

Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum

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The aims of this paper are to review previously published palaeovegetation and independent palaeoclimatic datasets together with new results we present from dynamic vegetation model simulations and modern pollen rain studies to: (i) determine the responses of Amazonian ecosystems to changes in temperature, precipitation and atmospheric CO₂ concentrations that occurred since the last glacial maximum (LGM), *ca.* 21 000 years ago; and (ii) use this long-term perspective to predict the likely vegetation responses to future climate change. Amazonia remained predominantly forested at the LGM, although the combination of reduced temperatures, precipitation and atmospheric CO₂ concentrations resulted in forests structurally and floristically quite different from those of today. Cold-adapted Andean taxa mixed with rainforest taxa in central areas, while dry forest species and lianas probably became important in the more seasonal southern Amazon forests and savannahs expanded at forest–savannah ecotones. Net primary productivity (NPP) and canopy density were significantly lower than today. Evergreen rainforest distribution and NPP increased during the glacial–Holocene transition owing to ameliorating climatic and CO₂ conditions. However, reduced precipitation in the Early–Mid-Holocene (*ca.* 8000–3600 years ago) caused widespread, frequent fires in seasonal southern Amazonia, causing increased abundance of drought-tolerant dry forest taxa and savannahs in ecotonal areas. Rainforests expanded once more in the Late Holocene owing to increased precipitation caused by greater austral summer insolation, although some of this forest expansion (e.g. in parts of the Bolivian Beni) is clearly caused by palaeo Indian landscape modification. The plant communities that existed during the Early–Mid-Holocene may provide insights into the kinds of vegetation response expected from similar increases in temperature and aridity predicted for the twenty-first century. We infer that ecotonal areas near the margins of the Amazon Basin are liable to be most sensitive to future environmental change and should therefore be targeted with conservation strategies that allow ‘natural’ species movements and plant community re-assortments to occur.

Keywords: Amazon tropical forest; palaeoclimate; carbon dioxide; last glacial maximum; Holocene

1. INTRODUCTION

The Amazon Basin is predicted to experience an increase in temperatures by *ca.* 3 °C coupled with a reduction in precipitation by *ca.* 20% over the twenty-first century (Houghton *et al.* 2001). These climatic changes would reduce plant water availability and thereby increase drought stress for many Amazonian species. Climatically sensitive ecotonal areas are likely to be most vulnerable to increased drought and warmth; i.e. the rainforest–savannah and rainforest–dry forest ecotones at the northern and southern limits of the Basin, and the rainforest–Andean cloud forest ecotone at the western limit of the Basin. Given that different species have different climatic

tolerances, different species would be predicted to respond individually to climate change. Consequently, not only would one expect biome shifts (e.g. replacement of rainforest by seasonally dry forest or savannah), but also significant reassortment of species within plant communities in response to such changes.

Insights into the nature of such anticipated vegetation responses can be obtained from an understanding of how Amazonian ecosystems have responded to environmental changes in the past. The aim of this paper is therefore to determine the responses of Amazonian ecosystems to the significant changes in temperature, precipitation and atmospheric CO₂ concentrations that occurred since the LGM, *ca.* 21 000 calendar years before present (cal yr BP), and synthesize this information to facilitate predictions about likely vegetation responses to future climate change. Towards this aim, we (i) review previously published palaeovegetation and pollen rain datasets, independent multi-proxy palaeoclimatic data and dynamic vegetation model simulations; and (ii) present new pollen

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rain data from the Bolivian Amazon and vegetation simulations for the Amazon Basin.

2. AMAZONIA AT THE LAST GLACIAL MAXIMUM

(a) *Climate and carbon dioxide concentrations*

Elucidating species' responses to Amazonian climate at the LGM has long been problematical, in large part owing to the fact that, in the absence of other kinds of evidence, palaeoclimate and palaeovegetation reconstructions have generally both been obtained from the same proxy data, namely fossil pollen records. Aside from the obvious problem of circular reasoning, this approach is also flawed because it rests on the assumption that climate was the only important environmental variable responsible for controlling species distributions. It is now well established from ecophysiological experiments (Polley *et al.* 1993; Cowling & Sage 1998), dynamic vegetation models (Cowling *et al.* 2001) and stable carbon isotope records (Street-Perrott *et al.* 1997) that the carbon-depleted atmosphere of the LGM (*ca.* 180–200 p.p.m. atmospheric CO₂ versus pre-industrial values of 280 p.p.m.; Monnin *et al.* 2001) significantly reduced the water-use efficiency (water lost per unit of carbon uptake) of C₃ plants (i.e. all woody plants). Studies by Huang *et al.* (2001) suggest that this was especially important in the highly seasonal forest–savannah ecotones at the northern and southern limits of the Basin, where species already under climate-induced water stress were most vulnerable to additional water-stress brought about by low CO₂ concentrations. Clearly, Amazonian species, especially those in the distinctly seasonal southern half of the Basin, would have been affected, not only by different climatic conditions, but also low atmospheric CO₂ conditions.

Fortunately, an increasing body of evidence from independent climate proxies has enabled more reliable reconstructions of Amazonian LGM climate to be made. Analysis of noble gas concentrations in fossil groundwater in eastern Brazil (Stute *et al.* 1995) and tropical SST reconstructions from Barbados corals (Guilderson *et al.* 1994) show that the Amazon Basin at the LGM was *ca.* 5 °C cooler than today. This estimate is supported by δ¹⁸O analyses of Andean ice-core records at Huascarán, Peru (9°07' S, 77°37' W; Thompson *et al.* 1995) and Sajama, Bolivia (18°06' S, 68°53' W; Thompson *et al.* 1998; figure 1).

Precipitation values and patterns at the LGM are less well understood, for several reasons. First, in contrast to the temperature and CO₂ variables, precipitation is likely to have been highly spatially variable across the Amazon Basin, as it is today. Thus, large-scale extrapolations beyond the immediate site of investigation may well be highly erroneous. Second, in addition to differences in the magnitude of precipitation, the direction of precipitation change over time may also have differed across Amazonia, given that the orbital forcing of insolation between the Northern and Southern Hemispheres of the Basin are in anti-phase (Berger & Loutre 1991) and the relative dominance of different climate drivers is likely to have varied in different parts of this vast area. Notwithstanding these problems, significant progress has been made in recent years in reconstructing the precipitation regime across Amazonia at the LGM. Bush *et al.* (2002) used

Figure 1. (a) Map showing the location of sites discussed in the text. The shaded area shows the current distribution of humid evergreen broad-leaf forest (rainforest). The hatched area shows the Andes mountains. Lowland unshaded areas represent seasonally dry forests and savannahs. (b) Schematic broad-scale summary trends of climatic change and/or vegetation response for each site since 21 000 cal yr BP. N.B. These profiles are intended as simplified cartoons to summarize the information discussed in the text and should not be viewed as absolute quantitative depictions. Key for sites: HU, Huascarán ice core (Thompson *et al.* 1995; 9°07' S, 77°37' W); JU, Lake Junin (Seltzer *et al.* 2000; 11° S, 76° W); TI, Lake Titicaca (Baker *et al.* 2001a; 17° S, 69° W); SA, Sajama ice core (Thompson *et al.* 1998; 18°06' S, 68°53' W); SI, Siberia (Mourguiart & Ledru 2003; 17°50'00" S, 64°43'08" W); PI, Laguna El Pinal (Behling & Hooghiemstra 1999; 4°08' N, 70°23' W); LL, Laguna Loma Linda (Behling & Hooghiemstra 2000; 3°18' N, 73°23' W); MX, Maxus 4 (Weng *et al.* 2002; 0°27' S, 76°37' W); PA: Lake Pata (Colinvaux *et al.* 1996; Bush *et al.* 2002; 0°16' N, 66°41' W); CA, Lago Calado (Behling *et al.* 2001; 3°16' S, 60°35' W); VE, Porto Velho/Humaita (De Freitas *et al.* 2001; 8°43' S, 63°58' W to 7°38' S, 63°04' W); BV, Laguna Bella Vista (Mayle *et al.* 2000; Burbridge *et al.* 2004; 13°37' S, 61°33' W); CH, Laguna Chaplin (Mayle *et al.* 2000; Burbridge *et al.* 2004; 14°28' S, 61°04' W); SC, Serra dos Carajas (Absy *et al.* 1991; Sifeddine *et al.* 2001; 6°35' S, 49°30' W); FA1, Amazon Fan (Haberle & Maslin 1999; 5°12.7' N, 47°1.8' W); FA2, Amazon Fan (Maslin & Burns 2000; 5°45' N, 49°06' W); GA, Laguna La Gaiba (17°47'00" S, 57°43'00" W); MA, Laguna Mandioré (18°05'31" S, 57°33'46" W); SO, Laguna Socórros (16°08'30" S, 63°07'00" W); RP, Rio Piray (Servant *et al.* 1981; 17°55' S, 63°15' W); OS, Ostra (Andrus *et al.* 2002; 8°55' S); SS, Siches (Andrus *et al.* 2002; 4°40' S).

palaeolimnological data from a cluster of lakes (Lakes Pata, Verde and Dragao) on an inselberg in northwest Amazonia (0°16' N, 66°41' W; figure 1) to infer that lake levels were relatively high at the LGM (although below present-day levels) and that humid conditions existed in northwest Amazonia at this time. Corroborating evidence for a humid climate is supported by complete absence of charcoal in the sediment record from these sites (M. Bush, unpublished data), indicating that the climate was too humid to favour frequent forest fires. Further evidence for wet climatic conditions comes from palaeolimnological data from Lake Titicaca (16–17.5° S, 68.5–70° W; Baker *et al.* 2001a), located on the Peruvian–Bolivian Altiplano just beyond the southwest margin of the Amazon watershed. The water-level reconstruction from this site shows that precipitation on the Altiplano was even higher than today, and that the lake overflowed southwards to form the huge palaeolake 'Tauca' on the central Altiplano (Baker *et al.* 2001b). Hastenrath & Kutzbach (1985) and Blodgett *et al.* (1997) simulated the hydrological conditions on the Altiplano by using different models, incorporating surface energy and water budgets, which showed that precipitation must have been 20–75% above modern levels to produce Pleistocene lake Tauca, assuming a 5 °C temperature drop. Additional corroborating data for a wet Altiplano come from geochemical and ice-accumulation-rate data from the Sajama Mountain ice core (Thompson *et al.* 1998), south of Lake Titicaca in the Bolivian Andes, a site that also receives the bulk of its

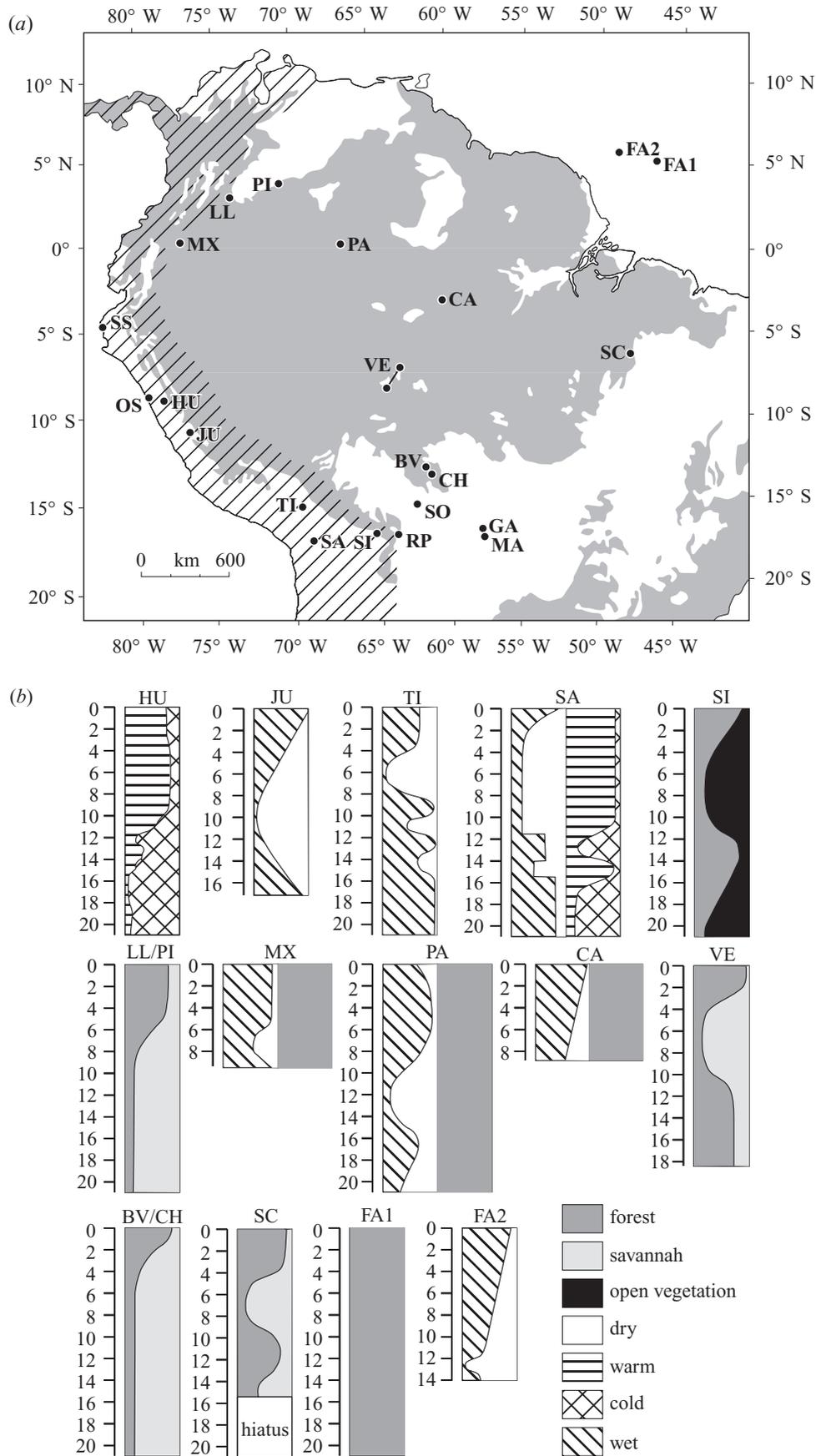


Figure 1. (Caption opposite.)

precipitation today from the Amazon Basin. It should be noted though, that although these ice-core data show that precipitation was continuously high between 25 000 and 16 000 cal yr BP, compared with the subsequent late glacial and Holocene, maximum precipitation occurred immediately before (25 000–22 000 cal yr BP) and after (18 000–17 000 cal yr BP) the LGM.

However, sedimentary hiatuses occurred between 22 000 ^{14}C yr BP and 13 000 ^{14}C yr BP (15 600 cal yr BP; Stuiver *et al.* 1998) at two lakes on the Serra dos Carajas (6°35' S, 49°30' W, Para State, east Amazonia) and between 38 000 ^{14}C yr BP and 11 000 ^{14}C yr BP (13 000 cal yr BP) at Laguna Bella Vista (13°37' S, 61°33' W, northeast Bolivia, southwest Amazonia). These lakes, located very close to the current rainforest limit (figure 1), therefore dried up, indicating that precipitation at the LGM must have been below present-day levels (Absy *et al.* 1991; Mayle *et al.* 2000; Sifeddine *et al.* 2001). Supporting evidence comes from Laguna Chaplin (14°28' S, 61°04' W; Mayle *et al.* 2000; Burbridge *et al.* 2004), located 100 km south of Laguna Bella Vista. The *Isoetes* record from this site shows that water levels were lower than today at the LGM, but precipitation cannot have been drastically lower because the sediment stratigraphy and age–depth plot (Burbridge *et al.* 2004) show that the lake, which is currently only 2 m deep in the dry season, has not dried up for any significant period (i.e. several millennia) over the past 50 000 years.

This LGM scenario of the southern Amazon lowlands being cooler and drier than today, and the Altiplano being cooler and wetter than today might, at first glance, seem difficult to explain, given that the Altiplano today receives the bulk of its precipitation in the austral summer from the lowland Amazon Basin to the northeast. However, analysis of local meteorological data, in combination with a GCM, has led Garreaud *et al.* (2003) to infer that the critical factor determining precipitation variability on the Altiplano is not moisture change in the source area *per se*, but instead the intensity and direction of upper-level large-scale zonal moisture transport (i.e. easterly winds enabling moisture transport from Amazonia versus dry westerly winds from the Pacific). Orbital forcing by the 19 000–22 000 year precession cycle of the Milankovitch Astronomic Theory would be predicted to have maximized austral summer insolation at 10–15° S at the LGM, thereby increasing deep convection over central South America, which would in turn maximize seasonal southerly migration of the ITCZ and intensify the Bolivian High (a prominent upper-level anticyclonic circulation centred at roughly 15° S, 65° W; Lenters & Cook 1997). These phenomena would not only increase precipitation in the southern half of Amazonia (which lies in the Southern Hemisphere), but also increase the intensity of moisture transport to the Altiplano by strengthening the easterly winds. However, the expanded Antarctic ice sheet and Patagonian glaciers at the LGM would be expected to have steepened the latitudinal temperature gradient across South America, despite the 5 °C cooling in the Amazon Basin, thereby counteracting the effects of precessional orbital forcing and reducing wet season convective activity over the southern Amazon Basin, thus producing greater precipitation in the northern half of the Basin compared with the south, relative to today. Furthermore, reduced

SSTs in the equatorial Atlantic would be expected to have reduced oceanic moisture transfer to the Basin. This combination of factors may explain the relatively high lake levels in northwest Amazonia (i.e. Lake Pata) compared with low levels and/or lake desiccation in southwest (e.g. Laguna Chaplin and Laguna Bella Vista) and southeast (e.g. Carajas) Amazonia. The difference in lake-level records between lowland Amazonian Bolivia and the Altiplano is reproduced in sensitivity tests with an atmospheric GCM (GENESIS 2.01; Hostetler & Mix 1999) using foraminiferal-based SST reconstructions (Mix *et al.* 1999), which simulate a stronger Walker circulation (an equatorial zonal pattern of ascending air over Indonesia, South America and Africa, and descending air over the eastern Pacific, Atlantic and western Indian oceans (Hostetler & Mix 1999)). It is likely that westerlies from the eastern Pacific or strengthened 'surazos' from Patagonia during the austral winter were the dominant mechanisms for moisture transport to the Altiplano at the LGM, rather than easterlies from the Amazon Basin.

(b) *Vegetation responses inferred from palaeodata*

(i) *Forest versus savannah*

Accumulating palaeoecological evidence indicates that most of the Amazon Basin remained forested at the LGM (figure 1), contrary to the rainforest refugia hypothesis of Haffer (1969). Colinvaux *et al.* (1996) and Bush *et al.* (2002) provide pollen data to show that the Lake Pata catchment in northwest Amazonia was forested at this time, and that, furthermore, it has been continuously forested over the past 170 000 years. Soil stable carbon isotope analyses by De Freitas *et al.* (2001) show that savannah islands within southern Amazonian rainforests (between Porto Velho, Rondonia State and Humaita, Amazonas State, Brazil, 8°43' S, 63°58' W–7°38' S, 63°04' W) were no more extensive at the LGM than today.

However, in contrast to these sites in northwest and south Amazonia, records from sites closer to the margins of the Basin do reveal changes in forest–savannah distribution between the LGM and today. The 50 000 year pollen record from Laguna Chaplin (Mayle *et al.* 2000; Burbridge *et al.* 2004) shows that Amazonian rainforest communities at the LGM were located at least 30 km north of their current southern limit in eastern Bolivia (figure 1), and that this ecotonal area was then dominated by open savannahs, with rainforest and/or dry forest species probably restricted to riverine gallery forests. Pollen evidence from Laguna El Pinal (4°08' N, 70°23' W), in the Colombian savannahs of the Llanos Orientales at the opposite end of the Basin (Behling & Hooghiemstra 1999; figure 1), shows that this site, which is currently bordered by localized gallery forests, was then surrounded by virtually treeless savannah. Mourguiart & Ledru (2003) present pollen data from a site, near the village of Siberia (17°50'0" S, 64°43'08" W) at the upper cloud forest ecotone in the Bolivian Andes, which shows an open grass-dominated landscape at the LGM, interpreted by the authors as a vegetation response to increased aridity. However, such an interpretation is at odds with the palaeoprecipitation record from the Altiplano (Baker *et al.* 2001*a,b*), and a far more likely explanation, argued by Baker *et al.* (2004), is that the grass-dominated LGM

pollen assemblages reflect expansion of high Andean puna vegetation and lowering of the tree-line, primarily in response to climatic cooling.

Although it would be unwarranted to extrapolate these isolated pollen records to the entire Amazon Basin, pollen data from Amazon Fan sediments (5°12.7' N, 47°1.8' W) can be considered a more reliable indicator of Basin-wide changes in vegetation, because these pollen assemblages have been deposited from the entire Amazon river catchment. Pollen spectra from these Amazon Fan cores show no significant changes in the relative proportions of forest versus savannah pollen taxa between the LGM and the Holocene (Haberle 1997; Hoorn 1997; Haberle & Maslin 1999). These findings corroborate the isolated terrestrial pollen records, showing that although there is evidence for more widespread savannahs at the northern and southern Amazonian margins relative to today, most of the Basin remained forested at the LGM.

(ii) *Seasonally dry forests versus rainforests*

Evidence from a variety of sources indicates that these environmental changes during the LGM had significant impacts upon the floristic composition and structure of the forest communities. The fossil pollen data (albeit from very few sites) indicate that the species composition of these glacial-age forests has no modern analogue. The climate cooling caused taxa that are currently largely restricted to the Andes (e.g. *Podocarpus* and *Alnus*) to spread throughout the Amazon Basin and form mixed communities with lowland Amazonian forest taxa (Colinvaux *et al.* 2000).

Notwithstanding these Andean elements, it has generally been assumed (Colinvaux *et al.* 1996) that these communities were dominated by evergreen rainforest taxa. However, recent biogeographical research raises the possibility that much of the Amazon Basin was instead occupied by seasonally dry tropical forests (i.e. semi-deciduous and/or deciduous forests) during the last glacial period. Seasonally dry forests today exist as isolated, disjunct distributions, widely separated from each other; for example, the Caatinga forests of eastern Brazil, the Chiquitano dry forest of eastern Bolivia and the Andean piedmont dry forests of southern Bolivia/northwest Argentina (Dinerstein *et al.* 1995). Prado & Gibbs (1993) and Pennington *et al.* (2000, 2004) found that these widely disjunct dry forest regions share many widespread species and inferred that they were therefore ancient refugia of a formerly much more extensive, contiguous distribution during the last glacial period, which they termed the '*Pleistocene Dry Forest Arc*'. Pennington *et al.* (2000) argued that full glacial pollen spectra from Amazonia, previously interpreted as a rainforest signal (albeit with Andean elements), could equally well be interpreted as a predominantly 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 (at least in terms of diagnostic species).

Determining the changes in spatial extent of dry forests versus rainforests in response to changing climate and atmospheric CO₂ concentrations since the last glacial period is important for several reasons. First, these two ecosystems have different carbon storage values; i.e. *ca.*

320 tons C ha⁻¹ (ha, hectare, =10⁴ m²) for tropical rainforest versus 260 tons C ha⁻¹ for seasonally dry forest (Adams & Faure 1998). Consequently, significant changes in their relative distributions and biomass over time would be expected to have resulted in corresponding shifts in the magnitude of the Amazon carbon store, which in turn are likely to have had implications for the global carbon cycle (Mayle & Beerling, 2004). Second, determining their respective biogeographic distributions at the LGM provides insights into understanding the importance of cyclic Quaternary climatic changes in explaining their present floristic composition, biodiversity and structure. Previous debate has dwelt on the relative distribution of rainforest versus savannah at the LGM (rainforest refugia hypothesis; Haffer 1969), and yet the possibility of dry forest expansion within Amazonia at this time has largely been ignored, as pointed out by Pennington *et al.* (2000), which is surprising given that both dry forests and cerrado savannahs grow under similar climatic conditions (generally 700–1800 mm yr⁻¹; Furley 1999).

(c) *Semi-deciduous dry forest versus evergreen rainforest modern pollen rain data*

Characterizing current rainforest and dry forest communities by their surface pollen spectra is crucial to determining whether or not these different vegetation types can be reliably distinguished by their pollen signatures, and hence whether or not their Amazonian distributions at the LGM can be elucidated by fossil pollen analysis. Although the available pollen data show that LGM plant communities were without modern analogues, owing to their unique mixture of Andean and lowland tropical forest taxa, modern pollen rain studies should at least give the potential to determine whether or not such communities were dominated by evergreen species or instead deciduous/semi-deciduous species.

Several modern pollen rain studies have been published from evergreen rainforests throughout the Neotropics, e.g. Central America (Bush 2000), the tropical Andes (Weng *et al.* 2004), Amazonia (Bush 1991; Bush *et al.* 2001) and the Atlantic coast of Brazil (Behling *et al.* 1997). However, the only data from semi-deciduous dry forests come from Panama (Bush 1991). Here, we present the first modern pollen rain data from the Chiquitano semi-deciduous dry forests of lowland eastern Bolivia, together with additional rainforest pollen rain data from the Bolivian Amazon (figure 2). The samples have been collected from both artificial pollen traps (Gosling *et al.* 2003) and sediment–water interface lake samples. It is immediately apparent that pollen percentages of the predominantly rainforest family, Moraceae, are significantly higher in evergreen forest (40–60%) than in semi-deciduous/deciduous forest (7–19%). Although such high Moraceae pollen percentages are a consistent, reliable signature of the seasonal humid evergreen forests of northeast Bolivia (Mayle *et al.* 2000), comparison with other pollen rain data shows far less consistency in abundance of this taxon in rainforests from other parts of the Neotropics (e.g. 10–50%, Bush *et al.* 2001). Clearly, abundance of this family, by itself, cannot serve as a reliable ecosystem indicator when considering an area as large as the Amazon Basin. Abundance of Poaceae pollen is also unreliable as a means of distinguishing between these ecosystems in the fossil record,

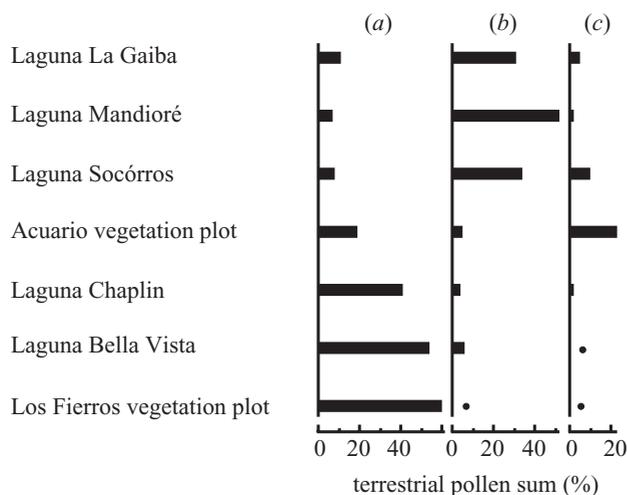


Figure 2. Modern pollen rain percentages of (a) Moraceae–Urticaceae, (b) Poaceae and (c) *Anadenanthera* pollen from semi-deciduous dry forest and humid evergreen forest sites in lowland Bolivia. The Acuario (15°14'58" S, 61°14'42" W) and Los Fierros (14°34'50" S, 66°49'48" W) sites are 20 m × 500 m permanent vegetation study plots. Pollen data from artificial pollen traps from these two plots (Gosling *et al.* 2003) constitute mean values of counts from 10 evenly spaced traps from each plot sampled over three consecutive years. Pollen samples from the five lakes were collected from the uppermost centimetre of sediment at the sediment–water interface. See Mayle *et al.* (2000) and Burbridge *et al.* (2004) for more detailed pollen data of the surface samples from Laguna Chaplin and Laguna Bella Vista.

as cogently argued by Bush (2002a). This is largely owing to the unknown contribution of shore-line aquatic grasses to the pollen assemblage (terrestrial and aquatic grass taxa cannot be distinguished palynologically). Although low Poaceae pollen percentages (i.e. less than 5–10%) are indeed generally characteristic of most rainforest surface pollen spectra, our artificial pollen traps from the Chiquitano semi-deciduous dry forests (figure 2) yield equally low Poaceae percentages. Interestingly, the surface pollen samples from the semi-deciduous dry forest sites Laguna La Gaiba, Laguna Mandioré and Laguna Socórrros (figure 2) all contain in excess of 30% grass pollen, although such high values may at least partly be attributed to localized patches of open cerrado savannah on neighbouring ridges (L. Mandioré) or nearby patches of savannah marsh and/or small local clearances (L. Socórrros and L. La Gaiba). The large surface areas of these lakes (e.g. L. Mandioré, 18 km × 8 km) would suggest that the relative contribution from shore-line aquatic grasses to the grass pollen sum was minimal. Similarly, high grass pollen percentages have been recorded from open savannahs (Ledru 2002; W. D. Gosling, unpublished data), further underlining the poor diagnostic value of Poaceae pollen abundance.

In contrast to the other pollen taxa in these surface pollen spectra, *Anadenanthera* pollen emerges as a key indicator taxon of semi-deciduous–deciduous tropical forest. Although *Anadenanthera colubrina* is restricted to seasonally dry forests (Prado & Gibbs 1993), the other species in this mimosoid genus, *Anadenanthera peregrina*, is also common in the southern cerrado savannahs of Sao Paulo state, Brazil (J. A. Ratter, unpublished data). Although

these species cannot be distinguished palynologically, we are confident that most pollen grains in these samples belong to *A. colubrina*, because this is by far the more common of the two species in neotropical dry forests. Prado & Gibbs (1993) found that *A. colubrina* was either dominant or frequent in all areas of South American seasonally dry tropical forests, with the exception of the Caribbean coasts of Colombia and Venezuela. They used the contemporary distribution of this taxon as a key basis for their argument that these patches are disjunct distributions that must have been formerly connected. This taxon reaches 19% in artificial traps and 2–10% in lake surface sediments of the Chiquitano Dry Forest (figure 2). It is completely absent from any neotropical rainforest modern pollen rain spectra, with the exception of Laguna Bella Vista and Laguna Chaplin, which are situated only a few kilometres north of the dry forest ecotone, and are therefore likely to contain low-level occurrences of a few dry forest taxa, which no doubt account for the negligible percentages (1% and 2%, respectively) of *Anadenanthera* pollen in the surface spectra of these two sites. Given that most seasonally dry forests are subject to frequent fires, whereas rainforests are not, a further distinguishing character between these two types of forest is the presence of charcoal within all these dry forest surface spectra, but absence of charcoal in rainforest spectra. It should be noted, however, that certain kinds of neotropical dry forest ecosystem, such as the xeric caatingas of eastern Brazil, do not experience frequent fires, borne out by their sizeable populations of cacti, which are poorly adapted to fire.

The LGM pollen spectra of the Lake Pata record contain no *Anadenanthera* pollen and no charcoal, suggesting either that semi-deciduous–deciduous forests were absent from the vicinity, or that if such forest types were present, they comprised communities of taxa that were quite different floristically and/or structurally from those of today.

(d) *Vegetation simulations*

(i) *Application of the University of Sheffield Dynamic Global Vegetation Model*

The poor spatial resolution of the fossil pollen data severely hampers efforts to map distributional changes in different ecosystems across the vast Amazon Basin over time. Dynamic vegetation models can therefore serve as useful tools for making process-based predictions about the nature of vegetation responses to past atmospheric CO₂ levels and climates across Amazonia. Here, we use data extracted from global equilibrium simulations using the SDGVM (Woodward *et al.* 1995; Beerling 1999; Beerling & Woodward 2001). The SDGVM calculates vegetation properties under steady-state conditions of climate and CO₂, and represents the physiological processes of plant nutrient uptake, C₃ and C₄ photosynthesis, respiration and stomatal control of canopy transpiration. Above-ground primary productivity is fully coupled to a below-ground model of soil carbon and nitrogen dynamics so that plant litter (leaves and surface roots) is subsumed through decomposition–nutrient cycling (Woodward *et al.* 1998; Beerling & Woodward 2001). The model predicts the distribution of different plant functional types on the basis of annual net primary production and biomass, competition for light and other resources, as well as

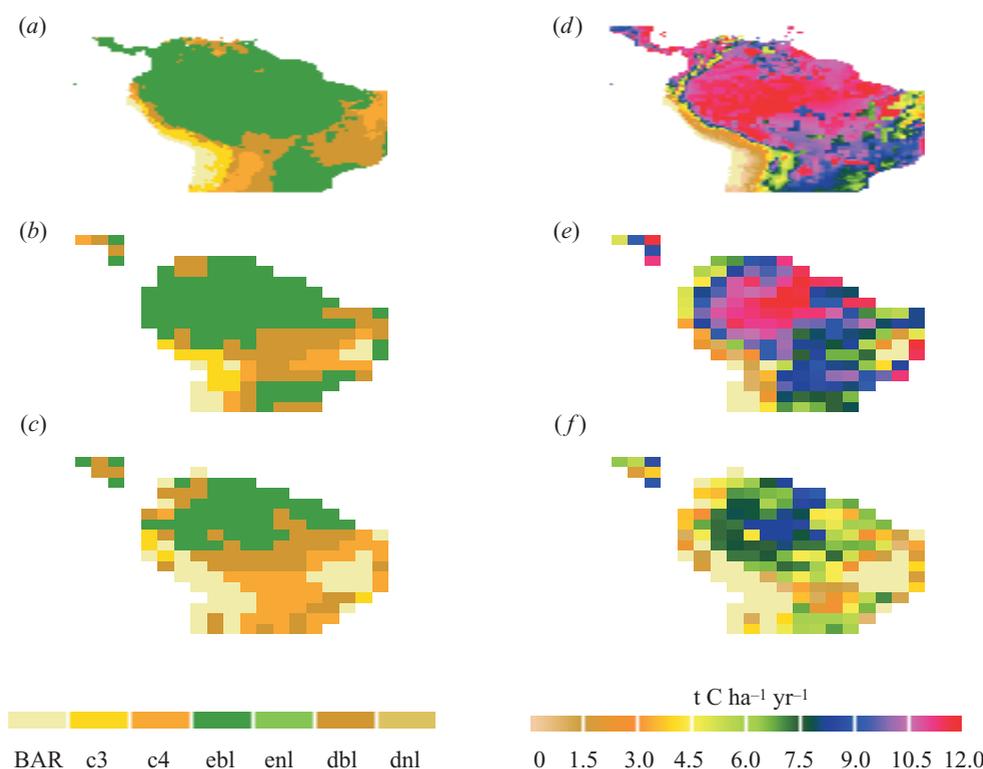


Figure 3. SDGVM model simulations forced with the UGAMP GCM. See § 2d(i). Key: c3, C₃ grasses; c4, C₄ grasses; ebl, evergreen broad-leaf forest; enl, evergreen needle-leaf forest; dbl, deciduous broad-leaf forest; dnl, deciduous needle-leaf forest. Amazonian vegetation distribution: (a) Pre-Industrial; (b) Mid-Holocene; (c) LGM; NPP of Amazonian vegetation: (d) Pre-Industrial; (e) Mid-Holocene; (f) LGM. (t C ha⁻¹ yr⁻¹, tonnes of carbon per hectare per year, where 1 hectare is 10⁴ m².)

probability of disturbance, and succession after disturbance (Cramer *et al.* 2001).

In this analysis, we focused on three time intervals for comparison: the Pre-Industrial, the Mid-Holocene and the LGM. The Pre-Industrial simulations of potential vegetation in the Amazon Basin were made by forcing the SDGVM with the historical land-surface climatologies produced by New *et al.* (1999, 2000) and averaging the results for the period AD 1901–1910. The two palaeovegetation simulations were forced by using the UGAMP GCM-derived climate (Hall *et al.* 1996*a,b*; Hall & Valdes 1997), which has a spatial resolution of 2.8° latitude × 2.8° longitude. The UGAMP GCM is based on the European Centre for Medium-Range Weather Forecasting model (ECMWF) and uses SSTs prescribed from palaeodata. Model bias was minimized by calculating locally differing monthly climate anomalies, i.e. GCM control (present-day) run minus GCM palaeorun, and imposing these onto a modern underlying climatology (cf. Beerling 1999). Atmospheric CO₂ concentrations for the Pre-Industrial, Mid-Holocene and LGM were 300, 280 and 180 p.p.m., respectively.

Figure 3 shows the predicted distribution of plant functional types and vegetation productivity in the Amazon Basin for the (a) present day (Pre-Industrial), (b) Mid-Holocene (6000 cal yr BP) and (c) LGM (21 000 cal yr BP). The Pre-Industrial simulation is for the potential vegetation, and does not account for anthropogenic land-cover change (e.g. crops, urban areas, forest clearance). Changes in land surface carbon storage of the different ecosystems in Amazonia for these time periods are

discussed in the context of Amazon carbon cycling elsewhere (Mayle & Beerling 2004).

The UGAMP GCM climate response to the LGM temperature (5 °C below present) and atmospheric CO₂ conditions (180 p.p.m.) is a basin-wide MAP of 1660 mm, which is 20% (338 mm) below present. The GCM computes mean monthly precipitation values (i.e. precipitation seasonality as well as MAP), which are used by the SDGVM.

(ii) Changes in biome distribution

The first key finding from these model simulations is that the Amazon Basin remained predominantly forested at the LGM (figure 3*c*), in agreement with the pollen data discussed in § 2b(i). The second significant result is that evergreen broad-leaf forests are simulated to have covered the northern half of Amazonia, while deciduous broad-leaf forests covered the southern half. These simulations suggest that the reduced precipitation in the southern half of Amazonia was sufficient to result in competitive replacement of evergreen species by the drought-adapted semi-deciduous and deciduous species found in seasonally dry tropical forests. They also support the hypothesis of Pennington *et al.* (2000), based on their phytogeographic studies, that much of the Basin was covered by seasonally dry forest rather than rainforest.

However, it should be noted that, despite a 20% decrease in precipitation in northwest Amazonia, our model shows that precipitation in this area (which includes Lake Pata) remained high enough to maintain evergreen broadleaf forest at the LGM, which supports

the inferences by Colinvaux *et al.* (1996, 2000) and ourselves, and contradicts the suggestion by Pennington *et al.* (2000) that it was regionally surrounded by seasonally dry forest. Furthermore, our LGM model simulation does not support the 'Pleistocene Dry Forest Arc' hypothesis. This hypothesis predicts that the Chiquitano Dry Forest of eastern Bolivia is a remnant of the central core of this postulated expanded Pleistocene distribution. Instead, the model simulates C_4 savannah grasses for eastern Bolivia, and shows that dry forest taxa were located north of their present-day disjunct distributions and were restricted to the southern half of Amazonia, which is currently occupied by rainforest. This vegetation simulation is corroborated by the pollen record from Laguna Chaplin. This site is located at the southernmost limit of Amazon rainforest, only 30 km north of the Chiquitano Dry Forest (figure 1), and was predominantly surrounded by open savannahs at the LGM, with deciduous–semi-deciduous forest taxa perhaps restricted to isolated edaphically suitable areas (e.g. riverine gallery forests). *Anadenanthera* did not arrive until the Early Holocene (Burbridge *et al.* 2004). These fossil pollen data (albeit from only one site), together with the model simulation, suggest that rather than being relict, refugial populations, the current distributions of dry forests are instead only Holocene in age, having arisen from populations spreading southwards from Amazonia since the LGM.

(iii) *Changes to forest structure and composition*

Vegetation modelling by Cowling *et al.* (2001) suggests that changes in vegetation structure could have been at least as important as changes in vegetation biomes or plant functional type. To distinguish between species' responses to lowered temperature, atmospheric CO_2 concentrations and precipitation, Cowling *et al.* (2001) simulated vegetation responses at the LGM to differing climate and atmospheric CO_2 conditions. They undertook multivariable sensitivity experiments to show that both conservative ($2^\circ C$) as well as extreme ($6^\circ C$) LGM cooling conditions, associated with both conservative and extreme values of decreased precipitation (20% versus 60% reduction) and CO_2 (220 p.p.m. versus 180 p.p.m.) resulted in significantly higher percentages of forest cover than those simulated under present-day temperature conditions. Cowling *et al.* (2001) attributed this response to improved carbon and water balance owing to reduced evapotranspiration and lowered rates of photorespiratory carbon loss, both of which would have favoured dominance of forests over savannahs. These authors further showed that atmospheric CO_2 concentrations would have been more important than precipitation levels in controlling canopy density (i.e. vegetation structure). For a decrease in 20% precipitation alone, they simulated an 11% decrease in basin-average LAI (an index of canopy density), whereas lowered atmospheric CO_2 concentrations alone (set at LGM values of 200 p.p.m.) were simulated to cause a 34% reduction in LAI.

From these sensitivity simulations we can infer that the changes in vegetation structure (i.e. reduced canopy density) and forest type (i.e. replacement of evergreen by deciduous–semi-deciduous species) were predominantly responses to carbon limitation and water stress due to lowered atmospheric CO_2 concentrations rather than water

stress due to lowered precipitation. Reduced precipitation (e.g. 20%) would no doubt have been sufficient to tip the ecological balance in favour of savannahs at the rainforest ecotones at the northern and southern Amazon Basin margins, where current rainfall approaches the precipitation threshold of ca. 1500–1800 mm yr^{-1} for evergreen rainforest. However, the cooler temperatures would have served to reduce evapotranspiration and thereby prevent more widespread replacement of forest by savannah in more central parts of the Basin.

Our model simulations of NPP corroborate the simulations of Cowling *et al.* (2001) of reduced LAI. Figure 3*f* shows that the cool, low CO_2 environment of the LGM severely restricted vegetation carbon uptake and lowered NPP compared with the Holocene (figure 3*d,e*). Irrespective of the composition or structure of forest communities that occupied the Amazon Basin at this time, it is clear that both modelling studies and palaeodata refute the 'glacial refugia hypothesis', advocated by Haffer (1969), Prance (1982), Whitmore & Prance (1987) and Haffer & Prance (2001), which states that most of the Amazon Basin was covered by savannah at the LGM. Furthermore, these studies suggest that, although seasonally dry forests appear to have been more extensive within Amazonia at the LGM than today, their overall spatial coverage throughout tropical South America does not appear to have been significantly greater at the LGM than today (before human clearance), but simply had a different spatial distribution in response to the differing climatic and CO_2 conditions at that time.

It is important to stress that although much of Amazonia was probably covered by tropical evergreen forest at the LGM, the structure, productivity and composition of the forests differed substantially from those of contemporary Amazonian rainforests. Insights into the nature of these ice-age forests may be gained by considering the structure and composition of the moist evergreen rainforests of southwest Amazonia (southern Peru and northern Bolivia) near the ecotone with savannahs and semi-deciduous dry forests. The latter, in contrast to other forests in more central parts of the Amazon, are dominated to a large extent by evergreen lianas (Killeen 1998) and/or bamboo, which have a greater ability to withstand water stress than other Amazonian rainforest taxa in these highly seasonal climates. It is therefore conceivable that these forests constitute the closest modern analogue to the evergreen forests that existed in Amazonia at the LGM. Furthermore, the low canopy density of these forests, in comparison with those growing in wetter, more central parts of Amazonia, is consistent with the low NPP values simulated in figure 3*f* and the low LAI simulated by Cowling *et al.* (2001). Such forests would not have been apparent from the fossil pollen records owing to the low pollen productivity of bamboo (Bush 2002*a*), the fact that different grass taxa cannot be distinguished by their pollen and because liana taxa are also generally indistinguishable palynologically from evergreen tree taxa.

(iv) *Vegetation–precipitation feedbacks*

Determining the responses of Amazonian ecosystems to climate forcing is further complicated by the fact that the climate (especially precipitation) is itself determined, to a large degree, by the vegetation. For example, ca. 50% of

Amazon precipitation is recycled through rainforest canopy transpiration (Shukla & Mintz 1982), thus reducing the relative importance of moisture transport from the Atlantic Ocean on total precipitation. Nepstad *et al.* (1994) have shown that this precipitation recycling process is in large part caused by the ability of tropical forest trees to access deep soil moisture with roots in some cases as deep as 18 m. Field studies have shown that this ability to draw upon large stores of water allows such forests to continue transpiration and maintain their foliage during extended dry periods. Kleidon & Lorenz (2001) included rooting depth as an additional parameter in climate models and thereby determined the impact of deep-rooted vegetation upon climate simulations for Amazonia at the LGM. They found that access to large soil-water stores by deep-rooted vegetation caused greater evapotranspiration in the dry season, which in turn produced a 4 °C surface cooling (owing to latent heat of evaporation) and an increase in precipitation of up to 2 mm day⁻¹. These results show that despite an anticipated reduction in precipitation coming from a cooler tropical Atlantic Ocean, precipitation recycling by vegetation would have been sufficient to maintain humid conditions, and consequently evergreen forest, throughout most of the Amazon Basin. Although these authors neglected to include the additional water stress expected from lowered LGM CO₂ concentrations, which could have tipped the ecological balance from evergreen to semi-deciduous dry forest, it is nonetheless clear that the vegetation itself would have counteracted to a significant extent any climate aridity inferred from independent climate data from outside the Amazon Basin, e.g. equatorial Atlantic SSTs.

These studies highlight the fact that the seasonal distribution of precipitation (i.e. the length and severity of the dry season) is the critical control upon vegetation, rather than mean annual precipitation. For example, the deciduous monsoon forests of India receive up to 5000 mm MAP, whereas the evergreen equatorial forests of peninsular Malaysia receive only 2000 mm MAP (O. Phillips, unpublished data). Sternberg (2001) developed a simple dynamic model simulating the dynamic feedback between dry-season precipitation and forest area. His simulations showed that a minimum of 100 mm dry-season precipitation (total precipitation over the driest three months) was required to maintain tropical evergreen forest, although only 50 mm imported dry-season precipitation was required, given the ability of such forests to recycle 50% of the rainfall.

In light of these studies, it is therefore important to point out that the palaeoprecipitation records gleaned from lake-level reconstructions provide information about past changes in MAP but unfortunately cannot provide information about the crucial parameter of dry-season precipitation. Furthermore, although our SDGVM simulations are based on precipitation seasonality, they do not incorporate any vegetation-climate feedbacks. Consequently, our simulations may underestimate the actual spatial cover and productivity of the rainforests that existed at the LGM. Clearly, understanding and quantifying these feedbacks remains an important goal for vegetation and climate modellers, although progress is being made (e.g. the TRIFFID terrestrial carbon cycle model (Cox *et al.* 2000; Cox 2001; Cowling *et al.* 2004)).

3. AMAZONIA DURING THE LATE-GLACIAL AND HOLOCENE

(a) *Climate and carbon dioxide concentrations*

The ice-core record from Dome Concordia (Dome C), Antarctica (Monnin *et al.* 2001) shows that atmospheric CO₂ concentrations rose by 76 p.p.m. across the last glacial–Holocene transition, from a mean of 189 p.p.m.v. between 18 100 and 17 000 cal yr BP to a mean of 265 p.p.m.v. between 11 100 and 10 500 cal yr BP, and that this rise took place in four incremental steps. However, the pattern of CO₂ changes across the Younger Dryas chronozone (GS-1, 12 900–11 500 cal yr BP; Björck *et al.* 1998) determined from the stomatal characters of fossil leaves remains controversial (McElwain *et al.* 2002). The Antarctic Taylor Dome ice core (Indermuhle *et al.* 1999) shows that CO₂ concentrations rose gradually from 260 p.p.m.v. to 285 p.p.m.v. through the Holocene until the Industrial Period.

Multi-proxy data from several sites (figure 1) show that the temperature and precipitation changes in Amazonia through the last glacial–Holocene transition were complex. Oxygen isotope, ice-accumulation and aerosol concentrations from Sajama Mountain (Thompson *et al.* 1998), together with geochemical, diatom, sedimentological and modelling studies from Lake Titicaca (Baker *et al.* 2001a; Cross *et al.* 2001), provide high-resolution estimates of temperature and precipitation changes on the Bolivian Altiplano, above the southwest rim of the Amazon Basin. These records show that, after the LGM, cold, wet conditions persisted until 15 500 cal yr BP, when temperatures and aridity rapidly increased until *ca.* 14 300 cal yr BP. However, new sedimentological data from Lake Titicaca and Lake Junin, Peruvian Andes (*ca.* 11° S, 76° W; Seltzer *et al.* 2002) show that the onset of this deglacial warming trend may have begun as early as 22 000–19 500 cal yr BP, coincident with the generally accepted date of the global LGM (i.e. 21 000 cal yr BP) inferred from the maximum extent of the North American Laurentide ice sheet. This episode of increasing temperatures and aridity correlates with lower lake levels in the Peruvian Andes (Seltzer *et al.* 2000) and central Amazonia (Bush *et al.* 2002) and rising equatorial Atlantic SSTs (Guilderson *et al.* 1994), indicative of similar climatic conditions throughout the Amazon Basin. Subsequently, temperatures decreased and precipitation increased once more on the Altiplano, culminating in a cold, wet climate between 13 000 and 11 500 cal yr BP, correlative with the North Atlantic Younger Dryas stadial (GS-1; Björck *et al.* 1998). However, this cold interval in lowland Amazonia appears to have been accompanied by the most arid conditions over the entire period of study (i.e. the past 21 000 years). At Lake Pata, northwest Amazonia, lowest water levels since the LGM occurred at 12 000 cal yr BP (Bush *et al.* 2002), coincident with a peak in dune growth nearby (00°23' S, 64°33' W; Filho *et al.* 2002) and a major reduction in Amazon river discharge (60% below present; Maslin & Burns 2000). Furthermore, the lake-level record from Lake Junin provides evidence for a peak in aridity during the Younger Dryas chronozone in the central Peruvian Andes above the western rim of the Amazon Basin (Seltzer *et al.* 2000). These regional comparisons suggest that, in contrast to the preceding interstadial warm

period and the present-day climate, moisture-bearing easterlies from the Amazon Basin were considerably weakened during the Younger Dryas, with precipitation instead perhaps predominantly originating from strengthened westerlies and/or anti-cyclones from the Pacific, as simulated by Hostetler & Mix (1999).

Proxy-temperature data from all these sites show that the termination of the Younger Dryas event was marked by a very rapid, large increase in temperatures at 11 500 cal yr BP to modern values, marking the onset of the present Holocene interglacial period. In contrast to the relatively stable Holocene climate of mid-high latitudes, the South American tropics have experienced major fluctuations in precipitation through the Holocene. Throughout southern Amazonia and the Bolivian Altiplano precipitation in the Early–Mid-Holocene was significantly below that of the preceding late-glacial period and subsequent Late Holocene. For example, maximum aridity at Lake Titicaca over the past 25 000 years occurred between ca. 8500 and 3600 cal yr BP (Cross *et al.* 2000; Baker *et al.* 2001a), when precipitation is modelled to have been 40% below modern values (Cross *et al.* 2001) and lake levels were 90 m below present (D'Agostino *et al.* 2002). Furthermore, Wolfe *et al.* (2001) inferred from oxygen isotope data from other Bolivian lakes that summer relative humidity values on the Altiplano were 20% lower than present 7500–6000 cal yr BP. There is widespread charcoal evidence to indicate that this reduction in precipitation caused an increase in fires in the Bolivian Amazon, i.e. the eastern flank of the Andes (Mourguiart & Ledru 2003), the vicinity of Santa Cruz de la Sierra just east of the Andes (ca. 17°55' S, 63°15' W; Servant *et al.* 1981), and the northeast Bolivian lowlands (Burbridge *et al.* 2004), as well as further afield in Para State (eastern Brazilian Amazonia; Soubies 1980; Turcq *et al.* 1998; Sifeddine *et al.* 2001). Although this reduction in rainfall appears not to have been great enough to cause extensive fires in the wetter, central and western parts of the Basin, pollen data do suggest more frequent low-water stands near Manaus (3°16' S, 60°35' W; Behling *et al.* 2001) and increased drought frequency in lowland Amazonian Ecuador (0°27' S, 76°37' W; Weng *et al.* 2002). Oxygen isotope records from the Peruvian Andes (Thompson *et al.* 1995) and Peruvian coastal waters (8°55' S, 4°40' S; Andrus *et al.* 2002) suggest that this Mid-Holocene period of aridity coincided with a Holocene thermal maximum, centred around 6000–6500 cal yr BP, with mean annual SSTs of coastal Peru ca. 3–4 °C higher than today. However, the lack of any apparent temperature change in the Sajama oxygen isotope profile (Thompson *et al.* 1998) calls into question the regional extent of such a warming and whether or not it affected the Amazon lowlands. In any event, any warming in lowland Amazonia would be expected to have been offset to some extent by the cooling effect of evapotranspiration from the rainforest.

There is evidence from all of these sites that precipitation increased in the latter half of the Holocene, especially after ca. 3000 cal yr BP. For example, Amazon river discharge (Maslin & Burns 2000) and water levels at Lake Junin (Seltzer *et al.* 2000), Lake Pata (Bush *et al.* 2002) and Lake Titicaca (Cross *et al.* 2000, 2001), together with marked decreases in charcoal concentrations at Lake Carajas (Turcq *et al.* 1998) and lakes Bella Vista

and Chaplin (Burbridge *et al.* 2004) all show higher precipitation in the Late Holocene than Early–Mid-Holocene. This trend of increasing precipitation can be attributed to progressively greater seasonal southerly penetration of the ITCZ, owing to increasing summer insolation at 10° S, which can in turn be attributed to the precession cycle of orbital Milankovitch forcing (Berger & Loutre 1991). The increased southerly migration of the ITCZ would be expected to have not only increased MAP, but, crucially with respect to the vegetation, shortened the duration of the dry season.

(b) *Vegetation responses inferred from palaeodata*

Over the last glacial–Holocene transition (ca. 21 000–10 000 cal yr BP), forests expanded in southern and eastern Amazonia. Cloud forests had become fully established on the eastern flanks of the Bolivian Andes between 12 500 and 10 000 ¹⁴C yr BP (14 900 and 11 500 cal yr BP; Mourguiart & Ledru 2003), most probably owing to increasing temperatures (Baker *et al.* 2004) and CO₂ concentrations, coincident with forest expansion in Rondonia–Amazonas states (based on stable carbon isotope data; De Freitas *et al.* 2001) and Para state (Absy *et al.* 1991). Populations of *Podocarpus* increased throughout Amazonia through the late glacial, suggesting that the combination of increasing CO₂ levels and precipitation, together with sufficiently cool temperatures, had reduced water stress sufficiently to allow expansion of this predominantly Andean genus throughout the entire Basin. It should be noted, though, that there is considerable temporal variation in the occurrence of this *Podocarpus* peak across the Amazon Basin (Mayle *et al.* 2000; Behling 2001; Ledru *et al.* 2001; Sifeddine *et al.* 2003; Burbridge *et al.* 2004), most probably reflecting the substantial temporal and/or spatial complexity of precipitation and temperature patterns in Amazonia over this interval. The temporal resolution of most of these pollen studies is insufficient to draw precise correlations with the high-frequency climatic oscillations that characterized this period. Humid evergreen rainforest remained significantly less extensive than today in NKMNPP (Mayle *et al.* 2000; Burbridge *et al.* 2004), indicating that dry-season precipitation was still below present-day levels at this time, at least in the Bolivian Amazon.

The Early–Mid-Holocene episode of aridity had a significant impact on plant communities throughout much of Amazonia. Stable carbon isotope data from soil organic matter show expansion of savannah islands at the border of Amazonas and Rondonia states, Brazil (Pessenda *et al.* 1998; De Freitas *et al.* 2001). The increased fire frequencies between 7000 and 3000 ¹⁴C yr BP (7800 and 3200 cal yr BP) in southern Amazonia would be expected to have caused significant structural and compositional changes to the forests, especially increases in drought-tolerant lianas and semi-deciduous tree species. For example the peaks in the dry forest taxa *A. colubrina*, *Astronium urundueva* and *Astronium fraxinifolium*, together with the savannah indicator *Curatella americana* and Poaceae pollen, in combination with high charcoal concentrations, from Laguna Chaplin and Laguna Bella Vista (Burbridge *et al.* 2004) show that the ecotonal area of NKMNPP in southwest Amazonia, which is currently dominated by evergreen rainforest, was instead covered by

a combination of seasonally flooded savannahs and semi-deciduous dry forests throughout most of the Holocene, until *ca.* 3000–1000 cal yr BP. Similarly, at the northern Amazon ecotone of Colombia (e.g. Laguna Loma Linda, 3°18' N, 73°23' W) there was greater extent of savannahs during the Early–Mid-Holocene than in the Late Holocene (Behling & Hooghiemstra 2000, 2001). Forests in the Ecuadorian Amazonian lowlands, which today experience the highest precipitation in Amazonia, remained as early successional communities, dominated by the pioneer tree *Cecropia*, between *ca.* 8700 and 5800 cal yr BP. Weng *et al.* (2002) critically assess the strength of evidence for different possible causes of such frequent forest disturbance (e.g. anthropogenic disturbance, flooding) and conclude that repeated droughts were the most probable reason for tree mortality, and hence increased gap formation.

Although increases in savannah and/or dry forest taxa clearly occurred both at the LGM and Mid-Holocene at ecotonal areas in response to increased water stress, the structural and compositional changes to the plant communities associated with these vegetation responses would be expected to have been significantly different owing to the markedly different climatic and CO₂ regimes driving these changes. Increased water stress at the LGM appears to have been caused primarily by 'ecophysiological drought' caused by the low glacial CO₂ concentrations (Cowling *et al.* 2001), whereas the increased water stress in the Early–Mid-Holocene was caused by 'climatic drought' owing to a reduction in precipitation and/or increased length of dry season, possibly in combination with a Holocene thermal maximum. The associated increase in fire frequencies would not only have driven the expansion of savannahs and fire-adapted dry forest taxa, but also the extinction of any remnant populations of heat-drought-sensitive Andean taxa remaining from the preceding late-glacial period. This climatic aridity caused reduction of the cloud forests in the Bolivian Andes and expansion of open, grass-dominated communities between *ca.* 10 000 and 4000 ¹⁴C yr BP (11 500 and 4500 cal yr BP; Mourguiart & Ledru 2003).

The precipitation increase in the Late Holocene caused renewed expansion of moist evergreen forest. Increasing abundance of Moraceae pollen, concomitant with a reduction in savannah and dry forest indicators, shows that MAP had exceeded the critical minimum threshold of *ca.* 1500 mm, and more importantly that dry season precipitation had exceeded the 100 mm minimum (Sternberg 2001), to allow rainforest communities to expand southwards, replacing savannahs and seasonally dry forests in northeast Bolivia, within the last three millennia to reach their current geographical limit at *ca.* 15° S (Mayle *et al.* 2000; Burbridge *et al.* 2004). Furthermore, these data show that the present-day rainforest boundary in eastern Bolivia constitutes the southernmost extent of Amazonian rainforest in South America over at least the past 50 000 years. Additional evidence for Late Holocene forest expansion comes from Brazil, namely: stable carbon isotope data from Rondonia and Amazonas in southern Amazonia (De Freitas *et al.* 2001) and pollen data from Carajas, Para State, in eastern Amazonia (Absy *et al.* 1991). Close correlation with the increasing water levels of Lake Titicaca (Cross *et al.* 2000; Baker *et al.* 2001a)

and increased precipitation on Sajama Mountain (Thompson *et al.* 1998) reveal that these rainforest expansions can clearly be attributed to increased precipitation, not only in Bolivia, but throughout southern and eastern Amazonia. The fact that forest expansion began somewhat earlier at the northern margin of Amazonia, *ca.* 6000 ¹⁴C yr BP (6800 cal yr BP; Behling & Hooghiemstra 2001), suggests that the increased precipitation was time transgressive. The latter would be expected from the trend of progressively increasing seasonal southerly migration of the ITCZ through the Holocene in response to increasing summer insolation at 10° S predicted by Milankovitch Astronomic Theory.

(c) *Vegetation simulations*

Our SDGVM simulations for plant functional type and NPP at the LGM, Mid-Holocene and Pre-Industrial are broadly consistent with the available palaeovegetation data. Interestingly, the model shows significantly greater evergreen broad-leaf forest and NPP (e.g. LAI or canopy density) at the Mid-Holocene than at the LGM (figure 3), despite the widespread independent palaeodata for Mid-Holocene climate aridity. This suggests that atmospheric CO₂ concentrations (180 p.p.m. at LGM versus 280 p.p.m. at Mid-Holocene) were the overriding control on Amazon vegetation between the LGM and Mid-Holocene, rather than temperature or precipitation, supporting the model sensitivity experiments by Cowling *et al.* (2001). Given that atmospheric CO₂ concentrations were above limiting values throughout the Holocene, and temperatures fluctuated only slightly, the southerly expansion of rainforest and increase in NPP between the Mid-Holocene and Pre-Industrial period must have been driven primarily by the increase in precipitation.

(d) *Anthropogenic influences*

There is archaeological evidence from the heart of the Amazon Basin (quartz spear points at Monte Alegre) that indigenous peoples have lived in Amazonia since at least 11 200 ¹⁴C yr BP (13 150 cal yr BP; Roosevelt *et al.* 1996), while Bush *et al.* (1989) show that maize has been cultivated in the Ecuadorian Amazon since *ca.* 6000 cal yr BP. These findings raise the possibility that ecosystem changes through the Holocene could, at least in part, have been caused by anthropogenic disturbance rather than climatic change. However, the sizes of these Pre-Conquest populations, and hence their ability to significantly alter the landscape, has long been a contentious issue. There is incontrovertible evidence from ceramics, artificial earthmounds and earthen causeways (Denevan 1966; Erickson 1995; Langstroth 1999; Erickson 2000) throughout the seasonally flooded Moxos savannahs of the Bolivian Amazon for major landscape modification by Pre-Conquest native peoples. Although many forest islands in these savannahs have been demonstrated to be natural remnants or fragments of gallery forests on ancient river levees (Langstroth 1999), other forest islands are clearly the result of human activity, whereby forests have invaded artificial earthmounds after abandonment by palaeo-Indians (Denevan 1966; Erickson 1995). Although Burbridge *et al.* (2004) argue against an anthropogenic explanation for the recent rainforest expansion in NKMNP, northeast Bolivia, the possibility that extensive

areas of Amazonian forest ecosystems contain a legacy of centennial–millennial-scale human disturbance (e.g. small-scale deforestation, burning) should not be discounted. It is certainly possible, for example, that some of the charcoal records reflect burning owing to human activity (Behling 1996) rather than climate change, although disentangling the relative importance of these disturbance agents is far from straightforward.

4. PREDICTED VEGETATION RESPONSES TO FUTURE CLIMATIC AND CARBON DIOXIDE CHANGES

The combination of continued large-scale deforestation in Amazonia and global warming due to the enhanced greenhouse gas effect is predicted to have a major detrimental effect upon Amazonian ecosystems, caused in large part by positive feedback between vegetation loss, climate warming and increased aridity. Fifty per cent of precipitation in western Amazonia is recycled from eastern Amazonia through repeated cycles of convective activity due to evapotranspiration from the rainforest, which ultimately receives its precipitation from the Atlantic Ocean. Interruption of this flow of moisture from the Atlantic, by deforestation in eastern Amazonia, would markedly reduce precipitation in central and western parts of the Basin (Shukla *et al.* 1990; Nobre *et al.* 1991). Several studies modelling the outcome of complete deforestation of Amazonia, with various GCMs, simulate a decrease of precipitation in western Amazonia by *ca.* 20–30% and a temperature rise of up to 3 °C (Shukla *et al.* 1990; Zhang *et al.* 2001; Avissar *et al.* 2002; Werth & Avissar 2002). Such a scenario is not beyond the realm of possibility. Laurance *et al.* (2001) simulate that, under their ‘nonoptimistic’ scenario of current deforestation trends, southern and eastern Amazonia will be largely deforested by AD 2020, with extensive forest fragmentation in central and northern parts of the Basin, and pristine forests confined largely to the western quarter of Amazonia. Furthermore, by AD 2050, when CO₂ concentrations are predicted to have doubled, Cox *et al.* (2000) simulate, using a fully coupled carbon-climate model, that the Amazon Basin will have changed from a net carbon sink to a net carbon source, thus accelerating climate warming and forest degradation.

Interestingly, the deforestation and rising CO₂ concentrations over the past 40 years have yielded no empirical evidence for overall drying of Amazonia, suggesting that the feedbacks between these different variables are more complex than previously thought (Curtis & Hastenrath 1999), and may relate to opposite precipitation anomalies between northern and southern Amazonia, which lie in opposite hemispheres (Marengo *et al.* 1993, 1998; Marengo 1995). Perhaps a critical threshold of deforestation (i.e. reduction in precipitation recycling through evapotranspiration) needs to be achieved before noticeable precipitation reduction ensues (Avissar *et al.* 2002).

What can the fossil pollen records and palaeovegetation model simulations tell us about the likely responses of Amazonian ecosystems to these predicted future climate changes? The proxy data and model simulations for the Early–Mid-Holocene (centred *ca.* 6000 cal yr BP), when aridity, and possibly temperatures, were higher than

present, suggest that future precipitation decreases coupled with warming would result in frequent widespread fires throughout southern and eastern Amazonia, which would lead to competitive replacement of lowland evergreen rainforest taxa by drought–fire-tolerant semi-deciduous dry forest taxa and cerrado savannahs. However, the Early–Mid-Holocene should not be considered a perfect analogue for the future for two key reasons. First, atmospheric CO₂ concentrations are projected to be at least twice Mid-Holocene levels by AD 2050, suggesting that mixed liana forest and/or semi-deciduous forest (dominated by C₃ plants) may be competitively favoured over savannahs, which are dominated by C₄ grasses. Secondly, the amplitude and frequency of ENSO, which causes increased aridity in most of Amazonia during strong El Niño years, is significantly greater today than it was in the Early–Mid-Holocene (Tudhope *et al.* 2001; Moy *et al.* 2002).

The pollen record from the eastern flank of the Bolivian Andes (Mourguiart & Ledru 2003) suggests that the cloud forests would be largely eliminated. This possibility is supported by Bush (2002*b*) who estimates that a 3 °C temperature rise would cause the cloud base and frost limit to rise up the Andes by 600 m (almost half the vertical space currently occupied by cloud forest). This would produce climatic conditions favourable for agriculture and settlement, and hence one would expect that in this ‘land-hungry’ part of Amazonia, any land below the cloud base would be rapidly deforested. As with the rest of Amazonia, rates of ongoing deforestation far exceed the natural ability of species to respond to climate change by migration. Consequently, ecotonal areas (e.g. between the puna, cloud forest and upland rainforest on the Andes, and between rainforest, cerrado savannahs and semi-deciduous dry forests in the lowlands) should be the target of conservation strategies to allow ‘natural’ species movements and plant community reassortments to occur.

5. CONCLUSIONS

Both fossil pollen data and dynamic, process-based vegetation simulations show that most of the Amazon Basin remained forested at the LGM, although there was some replacement of forest by savannahs at the ecotonal areas towards the northern and southern margins of the Basin. The combination of a 5 °C cooling, 32% reduction of atmospheric CO₂ concentrations, and a possible 20% reduction in precipitation, relative to Holocene levels, caused marked compositional and structural changes to these glacial-age forests. Populations of Andean taxa such as *Podocarpus* and *Alnus* increased throughout Amazonia to form mixed communities with rainforest taxa. Humid evergreen species dominated the wetter central and northwest parts of the Basin, although our model simulations suggest that the more seasonal southern parts of Amazonia were instead dominated by semi-deciduous dry forest taxa. These simulations suggest that water stress caused by a combination of reduced precipitation and lowered CO₂ concentrations caused a marked decrease in rainforest NPP and canopy density. Although the Bolivian–Peruvian Altiplano, above the southwest rim of the Amazon Basin, was 20–75% wetter at the LGM than today, palaeodata from the adjacent Amazon lowlands,

together with GCM models, suggest that the bulk of this precipitation did not come from Amazonia, as it did in the Holocene and does today, but instead from the Pacific Ocean.

Rainforest distribution increased in response to rising temperatures, atmospheric CO₂ concentrations and precipitation during the last glacial–Holocene transition, although not as far southward as today. During the Early–Mid-Holocene (*ca.* 8500–3600 cal yr BP) a marked decrease in precipitation (e.g. 40% below modern values on the Altiplano), possibly in combination with higher temperatures, affected much of the Amazon Basin, causing increased fires and consequently greater ecosystem disturbance, which would be expected to have caused structural as well as compositional changes to plant communities, such as expansion of drought-tolerant lianas and semi-deciduous taxa within forests and expansion of savannahs at forest–savannah ecotones. Populations of cold-adapted species (e.g. *Podocarpus*) were largely eliminated from the Amazon lowlands during this interval, and cloud forests on the eastern flanks of the Bolivian Andes diminished while open, grass-dominated ecosystems expanded.

Increased precipitation in the Late Holocene (*ca.* 4000–3000 cal yr BP) caused reduction in fire frequencies and consequently renewed expansion of rainforests. This long-term trend of progressively increasing precipitation between the Early Holocene and the present can be attributed to increased seasonal, southerly migration of the ITCZ, in turn owing to progressively higher December–January–February insolation at 10° S predicted by Milankovitch orbital forcing. The critical factor for these vegetation responses would not have been the increase in MAP *per se*, but instead the decreasing length or severity of the dry season.

The magnitude of impact of palaeo Indians upon Amazonian vegetation through the Holocene is largely unknown, owing to the paucity of archaeological artefacts, the difficulty in distinguishing anthropogenic from climatic agents of disturbance, and huge uncertainty over the size of Pre-Conquest palaeo Indian populations. The exception, however, is the Bolivian Beni in southwest Amazonia, where there is well-documented archaeological evidence that much of the forest–savannah mosaic in these seasonally flooded plains is an artificial landscape created by palaeo Indians.

The predicted 3 °C rise in temperatures and 20% reduction in precipitation in Amazonia over the twenty-first century, would, under natural conditions, be expected to cause similar vegetation responses to those of the Early–Mid-Holocene, i.e. renewed expansion of drought-adapted plants such as semi-deciduous–deciduous dry forest trees, lianas and savannahs in response to increased fires and water stress brought about by an increase in aridity and/or length of the dry season. The lower limit of tropical cloud forests would be expected to increase in elevation in response to the rising cloud base. Continued deforestation would no doubt accelerate these vegetation changes because a decrease in forests would itself lead to reduced evapotranspiration and hence increased temperatures and reduced precipitation.

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GLOSSARY

- ECMWF: European Centre for Medium-Range Weather Forecasting model
- ENSO: El Niño–Southern Oscillation
- GCM: general circulation model
- ITCZ: Intertropical Convergence Zone
- LAI: leaf area index
- LGM: last glacial maximum
- MAP: mean annual precipitation
- NKMNP: Noel Kempff Mercado National Park
- NPP: net primary productivity
- SDGVM: University of Sheffield Dynamic Global Vegetation Model
- SST: sea-surface temperature
- UGAMP: UK Universities Global Atmospheric Modelling Programme