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Observations on Late Pleistocene cooling and precipitation in the lowland Neotropics

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ABSTRACT: Although accurate reconstructions of Amazonian palaeoclimates are central to understanding the distribution and history of Neotropical biodiversity, current reconstructions based on proxy data are discordant and subject to intense debate. We review some current thinking in Amazonian climatology and incorporate some new ideas in an attempt to explain the apparently contradictory records of palaeoprecipitation from across the Amazon Basin. We suggest that palaeoecologists need to recognise that organised convective radiation, the process that induces most wet season rainfall in Amazonia, should be treated as a phenomenon related to, but separate from, the passage of the inter-tropical convergence zone (ITCZ). Decoupling ITCZ migration from larger convective activity provides a mechanism to account for observed palaeoclimatic heterogeneity. Patterns of observed precipitation change are consistent with the long-term persistence of closed forest across much of Amazonia, indicating that the greatest changes in precipitation during the last glacial maximum came during the wet season, which would have little negative impact on forest extent. Neotropical cooling at the last glacial maximum (LGM) is widely accepted, although the estimates of that cooling range between 1 °C and > 5 °C. In answering the basic question 'What is meant by cooling?' we observe that interhemispheric ice mass asymmetry may have caused cooling to be manifested differently according to location. A terrestrial cooling of ca. 5 °C, as well as radiative cooling and event-based cooling combined to induce vegetation change. Probably, both absolute temperature and mean monthly minima were reduced by polar air incursions in the northern Neotropics. However, in the southern Neotropics, mean monthly minima were reduced by more frequent incursions of Patagonian air masses, but absolute minima may have been largely unchanged. Copyright © 2004 John Wiley & Sons, Ltd.

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KEYWORDS: Amazonia; climate change; cold fronts; convection; ice age; ITCZ, precipitation; radiative cooling; trade wind.

Introduction

Modern climate distribution in the Amazon basin is complex, with annual rainfall varying from 1690 mm to 7900 mm over distances as short as 200 km, and mean annual temperatures varying from 22.5 °C to 28 °C (NOAA, 2004). Response to oceanic climatic forcing is equally varied, with some areas of the Amazon basin responding more strongly to changes in Pacific sea surface temperatures (SSTs) and others responding more to changes in Atlantic SST. Indeed, the same SST anomaly can either decrease or increase rainfall depending on location in the Amazon basin (Pezzi and Cavalcanti, 2001). Debate over past climates in Amazonia, however, has frequently been simplistic, polarized into arid versus wet, or cold versus warm (Colinvaux *et al.*, 1996; Hooghiemstra and van der Hammen, 1998).

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As modelled and empirical data replace conjecture, a complex image of Amazonian palaeoclimate emerges—one that, like modern climate, is both spatially and temporally heterogeneous. Recent general circulation models (Ganopolski *et al.*, 1998; Hostetler and Mix, 1999) for the last glacial maximum (LGM) support this view of complexity, suggesting that precipitation patterns did not change uniformly across Amazonia. The model of Hostetler and Mix (1999) predicts a reduction in wet season rainfall, with dry season rainfall (June–July–August (JJA) in southern Amazonia, December–January–February (DJF) in northern Amazonia) unchanged, or slightly increased. Such observations are entirely consistent with palaeoecological data suggesting that changes in precipitation across Amazonia were asynchronous and spatially variable (Absy *et al.*, 1991; Colinvaux *et al.*, 1996; Behling and Hooghiemstra, 1999; Colinvaux *et al.*, 2001; Ledru and Mourguiart, 2001; Bush, 2002; Bush *et al.*, 2002).

Rather than trying to look for climatic uniformity across Amazonia, it is more profitable to consider why predictable heterogeneity should be the norm rather than the exception, and how this heterogeneity might translate into predictable patterns of vegetation community change. In particular, we suggest that two simplifications that have been made: (1) the combination of two related but separate processes under 'migration of the ITCZ', and (2) the catchall term 'cooling', are too imprecise to be helpful. This paper presents a synthetic overview of South American climate, palaeoecology, and new ideas regarding Pleistocene palaeoclimatology and the eco-physiological effects of changing climatic conditions.

Differential forcing of the ITCZ and organized convection

The ideas that we advance within this section are well established within the climatological community, but have not been broadly adopted by palaeoecologists. The inter-tropical convergence zone (ITCZ) figures prominently in recent discussions of Neotropical palaeoclimate (Martin *et al.*, 1997; Hostetler and Mix, 1999; Mix *et al.*, 1999; Mayle *et al.*, 2000; Bush *et al.*, 2001; Ledru and Mourguiart, 2001; Haug *et al.*, 2003). Strictly defined, the ITCZ is formed by the convergence of the trade winds. The low-level convergence results in ascending limbs of the northern and southern Hadley cells marked by a cloud band and a high probability of thunderstorms (Horel *et al.*, 1989). This cloud band forms most strongly over the oceans where it migrates between about 5 °N of the equator in the northern hemispheric summer (JJA), and about 2 °S of the equator in the southern hemispheric summer (DJF). Over land the ITCZ is more diffuse, but occupies a similar latitudinal range. The cloudiness associated with the ITCZ over the Amazon basin, however, is predominantly due to organised convection rather than the ITCZ per se (Marengo, 1995; Hastenrath, 1997). Moisture carried onshore by the trade winds and the evapotranspirational loss of the forest itself provide the humidity that fuels organised convective activity as the solar equator moves over the South American continent, increasing heat energy in the atmospheric system (Fig. 1). Great cloud masses that extend to ~20 °S over Amazonia in the southern hemispheric wet season (DJF) are the combination of increased oceanic advection and increased evapotranspiration due to higher solar angles. The combination of wet air and a heated land mass produces rains throughout Amazonia.

The term ITCZ, as used by most palaeoecologists, generally does not distinguish between the ITCZ *proper* and the Amazonian convection centre (Hastenrath, 1997), or the Bolivian High (e.g. Martin *et al.*, 1997; Mayle *et al.*, 2000; Fritz *et al.*, 2001; Ledru *et al.*, 2001). At issue is whether the ITCZ truly develops a southern extension deep into Amazonia. If the ITCZ is regarded as an essentially marine phenomenon, it is depicted either disappearing over South America or only penetrating about 2 °S (e.g. Moran and Morgan, 1991). When storm activity is used to identify the location of the ITCZ the complexity of storm causation is overlooked. Storms can result from many phenomena, e.g. fronts, topographic effects, sea-breeze effects or the South Atlantic convergence zone (SACZ), rather than the direct influence of the ITCZ. Consequently, when cloudiness associated with storms is used as a surrogate to map the ITCZ, the position of the convergence is erroneously shown penetrating between 12 °S and 20 °S (e.g. Cerveny, 1999; Fritz *et al.*, 2001). Most recent models of palaeoclimatic change have used cloud location to infer the position of the ITCZ, and some show the ITCZ extending more than 20 °S (Martin *et al.*, 1997; Maslin *et al.*, 2000; Ledru and Mourguiart, 2001). However, we believe that this definition of the ITCZ obscures the underlying causes of the southern hemispheric wet season and, more importantly, masks factors important to past climate reconstructions. Specifically, changes in the strength of the trade winds will have large consequences for Amazonian rainfall (Marengo and Nobre, 2001). Strength of the trade winds and the Amazonian convection centre in turn controls moisture export to subtropical South America through interactions with the SACZ (Zhou and Lau, 1998). Both of these could be important controls on plant community changes at the southern margin of the Amazon basin (e.g. Mayle *et al.*, 2000).

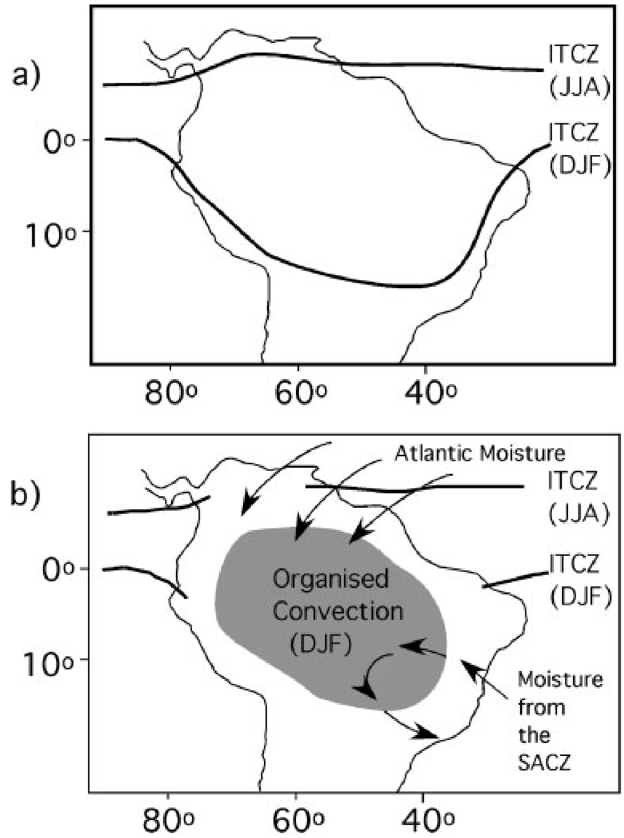

Figure 1 Two depictions of the inter-tropical convergence zone (ITCZ) over South America. (a) A common but misleading depiction of the ITCZ, which does not discriminate between the ITCZ proper and organized convection. (b) The ITCZ plotted as an essentially marine phenomenon following the upper tropospheric trough, discrete from the organized convection found over land

Solar forcing and the ITCZ

While the ITCZ and organised convection behave synchronously under modern conditions, they can respond in different ways to different forcing mechanisms (e.g. Milankovitch cycles, strength of the trade winds, convective activity, albedo changes due to changes in land cover, cooling of Amazonia). It is therefore important that they be regarded as separate entities in palaeoclimatic reconstructions (e.g. Baker *et al.*, 2001b).

On a millennial scale the relative strengths of the ITCZ north and south of the equator are asymmetric (Fritz *et al.*, 2001). The cycle of strong to weak phases of the ITCZ is defined by the 19 000 and 22 000 year rhythm of orbital precession (e.g. Berger, 1978). For example, at 22 000 yr BP the ITCZ was weak in the northern hemisphere (Fig. 2), but strong in the southern hemisphere. A weak ITCZ in the northern hemisphere would result in decreased wet season rainfall in northernmost South America, Central America and the Caribbean. In the southern

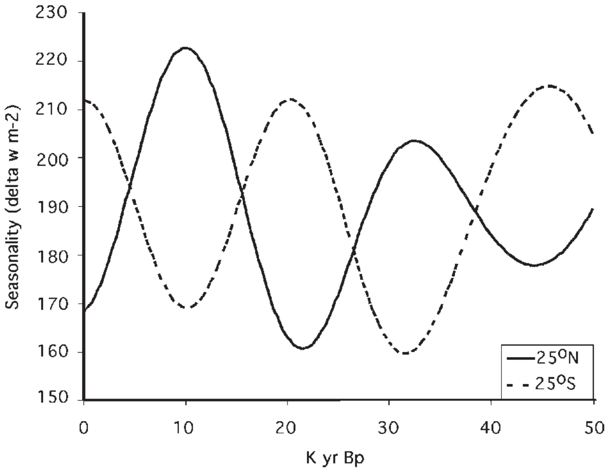

Figure 2 Variations in seasonality at 25 °N and S over the last 50 000 years, Seasonality is expressed as the difference in watts m^{2-1} between seasonal maximum and minimum insolation using December–January–February and June–July–August values. Data derived from Analyseries 2.1 (Paillard *et al.*, 1996) using the equations of Berger (1978)

hemisphere, the effect of a strengthened ITCZ would be strengthened trade winds and increased advection of moisture into northeastern Amazonia, thereby increasing moisture available to organised convection. Thus, seasonality, which we take to be the difference between wet season and dry season precipitation, should also follow this cycle, with maximal seasonality coinciding with the strongest occurrence of the ITCZ in that hemisphere.

Although the precessional signal is a pacemaker for ITCZ activity in each hemisphere, this basic pattern is modified by other influences such as sea-surface temperature and the size and proximity of ice masses. The following observations on both the influence of ice masses and the physical geography of North and South America lead to novel predictions regarding past Amazonian climates.

Ice sheets and temperature gradients

The development and extent of the Laurentide (northern hemisphere) ice sheet had the effect of increasing the temperature gradient between the ice front and the equator. The growth of this ice mass is thought to have split the north polar jet, forcing the southern limb ca. 10 °S towards the equator from its present position (CLIMAP, 1981). Although Heinrich events and Dansgaard–Oeschger cycles may have induced oscillations in the flow of the north polar jet (Bond *et al.*, 1993), the Laurentide ice mass was still large enough to dominate North American climate systems for the last 40 000 years of the Pleistocene. The consequent increase in the equator–ice front temperature gradient had the effect of inhibiting the northward migration of the ITCZ, keeping it positioned closer to the equator in the northern hemispheric summer (Markgraf, 1999).

The expansion of Antarctic sea ice led to a ca. 2–3° latitude northward migration of the southern polar jet and the westerlies (Markgraf, 1999; Bradbury *et al.*, 2001), although this temperature shift was less marked than that associated with the Laurentide ice sheet expansion in the northern hemisphere. The most pronounced influence that the southern hemispheric westerly migration would have had on Amazonia was more frequent incursions of winter cold fronts emanating from the south (Marengo and Rogers, 2001).

Physical attributes and climate

The physical setting of Amazonia strongly influences regional climates. High mountains lie to the west and north, with continent-wide plains stretching eastward to the Atlantic. To the north, the tepuis, Cordillera Oriental and Andean outliers form a ridge of high ground that isolates the Caribbean coast from the interior of northern Amazonia. Prevailing easterly winds drive moisture from the equatorial and mid-latitude Atlantic across the flat plain of Amazonia. Eventually those moist air masses leave Amazonia, either by being forced up over the Andes, or incorporated into the low-level jet east of the Andes, swinging south and east across the low Hills of the Mato Grosso towards the Atlantic (Curtis and Hastenrath, 1999).

The north–south axis of the Andes and lack of east–west orientation of mountain barriers promotes the flow of Antarctic air northward (Marengo and Rogers, 2001). Presently, incursions of cold wet air derived from the southern westerlies can occur 10 months of the year (Cerveny, 1999). These cold frontal systems are known locally as *friagen* (Brazil), *friajes* (Peru) or *surazos* (Bolivia). These fronts surge northward bringing night-time frosts to southern Brazil and dissipate as they spread across Amazonia, so that by the time they reach Manaus night-time temperatures are almost unaffected. However, the days are several degrees cooler than usual due to cloudiness (Marengo and Rogers, 2001). Consequently, frontal systems spawned in the high latitudes are clearly felt at Manaus (2 °S), Brazil, though their ecological impacts are probably much less marked than in southern Amazonia.

A similar north–south orientation of mountains in North America channels air flow southward. Outbreaks of continental polar air can penetrate deep into Central America, and are even given a local name, *Invierno de las Chicharras*, as far south as Venezuela. Under modern conditions, few air masses penetrate further south than 20 °N because they usually dissipate over the warm interior of Mexico or over the warm seas of the Gulf of Mexico and the Caribbean (Marengo and Rogers, 2001). However, some cold fronts penetrate to 7°N and last as long as 6 days while lowering temperatures by >5°C (Schultz *et al.*, 1998). The presence of the Laurentide ice mass and the southerly displacement of the north polar jet would have promoted deeper, colder, and more frequent incursions of these fronts.

In contrast to north–south flow of cold air, precipitation largely flows east to west across Amazonia. The lack of a topographic barrier within Amazonia allows the flow of easterly winds from the Atlantic to the Andes. The only interruptions to the flow of moisture are convectional cycles. Some estimates suggest that about 50% of precipitation in Amazonia is derived from water transpired within the basin, and that this effect is strongest in western Amazonia (Salati, 1985; Moran and Morgan, 1991).

What is 'cooling'?

For some years a troubling disparity has been evident between the sea surface temperature estimates of much of the tropical Atlantic (2–3 °C cooler at the LGM than present; Hostetler and Mix, 1999) and data for a stronger cooling of terrestrial environments (ca. 5 °C reduction at the LGM; e.g. Bush *et al.*, 2001). Attempts have been made to reconcile these data by invoking Pleistocene adiabatic lapse rates of >7°C per 1000 m of ascent (e.g. van der Hammen and Hooghiemstra, 2000). However, a marked increase in lapse rate at the LGM is improbable. For lapse rates significantly to rise above the modern value of ca. 5.2 °C per 1000 m of ascent requires low humidity conditions. Available evidence points to *equal to or wetter than modern* conditions at low to mid elevations at the LGM on the Andean flank, rather than the xeric conditions required for increased lapse rates (Liu and Colinvaux, 1985; Bush *et al.*, 1990; Baker *et al.*, 2001a, 2001b).

We argue that a likely explanation for the apparent discrepancies between the terrestrial and oceanic temperature histories is that the various data sets are measuring different parameters. The tropical sea surface temperature data (with the notable exception of the Cariaco Basin) are primarily from the deep ocean, and represent a strongly buffered system with very slow rates of sedimentation. The resolution of this record is probably centennial at best, and the resulting data provide long-term average temperatures (Lea *et al.*, 2000). Contrastingly, the coral reef isotopic data used by Guilderson *et al.* (1994) to determine a 5 °C Caribbean cooling at the LGM are effectively a series of snapshots of conditions affecting coral growth in shallow water. Growth of shallow water corals is more likely to be influenced by winter minima or circulatory changes than would be the growth of deep ocean organisms (Gagan *et al.*, 2000).

Because pollen assemblages reflect the distribution of local vegetation, they provide a proxy for both mean and absolute minimum temperatures (Bush and Colinvaux, 1990; Colinvaux *et al.*, 1997; Weng *et al.*, 2004). While no comprehensive distributional study has been undertaken for any Amazonian plant species, temperate plant distributions are often determined, not by mean conditions, but rather by extreme, episodic events (Shreve, 1921; Hocker, 1956; Nobel, 1980). Periodic frosts that kill coffee and other warm-climate plants are the best-documented examples of the sensitivity of tropical taxa to extreme temperatures (Marengo and Rogers, 2001). Susceptibility to cold events is often common to all members of a genus, or even family, in plants. Variability in response to chill damage starts in some families at temperatures as high as 12 °C (Scowcroft and Jeffrey, 1999; Allen and Ort, 2001).

Cooling: background and event-related

We suggest that the potential sources of the Pleistocene cooling can be divided into (a) a general, or background cooling, related to long-term changes in solar radiation due to orbital variations, concentrations of greenhouse gases and patterns of cloud formation, and (b) event-related cooling, related to weather. These factors may have been expressed differentially in lowered mean annual and monthly temperatures and in some, but not all cases, lowered absolute minimum temperatures.

Background cooling

While cooling of the oceans would bring cooler oceanic air into northern and eastern Amazonia, a more general trend of cooling may have been attributable to reduced atmospheric greenhouse gas concentrations (CO_2 and CH_4). At the LGM, CO_2 concentrations were only 180 ppmV (V = volume), i.e. half their modern value, making the atmosphere more transparent to long-wave radiation and allowing increased radiative exchange, which would cause more heat loss on clear nights. A first approximation of the magnitude of this effect can be made by adopting the estimate that a doubling of CO_2 concentrations induces a radiative change of $\sim 4\,\mathrm{W m^{-2}}$. Halving the modern CO_2 value (370 ppm) to the LGM level of 180 ppm yields a cooling of ca. 2.4 °C relative to present (Campbell and Norman, 1998; P. Foster, pers. comm.).

Increased radiative heat loss due to decreased atmospheric CO_2 and CH_4 concentrations is modulated by cloud cover. The degree of radiative cooling of objects depends on heat exchange with the night sky, which is, in turn, limited by the concentration of greenhouse gasses. This cooling is independent of frontal systems and is likely to have been even more extreme at higher elevations due to the less dense atmosphere and, in particular, the decreased absolute moisture content of the air. Consequently, a reduction in night-time cloud cover would cause significant radiative cooling. Thus, the radiative heat loss could produce effective temperatures of objects in the environment lower than those predicted by the mean air temperature, especially in dry or predominantly cloudless regions. Such cooling could lower the upper altitudinal boundary of plant species ranges, including timberline, not due to direct CO_2 effects (Jolly and Haxeltine, 1997), but rather by chill and freeze damage due to more extreme night-time radiative cooling induced by lowered partial pressures of CO_2 and CH_4. Beneath the cloud-free nights common in the Andes, additive radiative cooling supplementing background cooling may have induced the 6–8 °C cooling documented in many vegetation records (Hooghiemstra, 1984; Bush *et al.*, 1990; Bush *et al.*, 2004). The dry season in the lowlands combines increased penetration of cold air masses with a high proportion of clear days. Canopy trees exposed to cold temperatures and clear night skies could be especially affected by radiative cooling.

Lower cloud base formation and radiative fog would also be likely in a cooler Amazon basin if, as is suggested by current model and climate proxy data, moisture levels were similar to those of today (Hostetler and Mix, 1999). If the cloud base lowers with respect to decreasing temperature, as it has been demonstrated to rise with increasing temperature (Diaz and Bradley, 1997; Pounds *et al.*, 1999; Still *et al.*, 1999; Lawton *et al.*, 2001), lower montane forests, and perhaps even lowland Amazonian forests, may have experienced significant cloud immersion during the Pleistocene. The occurrence of radiative fog would also be expected to increase with lower CO_2 concentrations on clear nights due to the increased radiative loss causing stronger temperature inversions. Radiative fog is common in western Amazonia, occurring throughout the dry season and strongest on nights with clear skies and cool temperatures. At the LGM fog may have occurred more frequently and been slower to burn off, which would have had two ameliorating consequences regarding the effects of climate on plants. First, a major cause of chill damage in 'warm climate' plants is not cooling per se, but rather exposure to intense sunlight after cooling (Allen and Ort, 2001). Fog on the coldest nights would decrease radiative exchange between leaves and sky, whilst the presence of fog in the morning would increase the time leaves have to recover from cooling before they are exposed to direct sunlight. Furthermore, clear dry season nights in western Amazonia are accompanied by heavy dew due to radiative cooling of tree canopies. With increased nocturnal cooling, the harvesting of moisture from both dew and fog could have offset decreases in rainfall in Amazonian systems as it presently does in montane and temperate coastal systems (Cavelier and Solis, 1996; Dawson, 1998).

Event-related cooling

Extreme events such as outbreaks of polar fronts that penetrate toward the equator could provide short-lived but biologically important cooling. De Oliveira (1992), Ledru

(1993), Colinvaux *et al.* (2000) and Ledru and Mouguiart (2001) suggested the palaeoclimatic importance of high-latitude frontal systems. These fronts are strongest in the austral winter and result in subcontinental-scale cooling (Garreaud *et al.*, 2003). Describing the effect of such events on an Amazonian forest is germane to understanding the biological stresses imposed by *friajes*.

A typical *friaje* arriving in Madre de Dios, Peru, is presaged by a day of cloudiness. A sudden drop in temperature and a series of squalls marks the arrival of the front. Air temperatures ahead of the front are typically ca. 23–30 °C, with measured decreases of up to 12 °C in half an hour recorded at Cocha Cashu Biological Station, Peru, (12 °S 79 °W). On that occasion, the temperature reached a minimum of 9.8 °C (the coldest recorded is 8.5 °C, with temperatures of 10–12 °C recorded annually), accompanied by wind and heavy rain. The following day was wet, with a maximum temperature of 14 °C. Although in 2001 we experienced a *friaje* that lasted for 6 days, these phenomena typically last 2–3 days, with 10–20 per dry season. Most trees survive these *friajes* and no especially high rates of mortality appear to be directly linked to their arrival, save for cyclonic damage (Foster and Terborgh, 1998).

As the fronts proceed equatorward they weaken, so that in Cuyabeno, Ecuador (0 °S), the coldest recorded temperature is 13 °C (E. Asanza, pers. comm.). When sitting on the bank of the Rio Madre de Dios, Peru, with teeth chattering and breath visible in the air, the question came to mind: 'Would the Pleistocene really have been 5 °C colder than this?' Could Peruvian Amazonia at 240 m elevation really have been regularly subjected to temperatures of 3.5 °C? Most tropical plants would probably be severely damaged by regular exposure to such low temperatures (e.g. King and Ball, 1998; Scowcroft and Jeffrey, 1999; Allen and Ort, 2001), and yet this section of the Amazon basin is species-rich in all Amazonian taxa.

A key distinction needs to be made between absolute minimum temperatures and mean monthly minima. Often these climatic variables are closely correlated, but we suggest that the polar incursions of the LGM could have been manifested differently in the northern and southern hemispheres. We suggest that southerly fronts arrived with increased frequency and over more of the year, rather than being more intense. These fronts, spawned by the westerlies, would have started about 2–3 °N of their present position. Perhaps a little more intense at a given latitude than their modern counterparts in the temperate regions of South America, these air masses would have been weakened as they pushed northward. The basic geography of South America has not changed in the Quaternary. The fronts are channelled along the base of the Andes before splaying out and dissipating in the great interior plains of South America (ca. 20 °S). The cold dense air of the fronts drive beneath the relatively warm local air masses, which at the LGM may have been ca. 5 °C cooler than present, and therefore denser and harder to displace. Ultimately, as the polar air mass moves northward and is warmed, the front dissipates. Although starting from a few degrees further north, the fronts would have faced similar obstacles to those of the present. Thus, the penetration strength of fronts at the LGM may have been essentially similar to those of today and would not induce a 5 °C lowering of absolute minimum temperatures. However, their more frequent occurrence through more of the year would lead to a lowering of mean monthly and annual temperature minima, which is actually what the palaeoecological data probably reflect, rather than a 5 °C decrease in absolute minimum temperatures.

The asymmetry of ice masses at the LGM leads to different predictions for the influence of frontal cooling on the northern Neotropics. Although the barriers facing Antarctic polar air incursions were largely unchanged, the physical geography of the northern hemisphere was radically different. The vast Laurentide ice mass split the north polar jet and provided a much more southerly point of origin for cold air masses than at present and also a means to push that air southward. Furthermore, the mediating influence of the Caribbean was reduced because of lowered sea levels and cooler surface waters in the critical winter months. Under these conditions it has been suggested that polar air can be expected to penetrate deeper into Central and South America, reaching areas that currently do not have a direct polar influence (Ledru and Mourguiart, 2001). Consequently, in Central America and northern South America, not only were mean monthly temperature minima affected by more frequent incursions, but absolute minima would also have been reduced. In the lowlands of Panama and Colombia modern absolute minima are ca. 13–14 °C; a 5 °C cooling below these temperatures would still allow the survival of most stenothermic tropical species.

Palaeoprecipitation and forest extent

Palaeoclimatic models consistently point to a reduction in Amazonian precipitation at the LGM (e.g. CLIMAP, 1976; Ganopolski *et al.*, 1998; Kutzbach *et al.*, 1998; Hostetler and Mix, 1999; Maslin *et al.*, 2000). Although these models differ in the amount of reduction in paleoprecipitation, ranging from 1 mm per day to 5 mm per day in DJF, they all suggest that DJF—the wet season over much of Amazonia—was drier than modern. However, the dry season, JJA, was as wet as or wetter than present. The intensity and duration of the dry season are thought to be the dominant influences on plant diversity and forest composition in the modern Amazon basin (Gentry, 1988; Clinebell *et al.*, 1995). Hostetler and Mix (1999) observed that their Oregon State University model prediction of a 5 mm per day precipitation reduction in DJF was consistent with an arid Amazonia hypothesis. However, their conclusion was not justified and their data, as presented, are inconsistent with widespread changes in biome type. DJF is the wet season in much of Amazonia, a time of flooding and water surpluses in the system. Model simulations by Sternberg (2001) suggest that forests will be highly resistant to wet season shifts in precipitation. The model predicts that forest is only replaced by scrub or savanna when the rainfall of the three driest months falls below 28–37 mm (Sternberg, 2001). Hence the reduction of 5 mm per day during the wettest months of the year would not induce a shift of biome. Indeed, reductions in rainfall in the wet season are correlated with increased tree growth and reproduction in modern studies from rainforest in Central America (Clark and Clark, 1994; Wright *et al.*, 1999). Growth rates are more closely tied to dry season precipitation than wet season precipitation in deciduous species in Amazonian forests with marginal rainfall (Worbes, 1999).

While modern vegetation distributions are not sensitive to wet season precipitation, modern lake levels are. A decrease in wet season precipitation would present a drying signal in lacustrine systems that would not be manifested by widespread changes in forest cover, or even composition (e.g. Colinvaux *et al.*, 2000; Bush *et al.*, 2002).

Dry seasons are most pronounced along the southern and western edges of Amazonia (Fig. 3), contrasting with the general pattern of increasing precipitation from east to west across central Amazonia (Nix, 1983). As the amount of rain falling in the dry season is highest in eastern Amazonia, this region is likely to be rather resistant to biome shifts (contra Haffer, 1969; Bush, 1994; Hooghiemstra and van der Hammen,

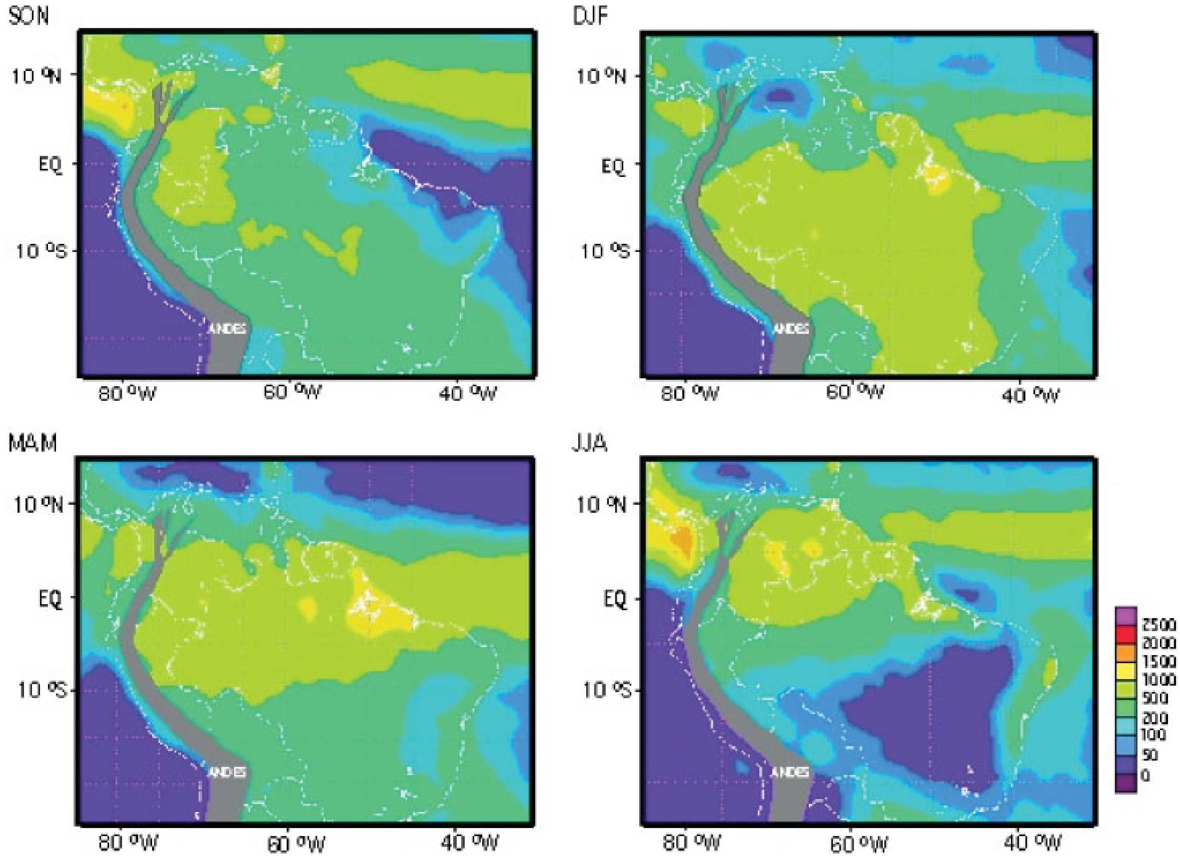

Figure 3 Quarterly precipitation data for Amazonia (1998–2001). DJF, December–January–February; MAM, March–April–May; JJA, June–July–August; SON, September–October–November. Data from Tropical Rainfall Measuring Mission (TRMM), courtesy Z. Liu

1998; van der Hammen and Hooghiemstra, 2000). The southern and southwestern boundaries of Amazonia have both low dry season and annual precipitation, making these areas sensitive to biome turnover. However, none of the models indicate stronger dry seasons for these latitudes at the LGM. At this southern margin, lake sediment records often contain substantial gaps or slowing of sedimentation rates that would be consistent with dry or intermittently flooded sites (Absy *et al.*, 1991; Ledru *et al.*, 1998; Burbridge *et al.*, 2004). Although such sedimentary hiatuses have been interpreted to indicate regional aridity (e.g. Absy *et al.*, 1991), they may only reflect a reduction in wet season precipitation sufficient to cause lake level to fall, but not enough to substantially change regional vegetation. The palynological observations that forest cover was not broken, in regions other than in areas of the most extreme climates (e.g. van der Hammen, 1974; Mayle *et al.*, 2000; Carneiro *et al.*, 2002), is entirely consistent with records of periodically reduced precipitation and reduced Amazon discharge.

Toward the ecotonal boundaries where modern drought stress favours C_4 over C_3 photosynthetic pathways, low atmospheric partial pressures of CO_2 at the LGM could have favoured some savanna expansion (Mayle *et al.*, 2004). In other areas where the combined, but partially offsetting, effects of low temperature and low CO_2 increased seasonal soil moisture deficits, the vegetational response may not have been a replacement of forest, but rather a simplification of forest structure. Cowling *et al.* (2001) model that such deficits may have reduced LGM net primary productivity and leaf area index across substantial portions of Amazonia. For the moment, the effect of lowered CO_2 levels on these forests remains an interesting but poorly documented issue (Mayle *et al.*, 2004).

It is important to note that even if, contrary to our expectations, much of Amazonia dried out by 25–40%, developed a strong 3-month dry season and experienced a 3 °C cooling, the new conditions throughout most of Amazonia would closely parallel those that exist today in western Amazonia from Pucallpa, Peru to northern Bolivia (NOAA, 2004); a region with one of the richest evergreen rainforests on the continent.

Conclusions

Late Pleistocene palaeoclimatic patterns within the Amazon basin were likely as diverse as those of today. Decoupling the migration of the ITCZ from organised convection over Amazonia shows two linked, but independent systems that are potentially driven by different forcing mechanisms. While the modern ITCZ responds to insolation and sea surface temperature (Marengo and Nobre, 2001), the ITCZ of the LGM was probably also influenced by a steepened thermal gradient between the Laurentide ice mass and the equator (Whitlock *et al.*, 2001). Organised convection is a function of moisture entering the system and evapotranspiration, which, in turn, is determined by the moisture of the soil surface and land surface temperature. Northern Amazonia is directly influenced by the ITCZ and the moisture it introduces, whereas southern Amazonia is primarily influenced by a combination of moisture derived from the ITCZ, convective activity and, especially in southeastern Amazonia, moisture from the SACZ (Zhou and Lau, 1998). Consequently, climatic heterogeneity over millennial to Quaternary time-scales is to be expected.

Model simulations and palaeoecological data suggest that precipitation change at the LGM was most profound in the wet season, with relatively little change, perhaps even wetter conditions, in the dry season. This reduction in seasonality would have slowed mineral weathering and lowered lake level, but in many areas would have had relatively little effect on vegetation.

Background cooling, radiative cooling, fog and event-based cooling contributed to a changing thermal environment for plants. The influences of these changes were not uniform geographically, temporally or taxonomically. In the northern Neotropics absolute temperature minima and mean monthly minima were lowered as a result of intensified and more frequent polar air incursions, by about 5 °C. In the southern Neotropics, the cold air incursions may have been no more intense than those of the present, but they probably occurred more often. If so, absolute minima would have been largely unchanged, but *mean* monthly and annual minima may have been lowered by 5 °C.

We conclude that the underlying mechanisms for changes in Neotropical precipitation, seasonality, and cooling led to regional climates that would have differed independently throughout the last glacial period. No empirical datum supports the turnover of biomes within Amazonia, except for areas that are presently ecotonal. As the climatic extremes of warming and cooling associated with the last glacial/interglacial cycle were possibly the largest experienced in the last 2 million years, the broad stability of Neotropical biomes is inferred for the Quaternary (Colinvaux *et al.*, 2000, 2001).

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