

Amazon Fan biomarker evidence against the Pleistocene rainforest refuge hypothesis?



MARK A. MASLIN,^{1*} VIRGINIA J. ETTWEIN,¹ CHRISTOPHER S. BOOT,² JAMES BENDLE^{2,3} and RICHARD D. PANCOST²

¹Environmental Change Research Centre, University College London, London WC1E 6BT, UK

²Organic Geochemistry Unit, Bristol Biogeochemistry Research Centre, School of Chemistry, The Cabot Institute, University of Bristol, Bristol BS8 1TS, UK

³Department of Geographical and Earth Sciences, University of Glasgow, Glasgow G12 8QQ, UK

Received 8 April 2011; Revised 14 November 2011; Accepted 16 December 2011

ABSTRACT: Ocean Drilling Program Leg 155 Site 942 on the Amazon Fan is an ideal location for monitoring palaeoclimatic changes within a significant proportion of the Amazon Basin. We present *n*-alkane $\delta^{13}\text{C}$ and taraxerol and laevoglucosan concentration records from this site covering the last 38 ka. The entire *n*-alkane $\delta^{13}\text{C}$ record is constrained between -31‰ and -34‰ , which is well within the isotopic range occupied by C_3 vegetation. The concentration and relative abundance of taraxerol, a mangrove indicator, varies by over an order of magnitude, but seems to have had no effect on the *n*-alkane $\delta^{13}\text{C}$ record. The laevoglucosan concentrations are extremely low during the last glacial period, suggesting a relatively low occurrence of forest fires. Laevoglucosan concentrations are highest between 13.5 and 12.5 ka, suggesting an increased incidence of Amazon forest fires at the very end of the Younger Dryas. These records, combined with previously published pollen records from Site 932, reveal no evidence for massive incursions of grasslands into Amazonia during the last glacial period, despite evidence of reduced outflow of the Amazon River indicating more arid conditions. We therefore suggest that savannah encroachment, as proposed by the Pleistocene refuge hypothesis, can be refuted as an explanation for high species endemism within the Amazon Basin, and alternative explanations are required. Copyright © 2012 John Wiley & Sons, Ltd.

KEYWORDS: Amazon; refugia; biomarker; Pleistocene; rainforest.

Introduction

Tropical rainforests display a level of biodiversity unmatched by any other vegetation type (e.g. Morley, 2000; Willis and McElwain, 2002; Hoon *et al.*, 2010). This has stimulated debate concerning the origin of this unparalleled biodiversity particularly in the Amazon Basin. This paper provides another test of one of these theories, namely the 'Pleistocene tropical rainforest refuge hypothesis' (e.g. Haffer, 1969; Haffer and Prance, 2001). It has been suggested that, during each glacial period, lower temperatures and precipitation in the Tropics allowed savannah to replace the majority of the tropical rainforest (e.g. Haffer, 1969; Prance, 1987; van der Hammen and Absy, 1994). However some of the tropical rainforest would have survived in small refugia (Prance, 1987). These isolated islands of rainforest would have become hotbeds of evolution by allopatric speciation, producing many new species. At the end of each glacial period the patchwork of rainforest merges back together with higher levels of species diversity and endemism (Prance, 1987; van der Hammen and Absy, 1994; Haffer and Prance, 2001; Behling *et al.*, 2010).

Little palaeoecological evidence, however, exists for this inferred massive incursion of savannah into the Amazon Basin during the last glacial period (Colinvaux and de Oliveira, 2000; Mayle *et al.*, 2004, 2009; Vonhof and Kaandorp, 2010). Many lake pollen records show no reduction of rainforest pollen at all (Colinvaux *et al.*, 1996; Bush *et al.*, 2002); in fact it is only at ecotonal margins that there is any evidence for savannah expansion (Mayle *et al.*, 2004; Burbridge *et al.*, 2004). Other evidence for a lack of savannah incursion includes the marine pollen record from the Amazon Fan, which shows large changes in the concentrations of pollen over the last 45 ka but almost no variation in the amount of arboreal pollen (Haberle and Maslin, 1999). However, phylogenetic studies of tropical flora and fauna provide conflicting interpretations as to whether there were

tropical rainforest refugia (e.g. Liu and Colinvaux, 1985; Fjeldsa and Lovett, 1997; Scheider and Moritz, 1999; Behling and Hooghiemstra, 1999, 2001; Moritz *et al.*, 2000; Bush *et al.*, 2004). Yet other studies emphasize the greater importance of the 'savannah refuge' in times of interglacial warming rather than forest refuge during glacial periods (Behling *et al.*, 2000; Flagstad *et al.*, 2001). Others suggest that during the glacial periods closed tropical dry forest ecosystems (i.e. trees) expanded more than savannah vegetation (Pennington *et al.*, 2004; Pennington and Dick, 2010). The additional problem is that it is very difficult palynologically to distinguish between evergreen forest and closed-canopy semi-deciduous dry forest (Pennington *et al.*, 2004; Mayle *et al.*, 2004; Pennington and Dick, 2010).

Hence there is still confusion over the changes in the Amazon rainforest extent over the last glacial–interglacial cycle (Morley, 2000; Behling *et al.*, 2010; Hoon *et al.*, 2010). In this study we present biomarker records from the Amazon Fan ocean sediments. These sediments can provide climate and vegetation records representative of a significant portion of the Amazon Basin catchment within a single, uninterrupted sedimentary sequence that can be radiocarbon dated to high resolution with foraminifera (Maslin and Burns, 2000). As noted above, a pollen record has been produced from the Amazon Fan at Ocean Drilling Program (ODP) Site 932 (Haberle and Maslin, 1999), and it suggests that forest persisted within the Amazon Basin during glacial periods. It is, however, frequently suggested that this pollen record is biased toward a coastal and gallery forest signal (e.g. Hooghiemstra and Van der Hammen, 1998; Behling *et al.*, 2002, 2010). Hence in this study we have used biomarker proxies as a complement to more traditional proxies to investigate and test the Amazon rainforest pleistocene refuge hypothesis.

Site location

ODP Leg 155 Site 942 on the Amazon Fan is an ideal location for monitoring palaeoclimatic changes on the adjacent continent (Damuth and Kumar, 1975; Flood *et al.*, 1995;

*Correspondence: M. A. Maslin, as above.
E-mail: m.maslin@ucl.ac.uk

Maslin and Burns, 2000). Site 942 is situated just to the west of the main Amazon Fan complex (Fig. 1), so it benefits from enhanced glacial sedimentation when terrestrial sediment is fed directly into the fan system but is sufficiently removed from the zones of active slope failure and sediment reworking (Flood *et al.*, 1995; Maslin *et al.*, 2000). A parallel study of high-resolution planktonic foraminifera $\delta^{18}\text{O}$ values, building on the work of Maslin and Burns (2000), indicates the constant influence of Amazon River water at this site (Maslin, 1998; Ettwein, 2005; Maslin *et al.*, 2011). This is supported by diatom analysis of the sediments (Mikkelsen *et al.*, 1997) revealing that $\sim 75\%$ of the assemblage is of a freshwater origin, by far the maximum representation of all the sites drilled (the remainder of which had 10–30% representation). Of all the Leg 155 sites drilled, 942 has experienced the greatest continual Amazon

River influence (Wilson *et al.*, 2011) and so has optimal potential to yield a representative terrestrial archive.

Methodology

ODP Leg 155 Site 942 was sampled for foraminifera and biomarker characterization over a depth of 20 m, representing the last 40 ka. A composite age model was developed for ODP Site 942, using a combination of 36 accelerator mass spectrometry (AMS) radiocarbon (^{14}C) ages (Fig. 2) that were measured on both multiple- and mono-specific planktonic foraminiferal samples. Radiocarbon analyses were conducted at the Leibniz-Labor für Alterbestimmung und Isotopenforschung, Kiel University, Germany (Maslin and Burns, 2000; Maslin *et al.*, 2000), the Center for Accelerator Mass

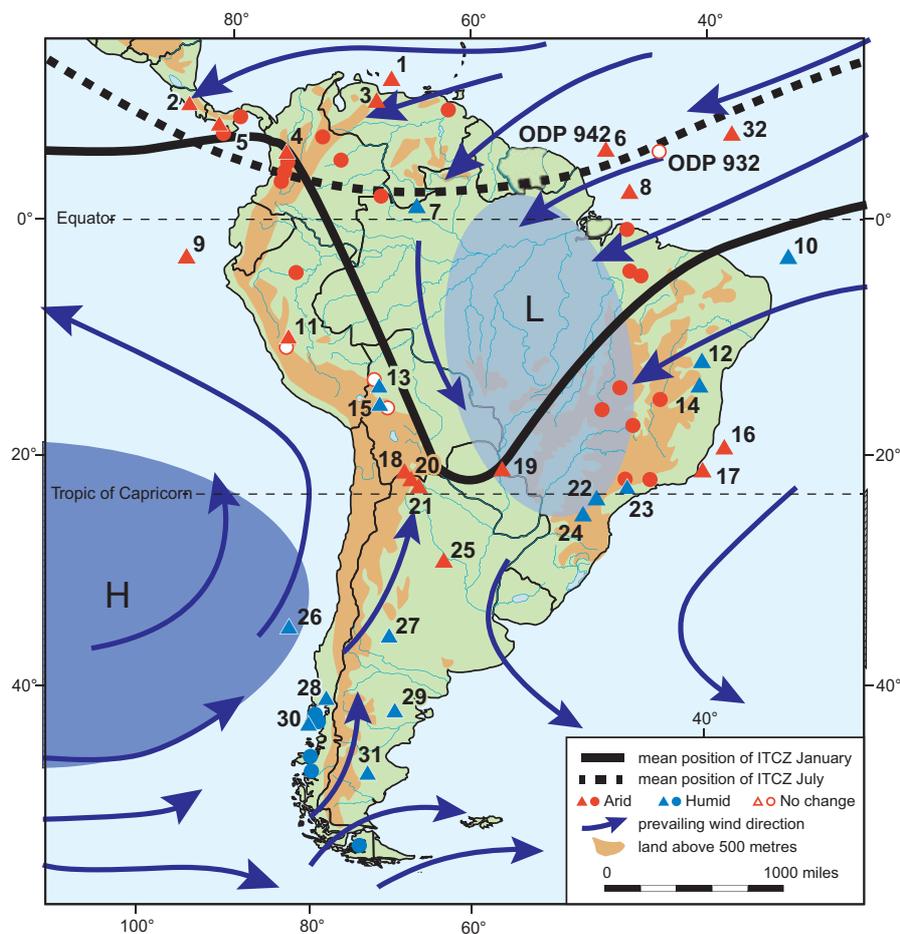


Figure 1. Map of the present-day summer and winter locations of the Intertropical Convergence Zone (ITCZ) and the major wind and hence moisture sources over the Amazon Basin. Locations of palaeoclimate records from the LGM and whether the authors found evidence for wetter (blue filled triangles/circles), drier (red filled triangles/circles) or no change (yellow open triangles/circles) compared to the present. Circles are used for key pollen records compiled by Marchant *et al.* (2009). 1, Cariaco Basin (Hughen *et al.*, 1996; Peterson *et al.*, 2000; Haug *et al.*, 2001; Lea *et al.*, 2003); 2, La Chonta Bog, Costa Rica (Islebe *et al.*, 1995); 3, Lake Valencia, Venezuela (Leyden, 1985); 4, Lake Fuquene, Columbia (Van der Hammen and Hooghiemstra, 2003); 5, El Valle Lake, Panama (Bush, 2002); 6, Amazon Fan ODP Site 942 (Maslin and Burns, 2000; Maslin *et al.*, 2000, 2011, this study); 7, Lake Pata, Brazil (Colinvaux *et al.*, 1996); 8, Amazon Fan (Damuth and Fairbridge, 1970); 9, Equatorial Eastern Pacific (Heusser and Shackleton, 1994); 10, Fortaleza, Brazil and North Brazilian Current (Arz *et al.*, 1998, Arz *et al.*, 1999); 11, Huascarán, Peru (Thompson *et al.*, 1995); 12, East Brazil (Auler and Smart, 2001); 13, Sajama, Bolivia (Thompson *et al.*, 1998) and Illumani, Bolivia (Ramirez *et al.*, 2003); 14, Bahia State, Brazil (Wang *et al.*, 2004, Wang *et al.*, 2006); 15, Lake Titicaca, Peru (Baker *et al.*, 2001a, 2001b; Fritz *et al.*, 2007); 16, South Atlantic Ocean core GeoB 3229-2 (Arz *et al.*, 1998, Arz *et al.*, 1999; Behling *et al.*, 2002); 17, South Atlantic Ocean core GeoB 3202-1 (Arz *et al.*, 1998, Arz *et al.*, 1999; Behling *et al.*, 2002); 18, Salar de Atacama, Chile (Bobst *et al.*, 2001); 19, Alto Parana, Argentina (Stevaux, 2000); 20, Lakes Lejia and Miscanti, Chile (Grosjean, 1994; Grosjean *et al.*, 2001); 21, Santa Maria Basin and Quebrada del Torro, Argentina (Trauth and Strecker, 1999; Trauth *et al.*, 2000); 22, St8 Santana Cave, Brazil (Cruz *et al.*, 2006, 2009); 23, Colonia, Brazil (Ledru *et al.*, 2005); 24, Botuvera Bt2, Brazil (Cruz *et al.*, 2006, 2009; Wang *et al.*, 2006); 25, Mar Chiquita, Argentina (Piovano *et al.*, 2008); 26, South East Pacific Ocean core GeoB 3302-1 (Lamy *et al.*, 1999); 27, Salinas Bebedero, Argentina (González, 1994; González and Maidana, 1998); 28, Chilean Lake District, Chile (Heusser, 1989; Markgraf, 1989; Moreno *et al.*, 1999); 29, Cari Laufquen, Argentina (Galloway *et al.*, 1988); 30, Huelmo Site, Chile (Massaferro *et al.*, 2009); 31, Cardiel, Argentina (Stine and Stine, 1990); 32, Ceara Rise (Harris and Mix, 1999). This figure is available in colour online at wileyonlinelibrary.com/journal/jqs.

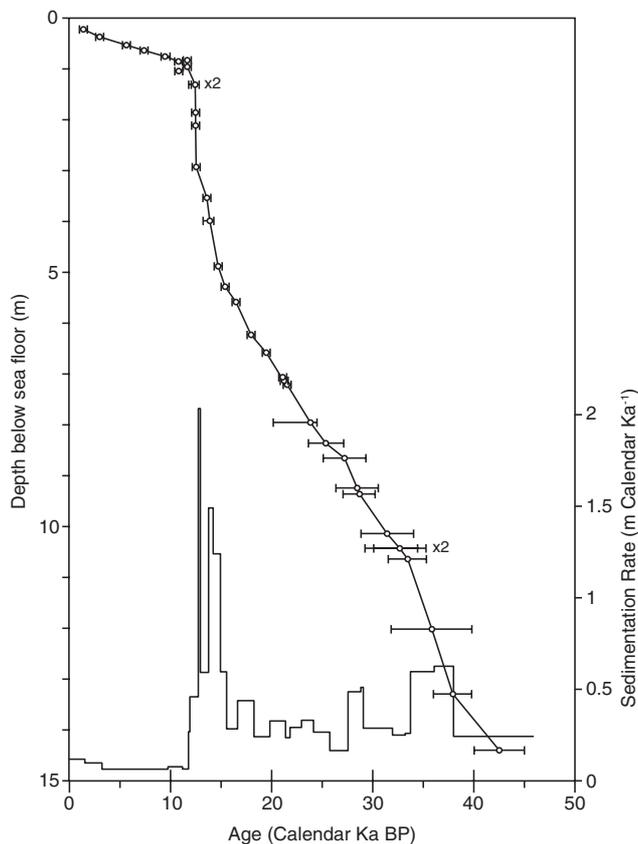


Figure 2. Site 942 composite age–depth plot and estimated sedimentation rates using the selected 36 AMS radiocarbon dates (Maslin and Burns, 2000; Ettwein, 2005; Maslin *et al.*, 2011).

Spectrometry, Lawrence Livermore National Laboratory (USA), and the Scottish Universities Environmental Research Centre. Each ^{14}C analysis was corrected for isotope fractionation through normalization using $\delta^{13}\text{C}$ values measured on the same samples. In order to translate the ^{14}C chronology into equivalent GISP2 ice core years, non-reservoir corrected ^{14}C ages from ODP Site 942 were correlated with similar data from nearby ODP Site 1002 in the Cariaco Basin (Hughen *et al.*, 2004a, 2004b) that has been tuned to the GISP2 age scale (Meese *et al.*, 1997). Sedimentation rates calculated from the age model (see Fig. 2) show that between 45.0 and 13.7 ka sedimentation rates varied between ~ 0.2 and 0.6 m ka^{-1} . Sedimentation rates peak at between 15 and 14 ka at $\sim 1.5 \text{ m ka}^{-1}$ and between 13.6 and 13.5 ka at over 5 m ka^{-1} (Fig. 2), which coincides with an abrupt increase in the abundance of terrestrial detritus in the record (Maslin *et al.*, 2000). This may be evidence for a shift of the main active channel system towards Site 942 (Maslin *et al.*, 2006) or of a flushing of river sediment following deglaciation in part of the Andes (Thompson *et al.*, 1998; Maslin and Burns, 2000; Bendle *et al.*, 2010). Thereafter, until 10.9 ka sediment accumulation rates were approximately 0.45 m ka^{-1} . At ca. 10.9 ka, sedimentation rates fall abruptly to a more typical oceanic pelagic sedimentation rate of $\sim 0.05\text{--}0.10 \text{ m ka}^{-1}$, when higher sea levels flooded the continental shelf and the river deposited its load further inland (Maslin *et al.*, 2006).

Samples to be analysed for biomarker distributions were freeze dried, ground and extracted via ultrasonication in a sequence of solvents with increasing polarity: hexane twice; a 1:1 (v/v) azeotrope of dichloromethane:methanol (DCM:MeOH) twice; MeOH twice. After extraction, the samples were evaporated to approximately 3–4 mL and then transferred to glass vials. The remaining solvent was evaporated

under a stream of N_2 after the addition of a standard mixture containing androstane and hexadecyloctadecanoate. In order to achieve gas chromatography (GC)-resolved peaks for isotopic analysis, each total lipid extract was further separated into five fractions using silica gel chromatography. The activated silica column (5 cm long, 5 mm wide) was eluted with: 3 mL hexane for saturated hydrocarbons; 1.5 mL of 9:1 (v/v) hexane:DCM for aromatic hydrocarbons; 5.5 mL DCM for ketones and wax esters; 3 mL of 1:1 (v/v) DCM:MeOH for alcohols and sterols; 3 mL of MeOH for more polar compounds.

Compounds in each of the fractions were initially screened using GC (see Boot *et al.*, 2006). After dissolving in 100 μL ethyl acetate, each sample was injected into a Carlo Erba 5300 series gas chromatograph fitted with a CP-Cil 5CB silica column (internal diameter 0.32 mm, length 50 m, d.f. 0.11 μm), which was heated from 40 to 140 $^{\circ}\text{C}$ at $20^{\circ}\text{C min}^{-1}$, then at $4^{\circ}\text{C min}^{-1}$ to 300 $^{\circ}\text{C}$, at which temperature it was held for 20 min. All fractions were subsequently analyzed using gas chromatography–mass spectrometry (GC-MS) with a Thermoquest Finnigan Trace chromatograph interfaced to a Thermoquest Finnigan Trace mass spectrometer operating with electron ionization at 70 eV and scanning an m/z range of 50–850. GC conditions for GC-MS were identical to those used for GC analysis. Compound identifications were assigned by comparing mass spectra and relative retention times with those in the literature. Compounds were quantified against the known concentrations of internal standards described above, with n -alkanes and n -alkanols quantified using GC, and taraxerol and laevoglucosan, which occur at lower concentrations, quantified using GC-MS. Sedimentation rates derived from the AMS age model described above were used along with the dry bulk density to calculate mass accumulation rates (MARs) for the various molecular components along with the average chain length (ACL) for the n -alkanes (Boot *et al.*, 2006).

$$\text{MAR}_{\text{component}} = (\text{Conc}_{\text{component}} \cdot \text{SR} \cdot \text{DBD})$$

where $\text{MAR}_{\text{component}}$ is the MAR ($\text{ng cm}^{-2} \text{ ka}^{-1}$), $\text{Conc}_{\text{component}}$ is the mass of component (ng g^{-1}) dry sediment, SR is the sedimentation rate (cm ka^{-1}) and DBD is the dry bulk density (g cm^{-3}).

ACLs for the n -alkanes were calculated as

$$\text{ACL}_{27-33} = (27 [C_{27}] + 29 [C_{29}] + 31 [C_{31}] + 33 [C_{33}]) / ([C_{27}] + [C_{29}] + [C_{31}] + [C_{33}])$$

with $[C_x]$ signifying the concentration of the n -alkane with x carbon atoms. Carbon preference indices (CPIs) were calculated for n -alkanes and n -alkanols as

$$\text{CPI} = \left[\frac{0.5 \sum (X_i + X_{i+2} + \dots + X_n)}{\sum (X_{i-1} + X_{i+1} + \dots + X_{n-1}) + 0.5 \sum (X_i + X_{i+2} + \dots + X_n)} \right]$$

where $i=25$ and $n=33$ in the case of n -alkanes, and $i=21$ and $n=31$ in the case of n -alkanols.

Gas chromatography–isotope ratio monitoring mass spectrometry (GC-IRMMS) was used to measure the carbon isotopic composition of compounds in the n -alkane fraction. Each sample was dissolved in 100 μL ethyl acetate and placed in 1 mL auto-sample vials before being analysed on a Varian gas chromatograph fitted with a ZB-1 column linked to a ThermoFinnigan Mat DeltaS mass spectrometer via a combustion interface; the gas chromatograph temperature programme was the same as that used for standard GC analysis. Each sample was analysed twice, with an equipment precision of

0.3‰; values are expressed in standard $\delta^{13}\text{C}$ notation as parts per mil (‰) deviations from the Vienna Pee Dee Belemnite (VPDB) standard.

The planktonic foraminifera oxygen isotope record was constructed using the following methodology. The samples were freeze dried and then wet sieved through a 63 μm mesh sieve, dried in a 60°C oven and weighed. The samples were then dry sieved at convenient intervals between 300 and 355 μm , from which 30 individual *Globigerinoides sacculifer* (with sac) planktonic foraminiferal tests were picked for each species per sample. Samples from 40 to 0 ka were measured for $\delta^{18}\text{O}$ using a Finnigan Delta XL+ ratio mass spectrometer linked to an automated carbonate preparation system (Kiel III) at the Stable Isotope Laboratory, Department of Geosciences, University of Massachusetts, Amherst, MA, USA. Higher-resolution samples from 22 to 13.9 ka were measured for $\delta^{18}\text{O}$ using an automated common acid bath VG Isocarb+Optima mass spectrometer at the NERC Isotope Geosciences Laboratory, Keyworth, Nottingham, UK. All $\delta^{18}\text{O}$ values were measured in per mil (‰) and expressed as deviations relative to the VPDB standard. Analytical sample reproducibility errors were <0.07‰ at each facility, based on replicate measurements of within-run laboratory standards, calibrated against standards from the International Atomic Energy Agency and the National Bureau of Standards. Data from each lab were spliced together and harmonized by comparing the $\delta^{18}\text{O}$ measurements of the laboratory sample standards and inter-laboratory replicate sample data; a correction factor was applied where appropriate. The global mean glacioeustatic component of foraminiferal $\delta^{18}\text{O}$ was removed using the independently Th/U-dated Barbados sea-level record (EPICA Community Members, 2006; Peltier and Fairbanks, 2006) scaled to $\delta^{18}\text{O}$, assuming a modern–Last Glacial Maximum (LGM) amplitude of $\sim 1\text{‰} \pm 0.1\text{‰}$ (Adkins *et al.*, 2002). The foraminiferal $\delta^{18}\text{O}$ record was corrected for temperature fractionation by scaling the Mg/Ca Site 942 SST record assuming a standard temperature– $\delta^{18}\text{O}$ fractionation of $0.21\text{‰} \text{ }^\circ\text{C}^{-1}$ (mean of $0.20\text{--}0.22\text{‰} \text{ }^\circ\text{C}^{-1}$; Maslin and Swann, 2005); see Maslin *et al.* (2011) for full details.

Discussion and results

Figure 2 shows the ice-volume corrected planktonic foraminifera oxygen isotope record, the biomarker MARs and distributions and *n*-alkane $\delta^{13}\text{C}$ values. The planktonic foraminifera oxygen isotope record provides a stratigraphic context and may provide an estimation of the outflow of the Amazon River (Maslin and Burns, 2000; Maslin *et al.*, 2000, 2011). Analysis of the diatom fraction of surface sediments from Site 942 reveals that freshwater taxa make up $\sim 75\%$ of the diatom assemblage, compared to just 10–30% elsewhere on the fan (Mikkelsen *et al.*, 1997). This higher percentage abundance reflects the influence of the Amazon River freshwater plume at this location (Maslin *et al.*, 1997; Mikkelsen *et al.*, 1997). Moreover, Wilson *et al.* (2011) used planktonic foraminiferal oxygen isotopes and Mg/Ca sea surface temperatures (SSTs) to show that during the late Glacial period, Younger Dryas, mid Holocene and Modern time slices ODP Site 942 and surrounding sites consistently exhibit the most negative oxygen isotope values, suggesting a continual influence of the Amazon River freshwater plume over this part of the Amazon Fan. A comparison of oxygen isotope records either side of the Amazon River outflow also confirms this influence. For example, the Glacial to late Holocene uncorrected $\delta^{18}\text{O}$ range is 2.5‰ for *G. sacculifer* and 2.2‰ for *G. ruber* (Ettwein, 2005). This compares with marine records to the east of the Amazon outflow, which have a range of 1.9‰

for *G. sacculifer* and 1.6‰ for *G. ruber* (Arz *et al.*, 1999). If we assume that the ice volume and SST effects are broadly similar either side of the Amazon outflow, then it suggests the Amazon outflow has an influence of approximately 0.6‰ on the surface water oxygen isotope composition.

In order to isolate the local freshwater impact on surface water salinity, we have removed the global mean glacioeustatic component and local Mg/Ca-derived SST data from the $\delta^{18}\text{O}$ time series (Fig. 3). The residual $\Delta\delta^{18}\text{O}$ can be explored using a two-component mixing model between an Amazon and a tropical Atlantic Ocean end-member, which have average modern-day isotopic values of $\sim -5.5\text{‰}$ and $\sim +1\text{‰}$ respectively (see references in Wilson *et al.*, 2011). Consequently, $\delta^{18}\text{O}$ values at Site 942 are comprised of a combination of these two isotopic signals dependent on the relative mixing ratio of the two water masses over Site 942. Although these end-members will have altered in the past, they cannot reverse, so the construction of a model of river outflow shows that a relative enrichment (depletion) in the $\Delta\delta^{18}\text{O}$ represents a decrease (increase) in the amount of fresh water mixed over Site 942, arising from changes in the outflow of the Amazon River (Maslin and Burns, 2000). Maslin *et al.* (2011) therefore suggest that Site 942 $\Delta\delta^{18}\text{O}$ reflects changes in Amazon River outflow and thus may be indicative of how wet or dry the Amazon Basin was in the past. During the last glacial period between 40–17 ka and 15–13 ka the Amazon Basin was drier than today, while between 17–15 ka and 12–0 ka the Amazon Basin seems to have been as wet as today.

The laevoglucosan, *n*-alkane and *n*-alkanol MARs, as well as the taraxerol:C₂₈ alkanol and taraxerol:C₂₉ alkane ratios, are largely invariant through the last 38 ka. The exceptions are the peaks in all five records at 13–12 ka (see Fig. 3B, C, D) and the peaks in the taraxerol:C₂₉ alkanol and taraxerol:C₂₉ alkane ratios at ca. 38 ka and ca. 27 ka. The *n*-alkane ACL and $\delta^{13}\text{C}$ records are also largely invariant throughout the last 38 ka, generally ranging from 29.5‰ to 30‰ and from –30‰ to –34‰, respectively.

Terrestrially derived lipid biomarkers provide a number of tracers for palaeovegetation and complementary insights into pollen analysis. One such class of biomarkers are the *n*-alkanes (straight-chain hydrocarbons), common leaf wax components in vascular plants (e.g. Eglinton *et al.*, 1962; Eglinton and Hamilton, 1967). Vascular plants are characterized by a predominance of *n*-alkanes with high carbon numbers (C₂₇–C₃₃), preferentially favouring odd rather than even carbon numbers ('high' carbon preference index (CPI), reviewed by Pancost and Boot, 2004). Although some bacteria and algae can produce *n*-alkanes of higher carbon number, they rarely have high CPIs (Bird *et al.*, 1995). Although interpretation of *n*-alkane concentrations is generally limited, their carbon isotopic compositions can have great utility in palaeovegetation investigations. Typical $\delta^{13}\text{C}$ values of C₃ (Calvin–Benson or non-Kranz) photosynthetic pathway plants range from –22‰ to –30‰ (average –27‰) (Ehleringer and Monson, 1993), whereas values of C₄ (Hatch–Slack or Kranz) photosynthetic pathway plants, which include tropical and marsh grasses, range from –9‰ to –16‰ (average –13‰) (Ehleringer and Monson, 1993). C₃ and C₄ plant species therefore each have distinct isotopic signatures (see references in Maslin and Swann, 2005). Although this plant species mixture can be recorded by bulk sedimentary organic matter (e.g. Kastner and Goñi, 2003), it can be skewed by contributions from marine inputs. Compound-specific $\delta^{13}\text{C}$ analysis of refractory *n*-alkanes of exclusively higher plant origin avoids this problem, and has been shown to record C₃ and C₄ species differences with fidelity in modern and geological materials (e.g. Collister *et al.*, 1994; Schefuss

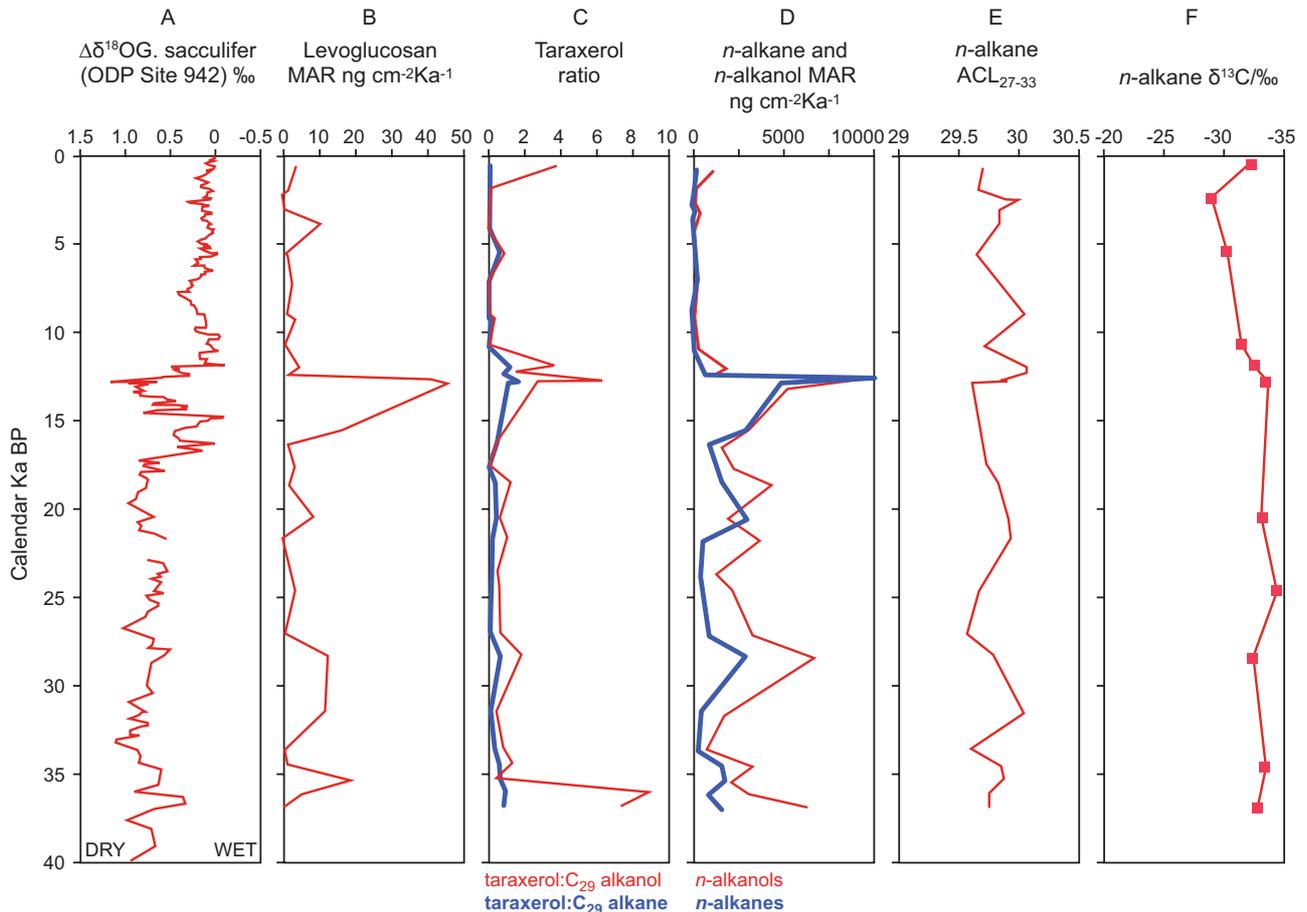


Figure 3. Comparison of the (A) ODP Site 942 *G. sacculifer* oxygen isotope record corrected for ice volume with the (B) laevoglucosan MARs, (C) taraxerol:C₂₈ alkanol and taraxerol:C₂₉ *n*-alkane ratios, (D) High molecular weight (HMW) *n*-alkane and *n*-alkanol MARs, (E) *n*-alkane ACLs (see text) and (F) *n*-alkane $\delta^{13}\text{C}$ values. This figure is available in colour online at wileyonlinelibrary.com/journal/jqs.

et al., 2003; Rommerskirchen *et al.*, 2003; Denison *et al.*, 2005). Collister *et al.* (1994) observed that in C₃ and C₄ species, the *n*-alkane $\delta^{13}\text{C}$ values were depleted relative to biomass by $\sim 5.9\%$ and $\sim 9.9\%$, making the observed C₃ range -28 to -36% (average -33%) and C₄ range -19 to -26% (average -13%) in *n*-alkanes.

As can be seen from Fig. 2, the *n*-alkane $\delta^{13}\text{C}$ values throughout the entire record is wholly constrained between -29% and -34% , which is well within the isotopic range for *n*-alkanes derived from C₃ vegetation (-28 to -36%). This result is consistent with the original biomarker work on Amazon Fan sediments by Kastner and Goñi (2003), which included carbon isotopic compositions of bulk organic matter and ratios of lignin-derived phenols. It is also consistent with the lack of variation in *n*-alkane ACLs (Boot *et al.*, 2006). Assuming that the signal at Site 942 is representative of the average vegetation across the Amazon River catchment, it implies that there has been continuous forest cover within the Amazon Basin with minimal/no significant encroachment of tropical grasslands over the last ca. 38 ka. However it may be possible that the *n*-alkane $\delta^{13}\text{C}$ record contains a sampling bias towards only coastal and river edge vegetation. This bias has also been suggested for the ODP 932 pollen record. In addition, the $\delta^{13}\text{C}$ values are unable to distinguish changes in floristic structure (e.g. variation in montane vs. lowland species); the intra-C₃ range of shift in the data remains in stark opposition to the refuge hypothesis.

Figure 3(C) also shows a down-core record of the taraxerol:C₂₉ *n*-alkane and taraxerol:C₂₈ *n*-alkanol ratios. Taraxerol has been shown to be a useful biomarker tracer

for mangrove organic matter contributions to deep-sea fan sediments (Versteegh *et al.*, 2004; Koch *et al.*, 2011). These ratios (Fig. 3C) can therefore reflect the relative inputs of mangroves relative to leaf wax inputs from the wider higher plant community. They have varied over the last 38 ka by over an order of magnitude, with particularly high taraxerol contributions at ca. 38 ka and the transition from Younger Dryas to the Preboreal period (13–11 ka). These trends appear to correspond to trends in the *Rhizophora* mangrove pollen signal from Site 932 on the Amazon Fan (Site 932; Haberle and Maslin, 1999). The ODP Site 942 $\delta^{18}\text{O}$ records shown in Fig. 3(A) suggest that the peak after the end of the Younger Dryas was coeval, with a rapid increase in outflow from the Amazon River. It also occurs both during and after the extremely high sedimentation rates between 13.8 and 13.5 ka (Bendle *et al.*, 2010), suggesting that the mangrove signal is not just responding to increased sediment input. The mangrove increased contribution may therefore be due to flushing out of the Amazon Basin with the first increase in moisture availability or increased erosion of coastal mangroves with increased sea level. A similar peak in taraxerol abundances relative to those of leaf waxes occurs ca. 36 ka; however, the relatively limited age control around this time prevents any relationship with changing sedimentation rates to be ascribed.

Nevertheless, the taraxerol:leaf wax ratios do have important implications for the interpretation of the $\delta^{13}\text{C}$ signal. Comparison with ratios from both the Congo and Amazon Fan sediments, where this biomarker ratio has been shown to match the mangrove pollen very well (Versteegh *et al.*, 2004; Koch *et al.*, 2011), suggests that mangroves contribute just

~10% of the total terrigenous organic matter to the sediment. Moreover, there are no isotopic shifts associated with the dramatic changes in the mangrove inputs inferred from either taraxerol or Site 932 pollen records. Combined, these two lines of evidence suggest that the $\delta^{13}\text{C}$ *n*-alkane signal is not driven by coastal mangrove inputs.

Further support for a lack of savannah expansion is provided by the ODP Site 942 laevoglucosan record (Fig. 3B). Laevoglucosan is derived from incomplete combustion of cellulose and is therefore thought to be a forest fire tracer when found in marine and lacustrine sediments (e.g. Simoneit *et al.*, 1999; Simoneit and Elias, 2000). Laevoglucosan MARS are relatively low throughout the record, apart from somewhat higher values between 14 and 13 ka, which corresponds to the increase in sedimentation rates. These higher values are not reflected in laevoglucosan concentrations, such that the increase could be a preservational artefact of increase sedimentation rates. Alternatively, it could record an increase in fires at the very end of the Younger Dryas due to extreme aridity. In contrast, the laevoglucosan record suggests that there was no large increase in fires in the Amazon Basin during the last glacial period, which would be expected if savannah had significantly expanded.

The biomarker data presented here add further weight to the increasing volume of evidence that forest cover persisted within the Amazon Basin throughout the last glacial cycle (e.g. Colinvaux, 1989; Colinvaux *et al.*, 1996; Haberle and Maslin, 1999; Colinvaux and de Oliveira, 2000; Kastner and Goñi, 2003; Marchant *et al.*, 2009). It adds credibility to palynological interpretations that, although the forest remained intact, there were significant changes in thermo-sensitive tree populations (Haberle and Maslin, 1999) due to suppressed temperatures $\sim 5^\circ\text{C}$ in the Amazonian lowlands (Bendle *et al.*, 2010). Figure 4 compares the Site 932, total arboreal pollen and Andean type tree pollen with the Site 942 *n*-alkane $\delta^{13}\text{C}$ record. Previously published pollen data from the Carajás Plateau, the site frequently used as the classic defence of the refuge hypothesis (e.g. Van der Hammen and Absy, 1994; Hooghiemstra and Van der Hammen, 1998) has since been

reanalysed and found instead to be responding to a strong local edaphic control (e.g. Colinvaux and de Oliveira, 2000). Marchant *et al.* (2009) suggest that of all the published pollen data only those from the extreme southwest edge of the modern forest provide substantial evidence for the past existence of savannah in the Amazon Basin. However, the biome replacement observed along this migrating ecotone boundary appears to correspond to insolation, suggesting it may be responding to precipitation driven by the Intertropical Convergence Zone (Wang *et al.*, 2004, 2006; Cruz *et al.*, 2005, 2009; Maslin *et al.*, 2011).

Nevertheless, it remains interesting that while the biomarker and pollen records imply the persistence of tree cover throughout the last 35 ka, other data, independent of vegetation, suggest that the Amazon Basin experienced a period of marked aridity during the last glacial period. This view of an arid glacial Amazon Basin is supported by (i) oxygen isotope reconstruction of Amazon River outflow (Maslin and Burns, 2000; Maslin *et al.*, 2000, 2011), (ii) inorganic sedimentary lake records from within the Amazon Basin that imply lower water levels or even complete desiccation (e.g. Van der Hammen, 1974; Colinvaux *et al.*, 1996; Ledru *et al.*, 1998; Servant *et al.*, 1993; Sifeddine *et al.*, 2001; Maslin and Burns, 2000); (iii) oxygen isotope records from speleothems (van Breukelen *et al.*, 2008; Cruz *et al.*, 2005, 2009); (iv) unweathered plagioclase deposits in the Amazon Fan (Damuth and Fairbridge, 1970; Irion *et al.*, 1995); and (v) $\delta^{18}\text{O}$ values of kaolinite within Andean soils (Mora and Pratt, 2001). This interpretation is also supported by drier conditions found in northern South America and southern Central America. For example, marine records from the Cariaco Basin clearly show a very dry LGM (Peterson *et al.*, 2000) and Younger Dryas (Haug *et al.*, 2001). In contrast, other authors have suggested that the Amazon Basin was wetter during the last glacial period. Evidence suggested includes lake level records from the Peruvian/Bolivian Altiplano (Seltzer *et al.*, 2000; Baker *et al.*, 2001a, 2001b; Seltzer *et al.*, 2002), pollen and lake level records from northwest Amazonia (Bush *et al.*, 2002) and speleothem evidence from southeast Brazil (Wang *et al.*, 2004, 2006; Cruz *et al.*, 2005, 2009). However, these records are distal and may have been strongly affected by local factors. For example, the Peruvian/Bolivian Altiplano (Seltzer *et al.*, 2000, 2002; Baker *et al.*, 2001a, 2001b) records are thought to be driven by increased moisture transport to higher altitudes as the southeasterly winds strengthen (Lenters and Cook, 1997; Marengo *et al.*, 2001; Leduc *et al.*, 2007) following the weakening of the South American monsoon, while rainfall in northwest Amazonia and southeast Brazil are strongly influenced by austral winter rainfall (Cruz *et al.*, 2009). The weight of evidence (see also Sylvestre, 2009; Mayle *et al.*, 2009; Marchant *et al.*, 2009; Maslin *et al.*, 2011) supports the interpretation that the Amazon was more arid during the last glacial period than today (see Fig. 1 for summary). However, the biomarker data suggest that this aridity did not result in a major change in Amazon Basin plants and especially not an expansion of savannah vegetation.

Indeed, persistent forest cover within the Amazon Basin despite cold-stage aridity is consistent with coupled climate–vegetation model results (e.g. Cowling *et al.*, 2001, 2004; Cowling, 1999, 2004; Prentice *et al.*, 2004) as the cooler temperatures mitigate the detrimental effects of the low carbon dioxide and aridity via reduced evapotranspiration and photorespiratory carbon loss in C_3 plants (Cowling *et al.*, 2001), allowing C_3 vegetation to outcompete C_4 species during glacial periods. Farrera *et al.* (1999) and Bendle *et al.* (2010) have shown temperatures to be at least 5°C lower during the last glacial period in the Amazon lowland,

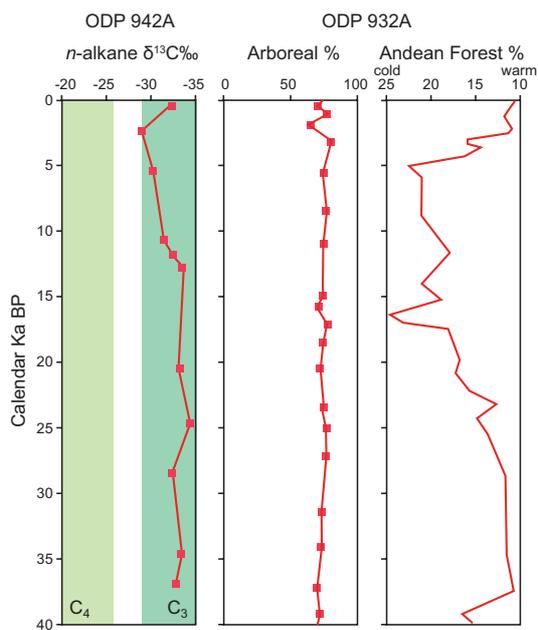


Figure 4. Comparison of the Site 942 *n*-alkane $\delta^{13}\text{C}$ values from this study with the Site 932 arboreal pollen and Andean forest pollen percentages (Haberle and Maslin, 1999). This figure is available in colour online at wileyonlinelibrary.com/journal/jqs.

supporting this proposed biological response. This allows us to reject the ephemeral view of the Amazon rainforest and confirms the theory that the Amazon rainforest is resilient and has adapted to past climate change and has been a dominant feature of the Earth climate system for at least the last 55 million years (Maslin *et al.*, 2005).

Conclusions

The biomarker data from the Amazon Fan reveals no evidence for massive incursions of grasslands into Amazonia during the last glacial period, despite more arid conditions. We therefore suggest that savannah encroachment, as proposed by the Pleistocene refuge hypothesis, may be refuted as an explanation for high species endemism within the Amazon Basin. The *n*-alkane $\delta^{13}\text{C}$ values, however, are incapable of discriminating between different forest types (e.g. montane vs. lowland) and, although C_3 plants remained dominant within the basin, there may have been a different floristic structure from that present within the Amazon Basin today, as proposed by palynological investigations and modelling simulations (Haberle and Maslin, 1999; Cowling *et al.*, 2001, 2004).

Acknowledgements. Many thanks to Ian Bull and Rob Berstan (Bristol Node of the NERC Life Sciences Mass Spectrometry Facility, School of Chemistry, University of Bristol) for analytical support, and Janet Hope for assistance in London. The compiling of figures by the UCL Drawing Office (Department of Geography) was much appreciated. We would like to thank the three reviewers and Jason Briner, whose comments and suggestions greatly improved the manuscript. This research was supported by NERC grant GST/02/2690.

Abbreviations. ACL, average chain length; AMS, accelerator mass spectrometry; CPI, carbon preference index; CPI, carbon preference index; DBD, dry bulk density; DCM, dichloromethane; GC, gas chromatography; IRMMS, visotope ratio monitoring mass spectrometry; ITCZ, Intertropical Convergence Zone; LGM, Last Glacial Maximum; MAR, mass accumulation rate; MS, mass spectrometry; ODP, Ocean Drilling Program; SR, sedimentation rate; SST, sea surface temperature; VPDB, Vienna Pee Dee Belemnite.

References

- Adkins JF, McIntyre K, Schrag DP. 2002. The salinity, temperature and $\delta^{18}\text{O}$ of the glacial deep ocean. *Science* **298**: 1769–1773.
- Arz HW, Pätzold J, Wefer G. 1998. Correlated millennial-scale changes in surface hydrography and terrigenous sediment yield inferred from last-glacial marine deposits off northeastern Brazil. *Quaternary Research* **50**: 157–166.
- Arz HW, Pätzold J, Wefer G. 1999. The deglacial history of the western tropical Atlantic as inferred from high resolution stable isotope records off northeastern Brazil. *Earth and Planetary Science Letters* **167**: 105–117.
- Auler AS, Smart PL. 2001. Late Quaternary paleoclimate in semiarid northeastern Brazil from U-series dating of travertine and water-table speleothems. *Quaternary Research* **55**: 159–167.
- Baker PA, Rigsby CA, Seltzer GO, *et al.* 2001a. Tropical climate changes at millennial and orbital timescales on the Bolivian Altiplano. *Nature* **409**: 698–701.
- Baker PA, Seltzer GO, Fritz SC, *et al.* 2001b. The history of South American tropical precipitation for the past 25,000 years. *Science* **291**: 640–643.
- Behling H, Hooghiemstra H. 1999. Environmental history of the Colombian savannas of the Llanos Orientales since the Last Glacial Maximum from lake records El Pinai and Carimagua. *Journal of Paleolimnology* **21**: 461–476.
- Behling H, Arz HW, Pätzold J, *et al.* 2000. Late Quaternary and vegetational dynamics in northeastern Brazil: inferences from marine core GeoB3104-1. *Quaternary Science Reviews* **19**: 981–994.
- Behling H, Hooghiemstra H. 2001. Neotropical savanna environments in space and time: late Quaternary interhemispheric comparisons. In *Interhemispheric Climate Linkages*, Markgraf V (ed.). Academic Press: San Diego, CA; 307–323.
- Behling H, Arz HW, Pätzold J, *et al.* 2002. Late Quaternary vegetational and climate dynamic in southeastern Brazil: inferences from marine cores GeoB3229-2 and GeoB3202-1. *Palaeogeography, Palaeoclimatology, Palaeoecology* **179**: 227–243.
- Behling H, Bush M, Hooghiemstra H. 2010. Biotic development of Quaternary Amazonia: a palynological perspective. In *Amazonia: Landscape and Species Evolution*, Hoorn C, Wesselingh F (eds). Wiley-Blackwell: Chichester; 335–348.
- Bendle JA, Weijers JWH, Maslin MA, *et al.* 2010. Major changes in Glacial and Holocene terrestrial temperatures and sources of organic carbon recorded in the Amazon Fan by tetraethers. *Geochemistry, Geophysics, Geosystems* **11**: Q12007.
- Bird MI, Summons RE, Gagan MK, *et al.* 1995. Terrestrial vegetation change as inferred from *n*-alkane $\delta^{13}\text{C}$ analysis in the marine environment. *Geochimica et Cosmochimica Acta* **59**: 2853–2857.
- Bobst AL, Lowenstein TK, Jordan TE, *et al.* 2001. A 106 ka paleoclimate record from drill core of the Salar de Atacama, northern Chile. *Palaeogeography, Palaeoclimatology, Palaeoecology* **173**: 21–42.
- Boot CS, Ettwein VJ, Maslin MA, *et al.* 2006. A 35,000 years record of terrigenous and marine lipids in Amazon Fan sediments. *Organic Geochemistry* **37**: 208–219.
- Burbridge RE, Mayle FE, Killen TJ. 2004. 50 000 year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research* **61**: 215–230.
- Bush MB. 2002. Distributional change and conservation on the Andean flank: a palaeoecological perspective. *Global Ecology and Biogeography* **11**: 463–473.
- Bush MB, Moreno E, de Oliveira PE, *et al.* 2002. Orbital-forcing signal in sediments of two Amazonian lakes. *Journal of Paleolimnology* **27**: 341–352.
- Bush MB, Silman MR, Urrego DH. 2004. 48,000 years of climate and forest change in a biodiversity hot spot. *Science* **303**: 827–829.
- Colinvaux PA. 1989. Ice-Age Amazon revisited. *Nature* **340**: 188–189.
- Colinvaux PA, de Oliveira PE. 2000. Amazon plant diversity and climate through the Cenozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology* **166**: 51–63.
- Colinvaux PA, de Oliveira PE, Moreno JE, *et al.* 1996. A long pollen record from lowland Amazonia: forest cooling in glacial times. *Science* **374**: 85–87.
- Collister JW, Rieley G, Stern B, *et al.* 1994. Compound-specific $\delta^{13}\text{C}$ analyses of leaf lipids from plants with differing carbon dioxide metabolisms. *Organic Geochemistry* **21**: 619–627.
- Cowling SA. 1999. Plants and temperature– CO_2 uncoupling. *Science* **285**: 1500–1501.
- Cowling SA. 2004. Tropical forest structure: a missing dimension to Pleistocene landscapes. *Journal of Quaternary Science* **19**: 733–743.
- Cowling SA, Maslin MA, Sykes MT. 2001. Paleovegetation simulations of lowland Amazonia and implications for neotropical allopatry and speciation. *Quaternary Research* **55**: 140–149.
- Cowling SA, Betts RA, Cox PM, *et al.* 2004. Contrasting simulated past and future responses of the Amazon rainforest to atmospheric change. *Philosophical Transactions of the Royal Society: Biological Sciences* **359**: 539–547.
- Cruz FW, Burns SJ, Karmann I, *et al.* 2005. Insolation-driven changes in atmospheric circulation over the past 116,000 years in subtropical Brazil. *Nature* **434**: 63–66.
- Cruz FW, Burns SJ, Karmann I, *et al.* 2006. Reconstruction of regional atmospheric circulation features during the late Pleistocene in subtropical Brazil from oxygen isotope composition of speleothems. *Earth and Planetary Science Letters* **248**: 495–507.
- Cruz FW, Vuille M, Burns SJ, *et al.* 2009. Orbital driven east–west antiphasing of South American precipitation. *Nature Geoscience* **2**: 210–214.
- Damuth JE, Fairbridge RW. 1970. Equatorial Atlantic deep-sea arkosic sands and ice age aridity in tropical South America. *Geo-Marine Letters* **3**: 109–117.

- Damuth JE, Kumar N. 1975. Amazon Cone: morphology, sediments, age, and growth pattern. *Geological Society of America Bulletin* **86**: 863–878.
- Denison S, Maslin MA, Boot C, *et al.* 2005. Precession-forced changes in South West African vegetation during marine oxygen isotope stages 100 and 101. *Palaeogeography, Palaeoclimatology, Palaeoecology* **220**: 375–386.
- Eglinton G, Hamilton RJ. 1967. Leaf epicuticular waxes. *Science* **156**: 1322–1335.
- Eglinton G, Gonzalez AG, Hamilton RJ, *et al.* 1962. Hydrocarbon constituents of the wax coatings of plant leaves: a taxonomic survey. *Phytochemistry* **1**: 89–102.
- Ehleringer JR, Monson RK. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology and Systematics* **24**: 411–439.
- EPICA Community Members. 2006. One-to-one coupling of glacial climate variability in Greenland and Antarctica. *Nature* **444**: 195–198.
- Ettwein V. 2005. The effective moisture history of the Amazon Basin for the last 40,000 years reconstructed from ODP Site 942 on the Amazon Fan. PhD thesis, University College London.
- Farrera I, Harrison SP, Prentice IC, *et al.* 1999. Tropical climates at the Last Glacial Maximum: a new synthesis of terrestrial palaeoclimate data. I. Vegetation, lake-levels and geochemistry. *Climate Dynamics* **15**: 823–856.
- Fjeldsa J, Lovett JC. 1997. Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodiversity and Conservation* **6**: 325–346.
- Flagstad O, Syvertsen PO, Stenseth NC, *et al.* 2001. Environmental change and rates of evolution: the phylogeographical pattern within the hartebeest complex related to climate variations. *Philosophical Transactions of the Royal Society of London B* **268**: 667–677.
- Flood RD, Piper DJW, Klaus A, *et al.* 1995. *Proceedings of the ODP Program*, initial reports 155. Ocean Drilling Program: College Station, TX.
- Fritz SC, Baker PA, Seltzer GO, *et al.* 2007. Quaternary glaciation and hydrologic variation in the South American tropics as reconstructed from the Lake Titicaca drilling project. *Quaternary Research* **68**: 410–420.
- Galloway RW, Markgraf V, Bradbury JP. 1988. Dating shorelines of lakes in Patagonia, Argentina. *Journal of South American Earth Sciences* **1**: 195–198.
- González MA. 1994. Salinas del Bebedero Basin (República Argentina). In *Global Inventory of Lake Basins*, Kelts K, Gierlowski-Cordesch E (eds). Cambridge University Press: Cambridge, UK; 381–386.
- González MA, Maidana N. 1998. Post-Wisconsinian paleoenvironments at Salinas del Bebedero basin, San Luis, Argentina. *Journal of Paleolimnology* **20**: 353–368.
- Grosjean M. 1994. Paleohydrology of the laguna Lejía (north Chilean Altiplano) and climatic implications for late-glacial times. *Palaeogeography, Palaeoclimatology, Palaeoecology* **109**: 89–100.
- Grosjean M, van Leeuwen JFN, van der Knaap WO, *et al.* 2001. A 22,000 ¹⁴C year BP sediment and pollen record of climate change from Laguna Miscanti (23°S), northern Chile. *Global and Planetary Change* **28**: 35–51.
- Haberle SG, Maslin MA. 1999. Late Quaternary vegetation and climate change in the Amazon basin based on a 50 000 year pollen record from the Amazon fan, ODP site 932. *Quaternary Research* **51**: 27–38.
- Haffer J. 1969. Speciation in Amazonian forest birds. *Science* **165**: 131–137.
- Haffer J, Prance GT. 2001. Climate forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. *Amazoniana* **16**: 579–607.
- Harris S, Mix A. 1999. Pleistocene precipitation balance in the Amazon Basin recorded in deep-sea sediments. *Quaternary Research* **51**: 14–26.
- Haug GH, Hughen KA, Sigman DM, *et al.* 2001. Southward migration of the intertropical convergence zone through the Holocene. *Science* **293**: 1304–1308.
- Heusser CJ. 1989. Southern Westerlies during the Last Glacial Maximum. *Quaternary Research* **31**: 423–425.
- Heusser LE, Shackleton NJ. 1994. Tropical climatic variation on the Pacific slopes of the Ecuadorian Andes based on a 25,000-year pollen record from deep-sea sediment core Tri 163-31B. *Quaternary Research* **42**: 222–225.
- Hooghiemstra H, Van der Hammen T. 1998. Neogene and Quaternary development of the neotropical rain forest: the forest refugia hypothesis, and a literature overview. *Earth Science Reviews* **44**: 147–183.
- Hoorn C, Wesselinghe FP, ter Steege H, *et al.* 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* **330**: 927–931.
- Hughen KA, Overpeck JT, Peterson LC, *et al.* 1996. Rapid climate changes in the tropical Atlantic region during the last deglaciation. *Nature* **380**: 51–54.
- Hughen KA, Lehman S, Southon J, *et al.* 2004a. ¹⁴C activity and global carbon cycle changes over the past 50,000 years. *Science* **303**: 202–207.
- Hughen KA, Baillie MGL, Bard E, *et al.* 2004b. Marine04: marine radiocarbon age calibration 26-0 ka BP. *Radiocarbon* **46**: 1059–1086.
- Irion G, Müller J, Nunes de Mello J, *et al.* 1995. Quaternary geology of the Amazonian lowlands. *Geo-Marine Letters* **15**: 172–178.
- Islebe GA, Hooghiemstra H, van der Borg K. 1995. A cooling event during the Younger Dryas Chron in Costa Rica. *Palaeogeography, Palaeoclimatology, Palaeoecology* **117**: 73–80.
- Kastner TP, Goñi MA. 2003. Constancy in the vegetation of the Amazon basin during the late Pleistocene: evidence from the organic matter composition of Amazon deep sea fan sediments. *Geology* **31**: 291–294.
- Koch BP, Souza Filho PWM, Behling H, *et al.* 2011. Triterpenols in mangrove sediments as a proxy for organic matter derived from the red mangrove (*Rhizophora mangle*). *Organic Geochemistry* **42**: 62–73.
- Lamy F, Hebbeln D, Wefer G. 1999. High-resolution marine record of climatic change in midlatitude Chile during the last 28,000 years based on terrigenous sediment parameters. *Quaternary Research* **51**: 83–93.
- Lea DW, Pak DK, Peterson LC, *et al.* 2003. Synchronicity of tropical and high-latitude Atlantic temperatures over the Last Glacial Termination. *Science* **301**: 1361–1364.
- Ledru MP, Bertaux J, Sifeddine A. 1998. Absence of Last Glacial Maximum records in lowland tropical forests. *Quaternary Research* **49**: 233–237.
- Ledru MP, Rousseau DD, Cruz JFW, *et al.* 2005. Paleoclimate changes during the last 100 ka from a record in the Brazilian Atlantic rainforest region and interhemispheric comparison. *Quaternary Research* **64**: 444–450.
- Leduc G, Vidal L, Tachikawa K, *et al.* 2007. Moisture transport across Central America as a positive feedback on abrupt climate changes. *Nature* **445**: 908–911.
- Lenters JD, Cook KH. 1997. On the origin of the Bolivian high and related circulation features of the South American climate. *Journal of the Atmospheric Sciences* **54**: 656–677.
- Leyden B. 1985. Late Quaternary aridity and Holocene moisture fluctuations in the Lake Valencia Basin, Venezuela. *Ecology* **66**: 1279–1295.
- Liu K-B, Colinvaux PA. 1985. Forest changes in the Amazon Basin during the last glacial maximum. *Nature* **318**: 556–557.
- Marchant R, Cleef A, Harrison SP, *et al.* 2009. Pollen-based biome reconstructions for Latin America at 0, 6000 and 18 000 radiocarbon years ago. *Climate of the Past* **5**: 725–767.
- Marengo JA, Nobre CA, McClain ME, *et al.* 2001. General characteristics and variability of climate in the Amazon Basin and its links to the global climate system. In *The Biogeochemistry of the Amazon Basin*, McClain ME, Victoria RL, Richey JE (eds). Oxford University Press: Oxford; 17–41.
- Markgraf V. 1989. Reply to Heusser's 'Southern Westerlies during the Last Glacial Maximum'. *Quaternary Research* **31**: 426–432.
- Maslin MA. 1998. Equatorial Western Atlantic Ocean circulation changes linked to the Heinrich events: deep-sea sediment evidence from the Amazon Fan. *Geological Society London, Special Publications* **131**: 111–127.

- Maslin MA, Burns SJ. 2000. Reconstruction of the Amazon Basin effective moisture availability over the past 14,000 years. *Science* **290**: 2285–2287.
- Maslin MA, Swann G. 2005. Isotopes in marine sediments. In *Isotopes in Palaeoenvironmental Research*, Leng M (ed.). Springer: Dordrecht; 227–290.
- Maslin MA, Burns S, Erlenkeuser H, et al. 1997. Stable isotope records from ODP Sites 932 and 933 ODP Leg 155 Scientific Results Volume; 305–318. http://www-odp.tamu.edu/publications/155_SR/CHAP_17.PDF [5 January 2012].
- Maslin MA, Durham E, Burns SJ, et al. 2000. Palaeoreconstruction of the Amazon River freshwater and sediment discharge using sediments recovered at site 942 on the Amazon Fan. *Journal of Quaternary Science* **15**: 419–434.
- Maslin MA, Mahli Y, Phillips O, et al. 2005. New views on an old forest: assessing the longevity, resilience and future of the Amazon Rainforest. *Transactions of the Institute of British Geographers* **30**: 390–401.
- Maslin MA, Knutz PC, Ramsay T. 2006. Millennial-scale sea level control on avulsion events on the Amazon Fan. *Quaternary Science Reviews* **25**: 3338–3345.
- Maslin MA, Ettwein VJ, Wilson KE, et al. 2011. Dynamic boundary–monsoon intensity hypothesis: evidence from the deglacial Amazon River discharge record. *Quaternary Science Reviews* **30**: 3823–3833.
- Massaferro JJ, Moreno PI, Denton GH, et al. 2009. Chironomid and pollen evidence for climate fluctuations during the Last Glacial Termination in NW Patagonia. *Quaternary Science Reviews* **28**: 517–525.
- Mayle FE, Beerling DJ, Gosling WD, et al. 2004. Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Philosophical Transactions of the Royal Society of London B* **359**: 499–515.
- Mayle FE, Burn MJ, Power M, et al. 2009. Vegetation and fire at the last Glacial Maximum in tropical South America. In *Past Climate Variability in South America and Surrounding Regions: From the Last Glacial Maximum to the Holocene*, Vimeux F, Sylvestre F, Khodri M (eds). Developments in Paleoenvironmental Research. Springer: Dordrecht; 89–112.
- Meese DA, Gow AJ, Alley RB, et al. 1997. The Greenland ice Sheet project 2 depth–age scale: methods and results. *Journal of Geophysical Research* **102**: 26411–26423.
- Mikkelsen N, Maslin MA, Giraudeau J, et al. 1997. Biostratigraphy and sedimentation rates of the Amazon Fan. In *Proceedings of the Ocean Drilling Program, Scientific Results*, Vol. 155, Flood RD, Piper DJW, Klaus A, Peterson LC (eds). Ocean Drilling Program: College Station, TX; 577–594.
- Mora G, Pratt LM. 2001. Isotopic evidence for cooler and drier conditions in the tropical Andes during the last glacial stage. *Geology* **29**: 519–522.
- Moreno PI, Lowell T, Jacobson GL, et al. 1999. Abrupt vegetation and climate changes during the last glacial maximum and last termination in the Chilean Lake District: a case study from Canal de la Puntilla (41°S). *Geografiska Annaler* **81**: 285–311.
- Moritz C, Patton JL, Schneider CJ, et al. 2000. Diversification of rainforest fauna: an integrated molecular approach. *Annual Review of Ecology and Systematics* **31**: 533–563.
- Morley RJ. 2000. *Origin and Evolution of Tropical Rain Forests*. Wiley: Chichester.
- Pancost RD, Boot CS. 2004. The palaeoclimatic utility of terrestrial biomarkers in marine sediments. *Marine Chemistry* **92**: 239–261.
- Peltier WR, Fairbanks RG. 2006. Global glacial ice volume and last Glacial Maximum duration from an extended Barbados sea level record. *Quaternary Science Reviews* **25**: 3322–3337.
- Pennington RT, Dick C. 2010. Diversification of the Amazonian flora and its relationship to key geological and environmental events: a molecular perspective. In *Amazonia: Landscape and Species Evolution*, Hoorn C, Wesselingh F (eds). Wiley-Blackwell: Chichester; 373–385.
- Pennington RT, Lavin M, Prado DE, et al. 2004. Historical climate changes and speciation: neotropical seasonally dry forest plants show both pattern of both tertiary and quaternary diversity. *Philosophical Transactions of the Royal Society of London B* **359**: 515–538.
- Peterson LC, Haug GH, Hughen KA, et al. 2000. Rapid changes in the hydrologic cycle of the tropical Atlantic during the Last Glacial. *Science* **290**: 1947–1951.
- Piovano E, Ariztegui D, Córdoba F, et al. 2008. Reconstrucciones paleohidrológicas en la región pampeana (Programa paleo-pampas). In *XII Argentine Meeting of Sedimentology*. XIIRAS: Buenos Aires, Argentina.
- Prance GT. 1987. Vegetation. In *Biogeography and Quaternary History in Tropical America*, Whitmore TC, Prance GT (eds). Oxford Science Publications: Oxford; 28–44.
- Prentice IC, Harrison SP, Bartlen PJ. 2004. Global vegetation and terrestrial carbon cycle data analysis. *Journal of Vegetation Science* **15**: 635–646.
- Ramirez E, Hoffman G, Taupin JD, et al. 2003. A new Andean deep ice core from Nevado Illimani (6350m), Bolivia. *Earth and Planetary Science Letters* **212**: 337–350.
- Rommerskirchen F, Eglinton G, Dupont L, et al. 2003. A north to south transect of Holocene southeast Atlantic margin sediments: relationship between aerosol transport and compound-specific $\delta^{13}\text{C}$ land plant biomarker and pollen records. *Geochemistry, Geophysics, Geosystems* **4**: DOI: 10.1029/2003GC000541
- Schefuss E, Schouten S, Jansen JHF, et al. 2003. African vegetation controlled by tropical sea surface temperatures in the mid-Pleistocene period. *Nature* **422**: 418–422.
- Scheider CJ, Moritz C. 1999. Rainforest refugia and evolution in Australia's wet tropics. *Philosophical Transactions of the Royal Society: Biological Sciences* **266**: 191–196.
- Seltzer GO, Rodbell DT, Burns SJ. 2000. Isotopic evidence for late Quaternary climatic change in tropical South America. *Geology* **28**: 35–38.
- Seltzer GO, Rodbell DT, Baker PA, et al. 2002. Early warming of tropical South America at the Last Glacial–Interglacial Transition. *Science* **296**: 1685–1686.
- Servant M, Maley J, Turcq B, et al. 1993. Tropical forest changes during the late Quaternary in African and South American lowlands. *Global and Planetary Change* **7**: 25–40.
- Sifeddine A, Martin L, Turcq B, et al. 2001. Variations in the Amazonian rain forest environment: a sedimentological record covering 30,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* **168**: 221–235.
- Simoneit BRT, Elias VO. 2000. Organic tracers from biomass burning in atmospheric particulate matter over the ocean. *Marine Chemistry* **69**: 301–312.
- Simoneit BRT, Schauer JJ, Nolte CG, et al. 1999. Levoglucosan, a tracer for cellulose in biomass burning and atmospheric particles. *Atmospheric Environment* **33**: 173–182.
- Stevaux JC. 2000. Climatic events during the Late Pleistocene and Holocene in the Upper Parana River: correlation with the NE Argentina and South-Central Brazil. *Quaternary International* **72**: 73–85.
- Stine S, Stine M. 1990. A record from Lake Cardiel of climate change in southern South America. *Nature* **345**: 705–707.
- Sylvestre F. 2009. Moisture pattern during the Last Glacial Maximum in South America. In *Past Climate Variability in South America and Surrounding Regions: From the Last Glacial Maximum to the Holocene*, Vimeux F, Sylvestre F, Khodri M (eds). Developments in Paleoenvironmental Research. Springer: Dordrecht; 3–27.
- Thompson LG, Mosley-Thompson E, Davis ME, et al. 1995. Late Glacial stage and Holocene tropical ice core records from Huascaran, Peru. *Science* **269**: 46–50.
- Thompson LG, Davis ME, Mosley-Thompson E, et al. 1998. A 25,000-year tropical climate history from Bolivian ice cores. *Science* **282**: 1858–1864.
- Trauth MH, Strecker MR. 1999. Formation of landslide-dammed lakes during a wet period between 40,000 and 25,000 yr B.P. in northwestern Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* **153**: 277–287.
- Trauth MH, Ricardo AA, Haselton KR, et al. 2000. Climate change and mass movements in the NW Argentine Andes. *Earth and Planetary Science Letters* **179**: 243–256.
- van Breukelen MR, Vonhof HB, Hellstrom JC, et al. 2008. Fossil dripwater in stalagmites reveals Holocene temperature and rainfall

- variation in Amazonia. *Earth and Planetary Science Letters* **275**: 54–60.
- Van der Hammen T. 1974. The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography* **1**: 3–26.
- Van der Hammen T, Absy ML. 1994. Amazonia during the last glacial. *Palaeogeography, Palaeoclimatology, Palaeoecology* **109**: 247–261.
- Van der Hammen T, Hooghiemstra H. 2003. Interglacial–glacial Fuquene-3 pollen record from Colombia: an Eemian to Holocene climate record. *Global and Planetary Change* **36**: 181–199.
- Versteegh GJM, Schefuss E, Dupont L, *et al.* 2004. Taraxerol and Rhizophora pollen as proxies for tracking past mangrove ecosystems. *Geochimica et Cosmochimica Acta* **68**: 411–422.
- Vonhof HB, Kaandorp RJG. 2010. Climate variations in Amazonia during the Neogene and the Quaternary. In *Amazonia: Landscape and Species Evolution*, Hoorn C, Wesselingh F (eds). Wiley-Blackwell: Chichester; 201–210.
- Wang X, Auler AS, Edwards RL, *et al.* 2004. Wet periods in northeastern Brazil over the past 210 kyr linked to distant climate anomalies. *Nature* **432**: 740–743.
- Wang X, Auler AS, Edwards RL, *et al.* 2006. Interhemispheric anti-phasing of rainfall during the last glacial period. *Quaternary Science Reviews* **25**: 3391–3403.
- Willis KJ, McElwain JC. 2002. *The Evolution of Plants*. Oxford University Press: Oxford.
- Wilson KE, Maslin MA, Burns SJ. 2011. Evidence for a prolonged retroflexion of the North Brazil Current during glacial stages. *Palaeogeography, Palaeoclimatology, Palaeoecology* **301**: 86–96.