), they all have Last Glacial Maximum pollen assemblages dominated by herbs (especially Poaceae), indicative of open, high-elevation *Campos* grasslands, which are today restricted, either to elevations over 1000 m, or high latitudes (> 27–28°S). This has led Behling to infer that Last Glacial Maximum temperatures were ca. 5–7°C colder than present, whilst peaks in *Eryngium* at Morro de Itapeva and Cambara do Sul are suggestive of drier conditions too.

4.4 Model Simulations of Last Glacial Maximum Vegetation

Our review of previously published Last Glacial Maximum pollen data shows that our knowledge of Last Glacial Maximum vegetation types, distribution, structure, carbon storage, and species composition, across tropical South America remains poorly understood, especially for Amazonia. This arises from the extreme paucity of Last Glacial Maximum pollen records, limitations of pollen taxonomy, and poor knowledge of modern pollen-vegetation relations. Use of vegetation models, forced by Last Glacial Maximum climatic and CO_2 conditions, has the potential to address several of these unresolved issues, and crucially, explore the underlying climatic controls and relative influences of climate versus CO_2.

4.4.1 Colombia

Marchant et al. (2002, 2004, 2006) used the BIOME-3 global vegetation model, developed by Haxeltine and Prentice (1996), to better understand how Colombian Andean and lowland ecosystems responded to glacial-interglacial temperature, precipitation, and atmospheric CO_2 changes. BIOME-3 is a biogeography-based model that predicts the dominance of different plant functional types (PFTs) based on ecophysiological constraints, resource availability, and competition (VEMAP members 1995). Their model outputs were in broad agreement with both the present-day ecoregion maps (Olson et al. 2001, Figs. 4.2 and 4.3) and the Last Glacial Maximum fossil pollen data, although the lowland *llanos* savannas (El Pinal), with their particular edaphic and hydrological conditions, were less accurately simulated (Marchant et al. 2002).

Temperature reduction was found to be the key driver for Last Glacial Maximum grassland expansion in the Bogota basin of the high Andes (2,550 m), whilst Last Glacial Maximum precipitation reduction was largely responsible for expansion of C_4 grasses in the lowland savannas/xeric woodlands (Marchant et al. 2004).

Marchant et al. (2002) examined the interactive effects of climate and CO_2 changes in the Bogota basin, with CO_2, temperature, and precipitation varying between 290–170 ppmV, 4–13°C, and 150–750 mm pa, respectively (these values were chosen to capture the full glacial-interglacial range). Unsurprisingly, low glacial CO_2 values (200 ppm), in combination with low precipitation, caused expansion of C_4 savanna grasses in the lowland savannas, as they would have had a competitive advantage over C_3 trees and shrubs in drought-stressed environments due to their greater water-use-efficiency (Farquhar 1997). However, Marchant et al. (2002) found that high altitude vegetation (as simulated by the BIOME-3 model) was not only affected by temperature reduction, but also CO_2 reduction, with a strong inter-dependence between these two variables. Once temperatures are reduced by at least 5ºC, and atmospheric CO_2 concentrations fall to below 225 ppmV, there is an abrupt biome shift in the Bogota basin from cool evergreen forest to cool grass/shrubland.

These model results are consistent with n-alkane δ^{13} C data from lacustrine sediments, not only from the Bogota basin (Boom et al. 2002), but also Mt. Kenya in Africa (Street-Perrott et al. 1997). These simulations suggest that the climatic and CO_2 conditions of the Last Glacial Maximum caused expansion of both high- and low-altitude grasslands, thereby compressing the altitudinal range of montane forests. Interestingly, the model suggests that these montane forests were largely semi-deciduous dry forests (akin to the xeric woodland scrub biome), a forest type which today has a highly scattered, disjunct distribution within isolated inter-Andean dry valleys (Prado and Gibbs 1993). These simulations therefore support the “Pleistocene Dry Forest Arc” hypothesis proposed by Prado and Gibbs (1993) and Pennington et al. (2000) which states that present-day pockets of montane dry forest constitute Holocene refugia, or remnants, of a more extensive and contiguous Andean dry forest distribution during the Last Glacial Maximum (Note though, that Mayle (2004, 2006) questions the validity of this hypothesis with respect to lowland dry forest biogeographic history in South America).

It is important to note, however, that the wettest, non-seasonal areas of the Colombian lowlands (e.g. Quibdo) remain unchanged as evergreen rainforest with this model, even under maximum temperature, precipitation, and CO_2 reductions (Marchant et al. 2004).

4.4.2 Amazon Basin

Beerling and Mayle (2006) used the University of Sheffield Dynamic Global Vegetation Model (SDGVM) to investigate the separate and interactive effects of climate versus CO_2 upon different parameters of Amazonian ecosystems (vegetation biomass, soil carbon storage, and biome type) between the Last Glacial Maximum and present day (pre-industrial). Model experiments were performed with an annual resolution, to allow the ecosystems within the Amazon Basin to continuously evolve from their initial equilibrium glacial state forwards in time to the present-day, and at a fine spatial scale (1° lat. × 1° lon.) to capture range shifts in forest distributions. Three transient 21 ka model experiments were performed, designed to assess the separate and interactive effects of changes in climate and CO_2 since the Last Glacial Maximum on Amazonian ecosystems: (i) changing CO_2 and climate (CT), (ii) changing CO_2 and constant pre-industrial climate (C), and (iii) changing climate and a constant pre-industrial CO_2 concentration (T). Their procedure gave a Basin-wide Last Glacial Maximum mean annual temperature decrease of 3–4°C below present and mean annual precipitation reduction of 20% below present, in broad agreement with fossil pollen and other palaeoclimate proxy data. Last Glacial Maximum-present CO_2 changes were obtained from Antarctic ice-core measurements by Indermühle et al. (1999) and Monnin et al. (2001). For full details of the approach see Beerling and Mayle (2006).

The climate and CO_2 experiment simulated dry forest/savanna cover at the Last Glacial Maximum to be 67% greater than today, whilst evergreen rainforest area was 14% below present. The near identical trends in forest cover in experiments CT and T, and contrasting trends in experiment C, indicate that broad-scale changes in lowland Amazonian vegetation distribution between the Last Glacial Maximum and present were primarily driven by climate. Reduced precipitation at the Last Glacial Maximum favoured expansion of the more drought-tolerant deciduous forests/savannas by increasing soil moisture deficits during a longer, more severe dry season (Beerling and Woodward 2001). The geographic patterns of these Last Glacial Maximum versus modern ecosystem changes (Fig. 4.4) match well with the fossil pollen data (Fig. 4.3); i.e. expansion of dry forests/savannas versus

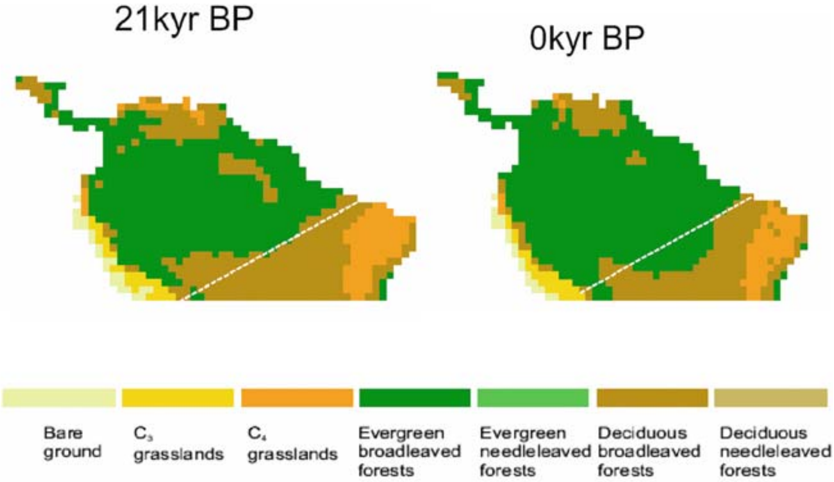

Fig. 4.4 Geographic distributions of Amazonian ecosystems simulated for the Last Glacial Maximum and pre-industrial (present day) using the University of Sheffield Dynamic Global Vegetation model as described in the text. Amazonia is defined as the area north of the diagonal line. Modified from Beerling and Mayle (2006)

evergreen rainforest in ecotonal areas (e.g. Chaplin) compared with present. The dominance of evergreen rain forest throughout most of the Amazon Basin at the Last Glacial Maximum (Fig. 4.4) is also consistent with the "Hill of Six Lakes" (Colinvaux et al. 1996; Bush et al. 2004b) and Amazon Fan (Haberle and Maslin 1999) pollen data (Fig. 4.3). These model simulations therefore do not support the rainforest refugia hypothesis of Haffer (1969) and Haffer and Prance (2001), and also suggest that the dry forest/savanna expansion in the "Dry Corridor" of eastern Amazonia (Fig. 4.4) was insufficient to divide the rain forest into two disjunct areas, as proposed by Bush (1994). These results suggest that a 20% reduction in mean annual precipitation would have been insufficient to disrupt rain forest cover, except in the most seasonal, ecotonal areas, especially since any soil moisture deficits would have been partially offset by reduced evapo-transpiration under a cooler climate.

These process-based vegetation simulations by Beerling and Mayle (2006) suggest that, in contrast to the rather minor climate-driven shifts in ecosystem geographic distribution between the Last Glacial Maximum and present, the low Last Glacial Maximum CO_2 concentrations (180 ppm versus pre-industrial 280 ppm) resulted in Amazonia's total above-ground carbon storage to be only half its pre-industrial value. This 50% reduction in carbon storage relative to present can be attributed to carbon limitation producing rainforests with markedly lower canopy densities and simpler structures than those of today (Fig. 4.5). Rainforest leaf area index (LAI) at the Last Glacial Maximum is simulated to be only 76% of its present-day value (5.25 versus 6.9, respectively). These results are in general

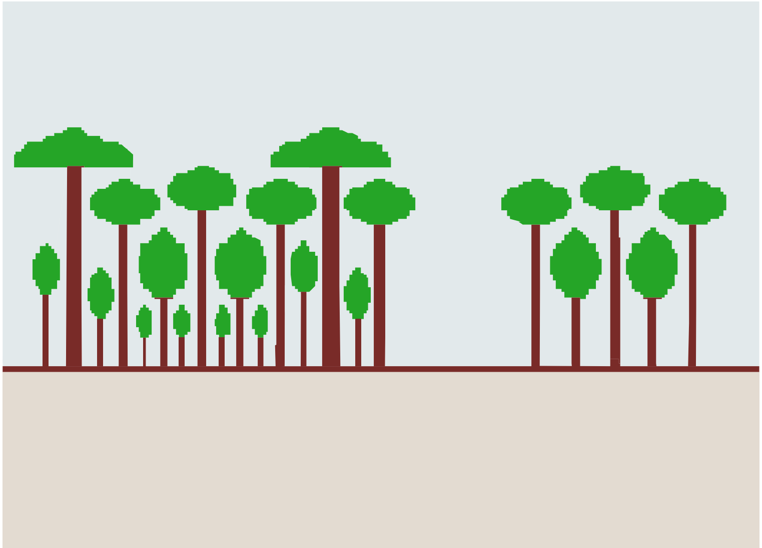

Fig. 4.5 Cartoon depicting hypothetical change in Amazon forest structure (*left*: present-day forests; *right*: Last Glacial Maximum forests). Modified from Cowling (2004)

agreement with those of Cowling (2004) and Cowling et al. (2001, 2004), who also showed that atmospheric CO_2 concentrations were more important than precipitation levels in controlling canopy density (i.e. vegetation structure). For a decrease in 20% precipitation alone, Cowling et al. (2001) simulated an 11% decrease in Basin-average LAI, whereas Last Glacial Maximum CO_2 concentrations alone caused a 34% reduction in LAI. These authors also argue that glacial cooling was likely the key factor responsible for maintaining Last Glacial Maximum Amazon forest cover via its effects in reducing photorespiration and evapotranspiration, which together improve plant carbon and water relations. Cowling et al. (2001) noted that, although their modelling studies simulated a largely forested Amazon basin (consistent with Beerling and Mayle 2006), there was considerable spatial heterogeneity in LAI (forest canopy density) across the basin, leading them to propose an interesting alternative to Haffer's rainforest refugium hypothesis as a mechanism of speciation. Instead of Haffer's model of allopatric speciation via fragmented rainforest populations isolated by open savannas (Haffer 1969), Cowling et al. offer the novel idea that these geographic variations in canopy density (Fig. 4.5) (and hence forest structure and productivity) could potentially have been sufficient to promote neotropical vicariance and thus allopatric speciation if gene pools were isolated. Increasing evidence for sympatric speciation over recent years among different organisms (e.g. Smith et al. 1997) raises the possibility that even if gene pools were not fragmented, environmental gradients associated with differences in forest structure may have been sufficient to promote sympatric speciation.

4.5 Last Glacial Maximum Fires

Although there are relatively few charcoal records for the Last Glacial Maximum (18–24 cal ka BP), most records show a pattern of less-than-present fire. Of the nine Last Glacial Maximum records (18–24 cal ka BP window) where charcoal has been searched for (Fig. 4.2), two sites are either devoid of charcoal or have negligible anomalies, five have significant negative anomalies (i.e. Z-score anomaly <–0.375 versus "present" (1–0.1 cal ka BP)), and two have positive anomalies (Z-score anomaly >+0.375 versus "present"), suggesting greater-than-present fire activity. The positive Last Glacial Maximum charcoal anomalies are unsurprising when one considers the contrasting vegetation at these sites between the Last Glacial Maximum and present. Morro de Itapeva is today surrounded by poorly flammable humid cloud forest, rainforest, and *Araucaria* forest (Figs. 4.2and 4.3), but at the Last Glacial Maximum was surrounded by grassland *Campos* (Fig. 4.3) which would be expected to have a higher fire frequency than the present-day humid forests (notwithstanding the cooler Last Glacial Maximum climate, see below). Likewise, Chaplin is today surrounded by humid evergreen rainforest, which is much less flammable than the open savannas which dominated this site's catchment during the Last Glacial Maximum.

The reduction in fire activity during the Last Glacial Maximum at several other sites can be explained in terms of the differences between modern and Last Glacial

Maximum vegetation and climate linkages. At Catas Altas, one might expect that the Last Glacial Maximum grasslands would have higher fire frequencies than the modern semi-deciduous forests, although grasslands have less fuel (and hence less potential for producing charcoal) than flammable dry forests. An overall reduction in biomass from lower CO_2 and the cooler Last Glacial Maximum climate would have limited fires. Sao Francisco de Assis, Caco, and Titicaca all have similar vegetation types (open and herbaceous) at the Last Glacial Maximum and present-day (Fig. 4.3), suggesting that the reduction in fires during the Last Glacial Maximum is likely a result of the colder than present Last Glacial Maximum climate (at least 5°C less than present). The absence of charcoal from Pata lake samples is consistent with the continued presence of humid rainforest during the Last Glacial Maximum and today. At Cambara do Sul, both the cool Last Glacial Maximum grasslands and cool, humid *Araucaria* forests produced little charcoal, suggesting similar-to-present fire activity.

4.6 Implications and Conclusions

Figure 4.3 shows the reconstructed Last Glacial Maximum vegetation for each pollen site mapped onto the distribution of present-day biomes/ecoregions, illustrating any differences/similarities between Last Glacial Maximum and modern (pre-clearance) vegetation types and their distribution. Although the paucity of sites does not allow for a detailed Last Glacial Maximum vegetation map to be drawn (hence we have not tried to do so!), some interesting conclusions can be made.

4.6.1 Last Glacial Maximum Climate

Despite the much wetter climate of the Altiplano compared with today (Baker et al. 2001), its vegetation during the Last Glacial Maximum was broadly similar to today's (an open herbaceous montane grassland or puna), indicating that temperatures were too low to support trees (e.g. Paduano et al. 2003). Cloud forests below the Altiplano descended downslope (Siberia et al. 2003; Baker et al. 2003) to form non-analogue mixtures of high Andean taxa and cloud forest taxa, demonstrating that temperatures must have been 5–9°C cooler than present (Bush et al. 2004a; Urrego et al. 2005), although precipitation must have been sufficiently high to support cloud forest taxa. A similar temperature depression is evident from the upper montane Colombian forest site, Fuquene-3, inferred from the downslope movement of grass-paramo to occupy the lake catchment during the Last Glacial Maximum (Van der Hammen and Hooghiemstra 2003).

Evidence that the lowland tropics also experienced a temperature reduction of at least 5°C during the Last Glacial Maximum comes from the mixture of Andean and lowland rainforest taxa at the Hill of Six Lakes (Bush et al. 2004b) and Amazon Fan (Haberle and Maslin 1999) sites, as well as presence of open tree-less grassland in areas of SE Brazil currently occupied by a mix of different types of tropical forests (e.g. Volta Velha, Behling and Negrelle 2001).

Although the Altiplano was significantly wetter than present during the Last Glacial Maximum (Baker et al. 2001), there was greater extent of savannas at the southern lowland Amazon margin (Chaplin, Mayle et al. 2000) and reduction in gallery forests in the Colombian *Llanos* (El Pinal, Behling and Hooghiemstra 1999) signifying reduced precipitation in the lowland tropics compared with present. Strong independent evidence for reduced Last Glacial Maximum precipitation throughout much of the lowland tropics comes from multi-millennial sedimentary hiatuses spanning the Last Glacial Maximum (Ledru et al. 1998) at six sites (Table 4.1). However, the Hill of Six Lakes (Pata, Dragao, and Verde), Amazon Fan, and vegetation modelling simulations together suggest that rainfall remained sufficiently high (under the cooler-than-present Last Glacial Maximum climate) to maintain closed-canopy forest and low fire activity across the Amazon basin. In fact, model simulations by Beerling and Mayle (2006) and Cowling et al. (2001) suggest that the low CO_2 concentrations at the time had a greater impact upon forests than lowered rainfall, through carbon limitation reducing LAI and resulting in forests with simpler structure and lower biomass than those of today.

Simulation of Colombian ecosystems using the BIOME-3 vegetation model (e.g. Marchant et al. 2002) reveals that high and low altitude ecosystems were controlled by differing climatic variables at the Last Glacial Maximum, with temperature being the key control on montane ecosystems, and precipitation the key driver in the lowlands. Furthermore, these authors show that low CO_2 concentrations not only favoured C_4 grass expansion in water-stressed lowland ecosystems (through their greater water-use-efficiency than C_3 trees/shrubs), but also in the high Andes.

4.6.2 Biogeography, Biodiversity, and Carbon Cycling

Considering tropical South America as a whole, the model simulations and fossil pollen data suggest that biome shifts between forest and grassland/savanna between the Last Glacial Maximum and present were not substantial. Biome shifts were largely restricted to ecotonal areas – depression of the Andean tree-line and encroachment of savanna into lowland rainforest. The exception, however, appears to be the Atlantic forests of SE Brazil, where, irrespective of the type of forest surrounding the site today (Table 4.1), all sites within the region are dominated by open *Campos* grasslands at the Last Glacial Maximum (Fig. 4.3), indicating substantial reduction in forest area. This expansion of grassland in SE Brazil points to a 5–7°C lowering of temperatures (Behling 1997), whilst taxa such as *Eryngium* indicate drier conditions. Today, these Atlantic forests receive most of their precipitation from the nearby Atlantic Ocean, but this moisture source would have been reduced during the Last Glacial Maximum due to reduced evaporation associated with lower tropical Atlantic sea-surface-temperatures (Guilderson et al. 1994; Pflaumann et al. 2003), which would account for the cold- and drought-tolerant glacial grasslands. Moreover, these sites were much further inland at the Last Glacial Maximum due to the 120 m lowering of sea-level (Fig. 4.3), which would perhaps have exacerbated this precipitation reduction.

Given the size of Amazonia's carbon store (10% of global terrestrial carbon stock), its wealth of biodiversity (possibly one third of global biodiversity), and hydrological importance for regional and global climates (Malhi and Phillips 2004), the nature of its ecosystems during the Last Glacial Maximum have naturally been the subject of intense interest and debate. Last Glacial Maximum pollen records from the centre and margin of the basin and the Amazon Fan, considered together with vegetation model simulations, suggest that Amazonia remained largely forested at the Last Glacial Maximum, contradicting the rainforest refugia hypothesis which argues for a savanna-dominated basin with rainforests restricted to isolated refugia (e.g. Haffer 1969; Haffer and Prance 2001). However, these studies suggest that Amazonia's forests have been far from static. The cyclic re-assortment of Andean and lowland species (Colinvaux et al. 1996; Bush et al. 2004b), combined with changes in forest structure and canopy density (Cowling et al. 2001), over glacial-interglacial cycles in response to temperature, precipitation and CO_2 changes, means that there would have been great opportunity for population fragmentation and allopatric speciation, which did not require large-scale biome shifts.

In terms of carbon cycling, a key finding of a dynamic vegetation model is that Amazonia remained covered by rainforest at the Last Glacial Maximum but with only half the present-day carbon store (due to reduced canopy density and biomass) (Beerling and Mayle 2006), although we acknowledge that the ability of the model to accurately differentiate between evergreen humid rainforest versus semi-deciduous dry forest is open to question. The model experiments by these authors also show that climate and CO_2 likely had quite distinct and separate effects on tropical ecosystems – Last Glacial Maximum-modern climate change driving biome replacements in ecotonal areas, and CO_2 driving changes in biomass per unit area, irrespective of the vegetation type.

Despite the insights into Last Glacial Maximum ecosystems from these data-model comparisons, large gaps in knowledge remain. Given the diversity of rainforest ecosystems (Olson et al. 2001) and heterogeneity of climatic regimes across Amazonia today (Fig. 4.1), similar, or perhaps greater heterogeneity likely occurred at the Last Glacial Maximum. Consequently, the two Last Glacial Maximum sites currently available from within the Amazon rainforest biome today are insufficient to draw a basin-wide vegetation reconstruction. This is compounded by questions over the interpretation of Last Glacial Maximum pollen assemblages – e.g. evergreen rainforest versus semi-deciduous dry forest (Pennington et al. 2000, with respect to Pata) and regional "terra firme" versus riparian seasonally-flooded rainforest (Burn and Mayle 2008, with respect to the Amazon Fan). Although new pollen rain data and pollen taxonomic advances (Burn 2008; Burn and Mayle 2008) have the potential to resolve some of these issues, the biggest problem is the paucity of Last Glacial Maximum records in the Amazon, due to the river-dominated landscape and predominance of young ox-bow lakes. Perhaps greatest research efforts, with respect to the Last Glacial Maximum environment of Amazonia at least, should therefore be directed to improving the quality of fully coupled vegetation-climate model simulations.

Acknowledgments We thank Francoise Vimeux and Florence Sylvestre for kindly inviting us to write this chapter, as well as the authors of all the records discussed here, whose research made this chapter possible. We also thank the two referees for their comments and suggestions which improved the paper.

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