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Colombian dry moist forest transitions in the Llanos Orientales—A comparison of model and pollen-based biome reconstructions

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Abstract

Colombian vegetation, at the ecological level of the biome, is reconstructed at six sites using pollen data assigned a priori to plant functional types and biomes. The chosen sites incorporate four savanna sites (Laguna Sardinas, Laguna Angel, El Piñal and Laguna Carimagua), a site on the transition between savanna and Amazon rainforest (Loma Linda) and a site within the Amazon rainforest (Pantano de Monica). The areal extent of tropical moist forest, tropical dry forest and steppe have been subject to significant change: differential responses of the vegetation to climatic shifts are related to changes in plant available moisture, duration of dry season and edaphic controls on the vegetation. The record from El Piñal shows that the present-day savanna vegetation, dominated by steppe (Poaceae) with little occurrence of woody savanna taxa (e.g. *Curatella*, *Byrsonima*), was present since the last glacial period of the northern hemisphere. Unfortunately, El Piñal is located on an edaphic savanna and is not particularly responsive to registering change. Most records cover the early Holocene; one site records the El Abra stadial (Younger Dryas equivalent), when forest expansion reflects more humid climatic conditions and higher plant available moisture. During the early and middle Holocene, the maximum expansion of steppe and tropical dry forest occurred, indicating that dry climatic conditions continued to around 4000 ^{14}C BP. The following period, from shortly before 4000 ^{14}C BP, is characterised by an increase in forest and gallery forests, reflecting a wetter period probably with a shorter annual dry season. Anthropogenic influence on the vegetation is recorded by all the records over the last millennial, particularly characterised by a reduction in forest cover and high amplitude changes in vegetation.

Biome transitions from one type to another, and the environmental controls on this shift, are investigated by applying a vegetation model (BIOME-3). The model uses climatic data from six meteorological stations that, encompass a range of environments within lowland Colombia, which are similar to the pollen data. The signals of vegetation change can be translated to the main environmental controls of temperature and moisture to indicate the degree of change needed in these parameters to record the vegetation change depicted by the pollen data. Moisture balance is the dominant control on driving vegetation change whether under seasonal or annual control. The combined reconstruction from pollen data and model output of biome-scale vegetation dynamics for lowland Colombia allows an understanding of the environmental controls to be developed.

Keywords: Biome; Colombia; Environmental change; Llanos Orientales; Pollen; Vegetation modelling

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1. Introduction

The history of dry ecosystems in the Neotropics, and in Colombia in particular, is poorly understood as few natural archives (lakes, mires) accumulate sediments over long time periods, subsequently recording evidence of environmental change. From those sites available, lowland tropical ecosystems are shown to be highly dynamic, even at the course ecological resolution of the biome. For instance, the vegetation at lowland sites has changed from tropical rain forest to tropical seasonal forest to steppe biomes since 18,000 ^{14}C BP (Marchant et al., 2002a). More broadly, a synthesis of all pollen data from Neotropical savannas, north and south of the equator, showed that these expanded in areal extent during the full glacial times due to markedly drier climatic conditions (Behling and Hooghiemstra, 2001). Spatial and temporal foci on Colombia have investigated vegetation change along an altitudinal gradient (Marchant et al., 2001a), during the past 6000 years at sub-millennial resolution (Marchant et al., 2001b), 3000 year intervals back to the Last Glacial Maximum (LGM) (Marchant et al., 2002a), and over the last 450,000 years (Marchant et al., 2002b). These previous applications demonstrate the sensitivity of the Colombian pollen data to register environmental change due to the underlying data being of a high quality (floristically diverse and with good radiocarbon dated chronologies) and quantity. In addition to providing a method to investigate vegetation response, biome-based environmental reconstructions can also provide an excellent validation tool for vegetation model-based reconstructions (Clausen and Esch, 1994; Marchant et al., in press; Jolly et al., 1998a,b) that can be used to isolate and manipulate environmental variables such as temperature, precipitation, the seasonal variations of these, and changes in CO_2 concentration ($[CO_2]_{atm}$) (Foley et al., 1996; Marchant et al., 2002b). New insights into vegetation response to environmental change derived from new techniques lead to a re-evaluation of how vegetation dynamics reflect climate change. For example, in Colombia analysis of compound-specific carbon-decay compounds has led to a re-evaluation of the oscillation of tropical vegetation belts in response to climate change; sub-components of the vegetation belts, particularly the balance between C_3 and C_4 grasses behave differentially to past climate change (Boom et al., 2002). The focus of the current investigation is to extend this approach to apply a vegetation model (BIOME-3) and compare the reconstruction with those derived from pollen data from the Llanos Orientales and its extension to dry/moist forest transitions.

2. Area descriptions, methods and material studied

2.1. Environment and vegetation

The Llanos Orientales is a large low-lying plain in the northeast of Colombia situated to the east of the Andes and to the north of Amazonia. Climate in Llanos Orientales can be classified as tropical diurnal; differences in monthly temperature are generally small although daily fluctuations may be large (20 °C), especially during the dry seasons. The climate is dominated by two systems: the Inter-Tropical Convergence Zone (ITCZ) and moisture derived from the Atlantic Ocean. The two rainy seasons, from March to May, and October to December, are separated by dry seasons January to February, and June to September. The average precipitation is 950 mm yr^{-1} with an average of 175 mm in March (Berrio et al., 2003); however, there is considerable variation in this (IGAC, 1998). A strong environmental gradient has an edaphic, rather than a climatic, basis: extensive sandstone areas in the east of Colombia provide a free-draining substrate, and hence a water-stressed environment for the vegetation that resulted in open tropical dry forest and steppe biomes.

The vegetation of lowland Colombia has been described by Cuatrecasas (1958) who determined vegetation zones based mainly on altitude, climate (predominately rainfall) and aspect. Dry forest ecosystems form a substantial part of the vegetation in Colombia, the composition of these, mainly based on data from the Caribbean, has been documented by Gentry (1995). Areas characterised by xerophytic vegetation are found in the Caribbean plains (Murphy and Lugo, 1995), Cauca, Magdalena and Patia valleys, and in the Chicamocha canyon. Dugand (1941, 1970) studied the dry forests in the Caribbean lowlands and the dry deciduous forest on the Magdalena floodplains. The main arboreal taxa on the flat valley floor and the hills, where fires occur frequently, are *Byrsonima crassifolia*, *Curatella americana* and *Scheelea butyraceae*. The flora of the Llanos Orientales is complicated by a dense drainage network that dissects plain feeding into the Orinoco drainage system (Fig. 1); along these rivers gallery forest grows with a floristic composition, at the generic and family level, similar to that of Amazonian rainforest (Salgado-Labouriau, 1997). Although steppe senso stricto does not occur in Colombia, this terminology maintains consistency with the Latin American reconstruction (Marchant et al., submitted for publication) rather than a more appropriate term such as ‘grass savanna’.

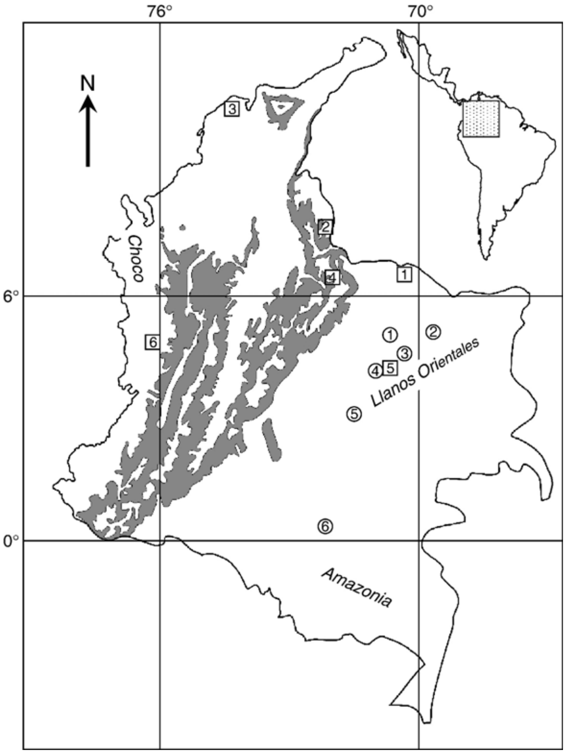

Fig. 1. Map of Colombia indicating the site locations refereed to in the text; those sites where pollen data are available are denoted by a circle, the meteorological station locations are denoted by a square. The numbers in each of the symbol relate to location details presented in Tables 1 and 4 for the palaeoecological sites and the meteorological stations, respectively.

2.2. Material studied

Over the past five decades, palynologists have collected numerous pollen-based records from Colombia. These were concentrated initially, in common with many tropical areas, at high altitudes (Van der Hammen, 1962; Van Geel and Van der Hammen, 1973); more recently there has been a focus on low altitude sites (Behling and Hooghiemstra, 1999; Berrío et al., 2000a,b, 2002). All data used here are the raw pollen counts that are currently being prepared for entry to the Latin American Pollen Database (http://www.ngdc.noaa.gov/paleo.html). The sites were chosen as they form a gradient of decreasing savanna nature; from strong edaphic savanna (El Piñal) to tropical rainforest (Pantano de Monica) (Table 1). To enable cross-site comparisons radiocarbon dates were used to apply a linear age–depth model for each site. Radiocarbon dates are standardised as calibrated ages by using calibration curves derived from the Calib 4.3 computer software (Stuiver et al., 1998; http://radiocarbon.pa.qub.ac.uk/calib/calib.html). Applicability of this method to provide dating control was checked, again on a site-by-site basis, for sedimentary contemporaneity (in terms of sedimentary hiatuses and rapid changes in sediment type about the radiocarbon data) and dating problems (such as age reversals and large standard errors attached to uncalibrated radiocarbon dates).

2.3. Method for translating pollen data to biomes

Before the pollen data can be analysed it is necessary to determine a classification of the potential vegetation types as sensed through the pollen data. The range of PFTs and biomes are determined specifically for dry moist forest, how the former combine to describe the latter, are presented in Table 2. The PFTs that characterise vegetation on the Llanos Orientales can be placed into two main groups: tropical (non-frost tolerant) and xerophytic (drought tolerant). The Colombian pollen taxa were assigned to one or more of the PFTs (Table 3) depending on the modern ecological range of the parent taxa responsible for producing the pollen. These assignments were made following reference to a wide body of evidence from several floras, botanical and palynological studies and personal communication with modern ecologists and palaeoecologists as collated within a dictionary of the distribution and ecological requirements of the parent taxa (Marchant et al., 2002c). Prior to the analysis aquatic and fern taxa were removed from the analysis as these commonly respond to very specific local environmental condi-

Table 1
Location of Colombian sites with pollen data that are included within our analysis

Site	No.	Longitude	Latitude	Altitude	Age range	Present biome	Sample type	RC	Site publications
El Piñal	1	−70.40	4.09	185	0–19,000	STEP	Lake	8	Behling and Hooghiemstra, 1999
Carimagua	2	−77.95	1.80	10	0–8270	TDFO	Lake	6	Behling and Hooghiemstra, 1999
Sardinas	3	−69.45	4.95	80	0–11,570	TSFO	Lake	7	Behling and Hooghiemstra, 1998
Angel	4	−70.58	4.45	205	0–10,000	STEP	Lake	7	Behling and Hooghiemstra, 1998
Loma Linda	5	−73.45	3.34	310	0–8700	TSFO	Lake	8	Behling and Hooghiemstra, 1998
Pantano de Monica	6	−72.08	−0.66	160	0–11,570	TRFO	Lake	9	Behling et al., 1999a

Each site is assigned a numerical code that relates to the site identifiers on Fig. 1.

Table 2
Plant functional types (PFTs) and biomes determined for the investigation on dry–moist forest dynamics

Codes	Plant functional types
g	Grass
Tr_1	Wet tropical raingreen trees
Tr_2	Dry tropical raingreen trees
Te_1	Wet tropical evergreen trees
Te_2	Dry tropical evergreen trees
txts	Tropical xerophytic trees and shrubs
tf	Tropical forbs/herbs
tef	Temperate forbs/herbs
sf	Steppe forbs/herbs
wte	Warm temperate broadleafed evergreen trees and shrubs

Codes	Biomes	Plant functional types
TRFO	Tropical Rain Forest	Tr_1, Te_1, tf
TSFO	Tropical Seasonal Forest	Tr_2, Te_2, tf, wte
TDFO	Tropical Dry Forest	Tr_2, Te_2, txts, sf, tef
WEFO	Warm Evergreen Forest	Te_2 tf, wte
STEP	Steppe	g, Tr_2, sf

The table also indicates how each biome is described by a unique set of PFTs.

tions, particularly hydrology, rather than being reflective of wider environment controls that are the focus of our investigation.

Output from the biomisation analysis is in the form of a range of 'affinity scores' to the a prior determined biomes for each depth analysed. In the previous large-scale applications the highest affinity score has been used for mapping as a colour-coded circle relating to the biome with the highest affinity score for each site in the analysis (Marchant et al., 2001b, 2002a). Although this is suitable for the reconstructions possible at a large continental/sub-continental scale, when investigating a small area, more information can be derived from the analysis.

2.4. Vegetation modelling

The BIOME-3 vegetation model is a biogeography-based model that predicts PFT dominance based on environmental conditions, ecophysiological constraints and resource limitations (Prentice et al., 1992). Inputs to BIOME-3 are temperature, precipitation, cloudiness, soil texture, atmospheric pressure and $[CO_2]_{atm}$ (Fig. 2). The level of $[CO_2]_{atm}$ prescribed to BIOME-3 has a direct influence on gross primary productivity via a photosynthetic algorithm and competitive balance between C_3 and C_4 plants (Haxeltine and Prentice, 1996). Following this input, a coupled carbon and water flux

Table 3
Assignment of pollen taxa from the sites presented in Table 1 to the PFTs presented in Table 3

PFT codes	Pollen taxa
g	Poaceae
Tr_1	*Acalypha*, *Aegiphila*, *Alchornea*, *Anthodiscus*, *Anthostomella fuegiana*, Apocynaceae, Araliaceae, Arecaceae, *Arcella*, Bombacaceae, *Croton*, *Crotalaria*, *Heliocarpus*, *Humiria*, *Inga*, *Lamanonia*, Loranthaceae, *Macrolobium*, Malpighiaceae, Malvaceae, *Mauritia*, Moraceae, *Oreopanax*, *Piper*, *Rhipsalis*, Rubiaceae, Rutaceae, Tiliaceae, Urticaceae, *Vismia*
Tr_2	*Acalypha*, *Alibertia*, *Andira*-type, *Annona*, Bignoniaceae, *Byrsonima*, *Casearia*-type, *Copaifera*, *Cordia*, *Coriaria*, *Cuphea*, *Curatella*, *Hieronima*, *Ipomoea*, *Mauritia*, Meliaceae, *Meliosma*, *Mimosa*, *Palicourea*, *Panopsis*, *Piper*, Rosaceae, *Schinus*, *Trema*, *Vallea*, *Warswiczia*, *Xylosma*
Te_1	*Alchornea*, *Amanoa*, Anacardiaceae, *Anemia*, *Apeiba*, Apocynaceae, Arecaceae, Astronium, Bombacaceae, *Brunellia*, *Cecropia*, Celastraceae, *Celtis*, *Clethera*, Combretaceae, *Didymopanax*, Euphorbiaceae, *Euterpe*, Fabaceae, *Ficus*, *Humulus*, *Iriartea*, *Mabea*, *Macrolobium*, *Mauritia*, *Maripa*, *Maytenus*, Meliaceae, Menispermaceae, Moraceae, *Myrsine*, Myrtaceae, *Ocotea*-type, *Oreopanax*, *Rauvolfia*, *Sapium*, Sapotaceae, *Sophora*, *Taperira*, *Tournefortia*, *Vismia*
Te_2	*Bauhinia*, Bignoniaceae, Boraginaceae, Bromeliaceae, *Brosimum*, *Brunellia*, *Bulnesia*, *Bursera*, Caryophyllaceae, *Casearia*-type, *Cecropia*, *Celtis*, *Crotolaria*, *Didymopanax*, *Humiria*, *Inga*, Leguminosae, *Macrocarpea*, *Metopium*, *Sapium*, *Schinus*, *Strutanthus*, *Taperira*, *Vitis*, *Xylosma*
txts	*Acalypha*, *Alternanthera*, Anacardiaceae, *Bauhinia*, *Byrsonima*, *Byttneria*, *Caryocar*, *Clusia*, *Copaifera*, *Cuphea*, *Curatella*, *Evolvus*, *Ipomoea*, *Protium*, *Siparuna*, *Stryphnodendron*
tf	Acanthaceae, Apiaceae, *Apium*, Asteraceae, *Begonia*, Bromeliaceae, Calyceraceae, *Genipa*, *Gomphorena*, *Gunnera*, *Hebenaria*, *Jungia*, *Justicia*, Ranunculaceae, Rubiaceae, Scrophulariaceae, *Siparuna*, *Thalictrum*, Urticaceae, Verbenaceae, *Viburnum*, *Xyris*
tef	Acanthaceae, *Apiaceae*, *Apium*, Asteraceae, *Borreria*, *Bravaisia*, Bromeliaceae, *Euphorbia*, *Galium*, *Genipa*, *Gomphrena*, *Gunnera*, *Halenia*, *Hebenaria*, *Iresine*, Iridaceae, *Jungia*, *Justicia*, Malvaceae, Moraceae, *Nertea*, *Stevia*, Umbelliferae, Urticaceae, *Xyris*, *Zornia*
sf	Amaranthaceae/Chenopodiaceae, Anarcardiaceae, Apiaceae, *Borreria*, Caryophyllaceae, *Ephedra*, *Eriocaulon*, *Eriogonum*, Euphorbiaceae, *Gaimardia*, *Gilia*, *Gleichenia*, *Gomphrena*, *Halenia*, *Hebenaria*, Lamiaceae, *Mutisia*, *Polygala*, Rhamanaceae, *Xyris*
wte	*Acalypha*, *Aegiphila*, *Alchornea*, *Alibertia*, *Allophylus*, Araliaceae, *Brunellia*, *Clusia*, *Croton*, *Crotolaria*, *Cydista*, *Euterpe*, *Genipa*, *Gentiana*, *Ludwigia*, *Luehea*, *Metopium*, *Mimosa*, *Panopsis*, Proteaceae, *Schinus*, Solanaceae, *Trema*, *Vernonia*

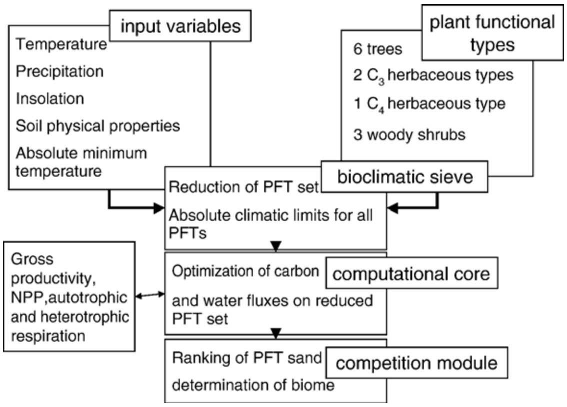

Fig. 2. Schematic of the BIOME-3 vegetation model indicating environmental inputs.

model is used to calculate leaf area index (LAI) and net primary productivity (NPP) for each PFT. The NPP is used to form a series of prescribed PFTs using resource availability (water, nutrient, CO_2 and light), which then combine to form biomes (Fig. 2). The translation of pollen data to biomes provides an opportunity to test the outputs from a vegetation model that similarly constructs biomes. Here we applied the BIOME-3 vegetation model that was developed as a tool for integrating the impacts of changes in climate and CO_2 on ecosystem structure and function (Haxeltine and Prentice, 1996). The model is based on the same environmental perspectives that govern our interpretation of the pollen data; that the vegetation is in equilibrium with the ambient environment. Similar to our treatment of the pollen data, output from BIOME-3 computes affinity (in the form of NPP) to a series of plant functional types. Recorded vegetation changes observed from the pollen data are compared to model output that is run at a range of boundary conditions. In conjunction with the data based approach we use the BIOME-3 model as a vehicle to describe how the vegetation will change in response to fluctuating environmental conditions. BIOME-3 is modified to represent vegetation change within a single pixel where data is available from a meteorological station (Fig. 1, Table 4). The model is run to determine the range of environmental conditions that would be incorporated in a transition from the present climatic condition to those of the last glacial maximum (LGM). Environmental conditions were controlled for temperature, precipitation and $[CO_2]_{atm}$. As the LGM is the origin for our reconstruction focus we run the model at 200 ppm $[CO_2]_{atm}$ with the other environmental parameters being kept constant. Temperature and precipitation were set to present day mean annual values, as recorded at the nearby meteorological station, and then set to reduce by approximately 8 °C and 600 mm yr^{-1}, respectively. This range was chosen as it encompasses the maximum climate change experienced at the LGM.

3. Results

Results from the biome analysis are portrayed as *X–Y* plots of biome affinity scores vs. time (Fig. 3). The six plots are arranged in a gradient of decreasing savanna nature, thus arranged from strong edaphic savanna (El Piñal (Fig. 3a) to tropical rainforest (Pantano de Monica, Fig. 3f). Results from the vegetation modelling are portrayed as box plots with the environment gradients of moisture and temperature forming the *X–Y* axes, respectively (Fig. 4). These plots are arranged in along a gradient of decreasing savanna nature.

3.1. Biome reconstructions from pollen data

Rather than describing change from each site, the pollen-based results will be portrayed as a series of periods: ‘late glacial and transition to the Holocene’, ‘early to mid Holocene’ and ‘mid to late Holocene’.

3.1.1. Late glacial and transition to the Holocene

The only site to extend to the late glacial is El Piñal (Fig. 3a), and this does so at quite a low resolution with only five samples comprising the lower 8000 years;

Table 4
Location details for the six meteorological stations used to run the BIOME-3 vegetation model

Site	Site no.	Longitude	Latitude	Altitude	Present biome
Arauca	1	−70.15	7.10	320	Xeric woodlands scrub
Cucuta	2	−72.50	8.00	800	Short grassland
Barranquilla	3	−74.95	11.00	100	Short grassland
Bucaramanga	4	−72.75	7.45	240	Tropical seasonal forest
Villavicencio	5	−74.05	4.80	300	Tropical rain forest
Quibdo	6	−76.85	5.85	240	Tropical rain forest

Each site is assigned a numerical code that relates to the site identifiers on Fig. 1.

however it is possible to show that tropical dry forest was present at the LGM. Interestingly, this changes little from the present vegetation although the more mesic biomes of tropical rain forest and tropical seasonal forest have their lowest affinity scores. There is a sharp increase in the affinity score of the tropical dry forest biome going into the Holocene with a concomitant rise in affinity to the tropical rain forest biome, possible coeval with the El Abra (Younger Dryas equivalent). The only other site to register this period (Laguna Sardinas, Fig. 3c) also records a rise in affinity score to the tropical dry forest biome about this time. The record from Pantano de Monica (Fig. 3f) interestingly records a steady decrease in the affinity to warm temperate forest in the early part of the Holocene, a trend that may be a continuation from the late glacial period.

3.1.2. Early to mid Holocene

All the sites record the early Holocene. Although there are site-specific signatures of change, the general trend is one of increasing affinities to steppe and tropical dry forest towards the mid-Holocene. El Piñal (Fig. 3a) shows very little change whereas Loma Linda (Fig. 3e)

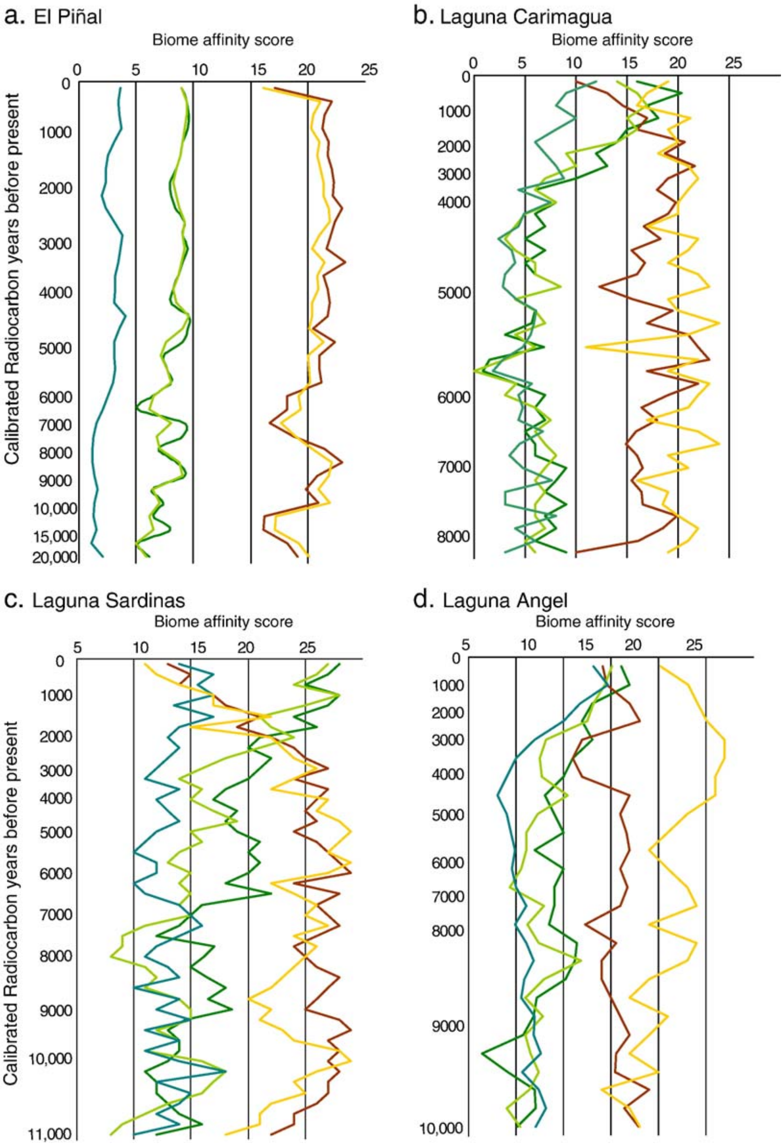

Fig. 3. *X–Y* plots of biome affinity scores vs. time arranged in a gradient of decreasing savanna nature, thus arranged from strong edaphic savanna (El Piñal, 3a) to tropical rainforest (Pantano de Monica, 3f).

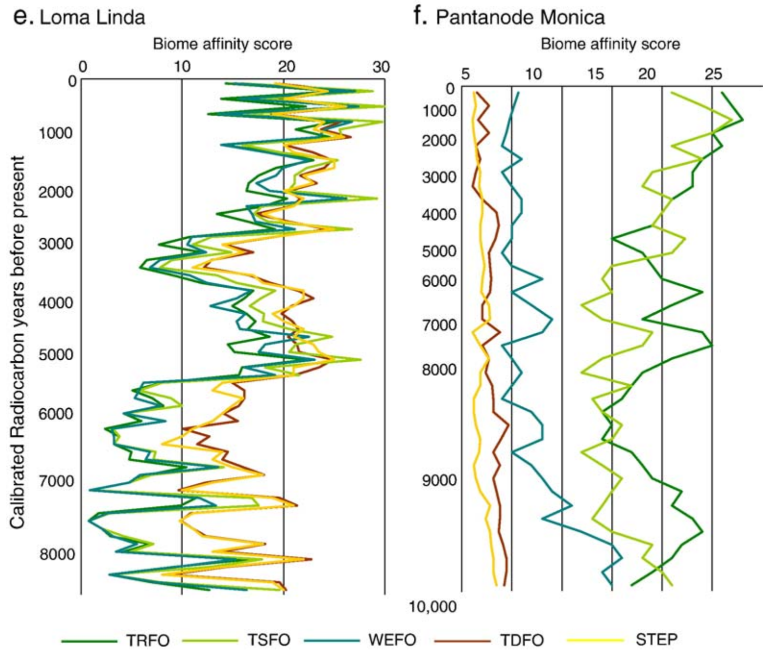

Fig. 3 (*continued*).

shows very high variability as the tropical dry forest biome becomes quite dominant at the site, as denoted by the strong anti-phase relationship with the more mesic biomes of tropical rain forest and tropical seasonal forest. Interestingly, a number of sites recorded the highest affinity to the tropical dry forest biome around 6000 ^{14}C BP, whereas at Pantano de Monica there is a decreased affinity to the tropical rain forest biome (Fig. 3f).

3.1.3. Mid to late Holocene

Again all the sites record the mid Holocene to late Holocene. The general trend observable at Laguna Carimagua (Fig. 3b), Laguna Sardinas (Fig. 3c), Laguna Angel (Fig. 3d) and Pantano de Monica (Fig. 3f) if a transition to more mesic vegetation; at the former three sites this is characterised by a reduction in tropical dry forest where as at the later site there is an increase in tropical rain and tropical seasonal forest biomes. The timing and magnitude of this change is quite synchronous and dramatic, appearing to occur between 5000 and 3000 ^{14}C BP. At Loma Linda (Fig. 3e) there is a rapid increase in the affinity scores to all the biomes although there are occasions in the last 4000 years where tropical seasonal forest biome dominates. Many of the records show a change in the last few thousand years, the common signal being a reduction in forest at all sites, apart from Laguna Sardinas (Fig. 3c) and Loma Linda (Fig. 3e), thought to stem from human activity. Laguna Sardinas and Loma Linda show a slightly different response, at the latter site there is high variation in the signal over the last 2000 years, again possibly a response to rapid vegetation change following human activity.

3.2. Vegetation modelling

The vegetation changes are broadly analogous to those recorded from our pollen-based reconstructions with one major exception: one benefit of BIOME-3 is its ability to separate grass-dominated biomes on the basis of NPP and the relative response of the C_3 and C_4 grasses; therefore, there are more grassland types than possible from the pollen data. Thus, the model output provides an indication on the range of potential vegetation types at the LGM. At the lowland sites of Cucuta (Fig. 4a) and Baranquilla (Fig. 4b) the importance of moisture reduction is again apparent as shown by the predominance of the horizontal boundaries between the biomes. Interestingly, moisture appears to be a less important control at Baranquilla (Fig. 4b) compared to Cucuta (Fig. 4a) as recorded by the stronger vertical gradient between the dry savanna and short grassland. The control of moisture continues to be important at the slightly higher sites of Bucaranmanga (Fig. 4c) and Arauca (Fig. 4d), both being characterised by xerophytic woods and shrub prior to the transition to grass-dominated biomes, again portrayed by strong vertical gradients. Two mesic lowland sites of Villavicencio

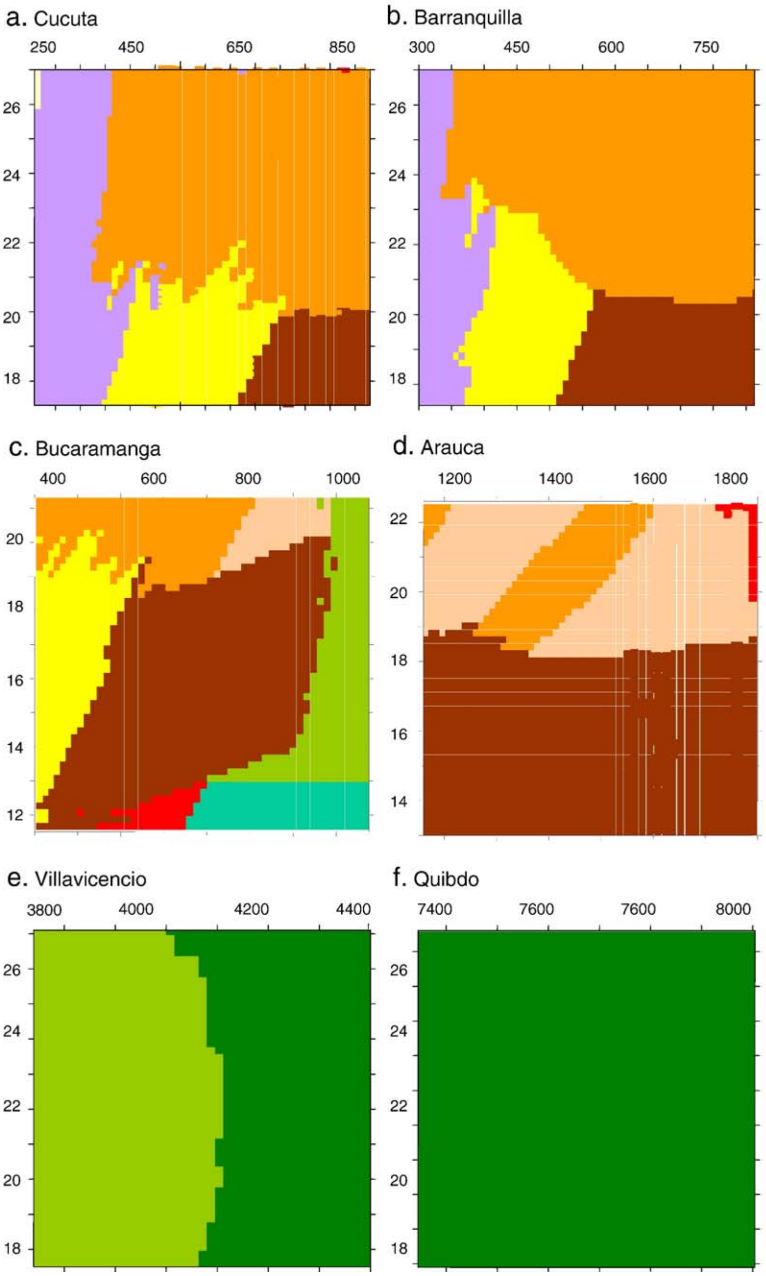

Fig. 4. Biome reconstructions derived from the BIOME-3 vegetation model for the six locations where meteorological data are available. Mean annual temperature (°C) is shown along the Y axis with mean annual precipitation (mm yr^{-1}) shown along the X axis. The present-day climate space is represented for each location by the top right hand corner in each plot—temperature and precipitation are set to reduce by 8 °C and 600 mm yr^{-1} to simulate the environment experienced since the LGM for the region of Colombia encompassed by our records.

(Fig. 4e) and Quibdo (Fig. 4f); both show the dominance of tropical rain forest and the dominance of the temperature gradient in precipitating vegetation change. Results from Quibdo (Fig. 4f), located in the hyperhumid area, shows that even under substantial moisture changes the tropical rain forest biome remains to be reconstructed.

4. Discussion

The discussion will be divided into five main sections: (1) a general section on Late Quaternary biome changes and palaeoenvironmental interpretations available from BIOME-3 model output and connections to the pollen data, (2) three sections that focus on the late glacial and transition to the Holocene, the early to mid Holocene, and the mid to late Holocene and finally, a section that discusses the more recent results relating to anthropogenic activity and evidence of this from the analysis.

4.1. Late Quaternary biome changes and palaeoenvironmental interpretations

In most previous applications of the biomisation technique to pollen data, only the most dominant biome has been used to describe the reconstructed vegetation (Jolly et al., 1998a,b; Tarasov et al., 1998; Marchant et al., submitted for publication). However, as discussed in a previous application of the technique to Colombian pollen data (Marchant et al., 2004a), this results in a large amount of lost information. Coarsening of the palaeoecological signal to a single biome can provide an erroneous vegetation reconstruction, for example, if the dominant biome (highest affinity score) would be applied to Laguna Angel (Fig. 3d), a steppe biome would be reconstructed throughout and the record would be viewed as unresponsive to environmental change. With interesting vegetation response recorded by biomes with relatively low affinity scores, it is crucial to interpret biome reconstruction with the realisation a large amount of information lies behind the biome dot maps that is ‘hidden’ but can be used to differentiate subtle intra-biome differences (Marchant et al., 2001b, 2002b; Marchant and Hooghiemstra, 2001). This understanding of ‘what lies beneath’ is particularly important when the pollen data are used for palaeoclimate reconstructions. Many palaeoclimate reconstructions are driven with a modern analogue-driven transfer function (Farrera et al., 1999), under the assumption that interactions between the abiotic and biotic environment remain constant through time, that commonly do not take into account non-climatic parameters such as volcanic activity, fire (Cavelier et al., 1998; Rull, 1999), UV-B insolation (Flenley, 1998) or atmospheric composition, in particular changing CO_2 levels (Marchant et al., 2002b). Such omissions can lead to significant errors in these estimates that are then used, sometimes indiscriminately, by other disciplines. Predicting and detecting forest responses to changes in non-climatic factors present significant challenges that require creative solutions (Graham et al., 1990) such as adapting a vegetation model. For example, concentrations of CO_2 reduced to glacial levels (200 ppmV, Petit et al., 1999) have been shown to have a very significant impact on tropical vegetation (Jolly and Haxeltine, 1997; Boom et al., 2002). Changes in dry–moist forest plant distribution are predominately driven by changes in moisture and how this interacts with low $[CO_2]_{atm}$; CO_2 change manifested as a variation in water use efficiency (WUE) (Farquhar, 1997). Under conditions of low $[CO_2]_{atm}$ plants have to transpire more to achieve the same level of photosynthesis and hence NPP; halving the $[CO_2]_{atm}$ is comparable to halving the rainfall (Farquhar, 1997). Although it has been shown that some C_3 plants can respond to decreased $[CO_2]_{atm}$ by increasing the amount of stoma on the leaf lamella (Wagner et al., 1999), this is difficult to apply to late glacial interglacial transitions as one of the main impacts on plants appears to be reduced water use efficiency rather than a physiological response to low $[CO_2]_{atm}$ (Cowling and Sykes, 2000). For example, if the stomata have a wider aperture, or are more numerous, this will result in more water being evaporated. Thus, no matter how the stomata compensate for the variation in $[CO_2]_{atm}$, C_4 plants will always have a competitive advantage under environments characterised by relative water stress (Boom et al., 2002).

One problem in palaeoenvironmental reconstructions from single sites is that vegetation change may result from multiple causes, i.e. a change in temperature may have a similar effect as a change in moisture or $[CO_2]_{atm}$. Indeed, our analysis shows that inter-site vegetation response varies considerably, emphasising the importance of understanding temporal and spatial variability and hence the misconception that climate change would, at any one time, give the same signal throughout a region (Huntley, 1999). Site selection is crucial in understanding controls on environmental change, and how the vegetation reflects this. The varied nature of vegetation change, as recorded by the pollen data, is also apparent from the BIOME-3 model output used to simulate the influence of changing environmental conditions. Applying a vegetation model allows separation, and subsequent investigation on the impact on, of change in a range of environmental parameters from the site to the region. Although BIOME-3 provides a useful tool to investigate impact of changing environmental conditions on vegetation, that can add value to the interpretation of palaeoecological data, a series of improvements would greatly improve its utility. Particularly important within the context of our investigation are soil–vegetation relationships and soil hydrology that are more variable than parameterised within the BIOME-3 model that currently has a two-layered simple bucket approach. Additional components that describe the length and character of dry seasons (such as when is the main concentration of rainfall) and soil hydrology would be useful model developments; this is highly achievable where there are good local meteorological and soils datasets locally available. These parameters are particularly important for moist and dry forest transitions in tropical regions where, unlike temperate areas, moisture is the main component that determines seasonality rather than temperature.

Late Quaternary vegetation history of the Neotropical phytogeographical realm is still poorly resolved: a significantly greater number of sites are needed to determine more precisely the complexities of environmental change and the driving mechanisms behind this. Such a wish is not purely academic with ensuing results being important in model testing (Peng et al., 1998), developing biogeographical theory (Tuomisto and Ruokolainen, 1997), and understanding issues concerned with biodiversity and early human-environmental interactions (Marchant et al., 2004b). New sites, located in key areas, combined with the application of a range of proxies of environmental change, are required to refine our understanding on the sensitivity of the Neotropics to Late Quaternary climatic variations, how the environment responds to this variation, and how this signal can be interpreted in light of comparable data from adjacent areas. An increased volume of physical data would be aided by a philosophical move for interpreting data away from the 'present is the key to the past' to the 'past is the key to the present'.

4.2. Late glacial period and transition to the Holocene

The precise dating of the LGM in Colombia, as elsewhere in South America, is problematic (Bush et al., 1990; Hooghiemstra and Van der Hammen, 1998; Ledru et al., 1998). In the Colombian lowlands El Piñal is the only site with sediments dating to the LGM. However, although there are good radiocarbon data to constrain sediments to the LGM, the sedimentation rate and the ensuing resolution of the vegetation reconstruction is very low. Although this is only one site from an edaphic savanna, results do not agree with the suggestion that closed *Byrsonima*-dominated savanna preceded the open savannas of today (Wijmstra and van der Hammen, 1966). The signals from the site are mirrored regionally (Behling and Hooghiemstra, 2001) with sparse vegetation characterising the Plateau of Mato Grosso (Servant et al., 1993) that extends to the coastal areas of Guyana and Surinam. Indeed, the reconstruction from El Piñal may reflect the majority of the area presently covered by drier types of tropical forest that were probably characterised by more open forest around the LGM. The modelled results show that the expansion of savanna would have been greatly aided by reduced CO_2 concentrations and the resultant competitive advantage attained by C_4 grasses over C_3 plants by better WUE (Haberle and Maslin, 1999; Marchant et al., 2002b), as is the case at higher altitudes (Boom et al., 2002). However, to see if lowland steppe expansion around the LGM is a spatially consistent signal, additional sites with sediments that date to the LGM are required. Given that significant sediment accumulation in moisture-stressed environments are quite rare, developments in vegetation modelling can help to fill in gaps where there are deficiencies in data.

4.3. Early to mid Holocene

Relative to the present day, the sites under analysis here mainly record a shift to more xeric vegetation during the early to mid Holocene. Relatively dry conditions have also been indicated for lowland Colombia for the mid-Holocene although the peak of dry conditions, occurring between 6500 and 4500 ^{14}C BP, varied considerably between sites (Behling et al., 1999a). This signal of mid-Holocene aridity is recorded regionally with dry environmental conditions in southern Brazil extending from the early Holocene until approximately 4500 ^{14}C BP when there was an increase in arboreal taxa (Alexandre et al., 1999). The driest phase in central Brazil is at approximately 5000 ^{14}C BP, with relatively moist climate conditions similar to today setting in after 4000 ^{14}C BP (Ledru, 1993). Although fire has been proposed as being responsible for late Holocene variation in the forest/savanna boundary in Brazil (Desjardins et al., 1996), this relative aridity is also thought to reflect an extended dry season during this period (Behling, 1997). A dry phase is also recorded at many Andean sites, for example, in northern Chile desiccation of the Puna ecosystem is recorded between 8000 and 6500 ^{14}C BP (Baied and Wheeler, 1993). On the central Peruvian Andes, a dry warm climate was encountered between 7000 and 4000 ^{14}C BP (Hansen et al., 1994). δ^{18}O measurements from the Huascarán ice core record taken from highland Peru shows that mid-Holocene climatic warming and drying was recorded from 8200 to 5200 ^{14}C BP, with maximum aridity between 6500 and 5200 ^{14}C BP (Thompson et al., 1995). On the Bolivian Andes, a dry phase is recorded from approximately 5500 ^{14}C BP (Abbot et al., 1997). Farther north, within the Lake Valencia catchment, dominant taxa during this period include *Bursera*, *Piper* and *Trema* (Bradbury et al., 1981), these tropical raingreen taxa indicate the presence of a seasonal climate with relatively dry conditions (Marchant et al., 2002c). Low lake levels in central Panama also indicate that environmental conditions at this period were more xeric (Piperno et al., 1991; Bush et al., 1992) whereas sites on the Yucatán peninsula show a shift to warm evergreen forest, characteristic of warmer conditions, persisted from the early Holocene until approximately 6500 ^{14}C BP (Brown, 1985). Despite a large body of evidence for a mid-Holocene dry period, there still remains a debate about the intensity, and even the occurrence, of this. Salgado-Labouriau et al. (1998) suggests that most savanna areas were characterised by increased rainfall between 7000 and 6000 ^{14}C BP.

One of the main mechanisms used to determine moisture shifts in Colombia is fluctuation in the Southern Oscillation and the migration of the ITCZ (Martin et al., 1997). Rather than changes in the median position of the ITCZ, changes in the character of the ITCZ oscillation, such as greater latitudinal range for annual migration, can be invoked to explain vegetation changes (Behling and Hooghiemstra, 2001). Martin et al. (1997) suggests that during the mid-Holocene, the ITCZ was located farther north than its present-day position, resulting in a summer rainfall deficit compensated by increased winter precipitation, in short greater seasonality. However, due to the topographical influence of the Andes and the convergence of westerly and easterly winds, the ITCZ has a sinusoidal profile over northern South America; therefore, to explain moisture changes over north-eastern South America, the importance of convective moisture sources cannot be overestimated. Reduced precipitation, particularly in mid latitude western South America, is likely to result from a reduction in the intensity of the westerly climate systems. It is also possible that episodic dry events that presently occur in South America in relation to sea-surface temperature anomalies of the Pacific Ocean were more frequent in the mid-Holocene (Markgraf, 1993). This later suggestion has also been used to explain increased fire frequency in southeast Brazil (Alexandre et al., 1999).

4.4. Mid Holocene to late Holocene

There are a growing number of studies from the South American tropics that document the timing and strength of mid to late Holocene environmental change that are a testament to the highly responsive nature of tropical sediment archives to climate change (Marchant and Hooghiemstra, 2004). In addition to these site-specific studies, a number of synthesis studies documented broad-scale patterns of vegetation change (Behling and Hooghiemstra, 2001; Behling, 2002; Marchant et al., 2002a). Vegetation at numerous Colombian sites record a shift between 4000 and 3500 ^{14}C BP indicative of relatively moist environmental conditions resulting from increased precipitation, decreased evaporation, a shorter dry season or a combination of these factors (Marchant et al., 2001a). The strength of this climatic signal was remarkable, for example, the level of Lake Titicaca increased by some 100 m about 3800 ^{14}C BP (Cross et al., 2000). Farther to the south, increased moisture levels recorded in the high altitude ice-core record of Sajama followed an increase in snow accumulation as recorded by a decrease in aerosols from 3400 ^{14}C BP (Thompson, 1992; Thompson et al., 2000). However, this was not a single uni-directional event: mid Holocene environmental variability was recorded by four noticeable dust events dated between 5550 and 2350 ^{14}C BP (Thompson et al., 1995). A similarly complex signal was recorded in the Quelccaya ice cap (Thompson et al., 1984).

A relatively synchronous climatic signal to wetter climatic conditions was centred about 4000 ^{14}C BP as relatively mesic forests extended across the Llanos Orientales, herb savanna changed to a shrub-dominated savanna, and shrub savanna to tropical moist forests (Berrío et al., 2002a,b). In addition to general forest expansion, a trend that may still be in progress (Behling and Hooghiemstra, 1998), this period of vegetation change is specifically characterised by a marked increase in palms (*Euterpe*/*Geonoma*, *Mauritia* and *Mauritella*) (Behling and Hooghiemstra, 1999). This vegetation shift may be in response to a wetter climate, probably with a short dry season and/or human influence (Behling and Hooghiemstra, 1998, 1999; Berrío et al., 2002a,b). Interestingly, *Mauritella* increases around Laguna Angel, whereas *Mauritia* is the main taxon to increase around Laguna Sardinas (Behling and Hooghiemstra, 1998). In addition to being an indicator of human activity, *Mauritia* is also known to grow under higher moisture availability (Berrío et al., 2002a,b; Marchant et al., 2002c).

More regionally, the stratigraphy from a site situated in the hyper-humid (precipitation >10,000 mm yr^{-1}) lowland rainforest near the Pacific coast (El Caimito) records sandy sediments at about 4200 years which are indicative of increased fluvial activity in response to greater moisture levels (Velez et al., 2001, 2005). On the northern boundary of the Amazonian rainforest in French Guinea, fires have been less frequent since 3000 ^{14}C BP when forests appeared to be relatively humid in comparison to the present-day (Charles-Dominique et al., 1998). In Amazonia, a pollen record from along the Rio Curuá indicates a rise in river level following relatively wet conditions around 3500 ^{14}C BP (Behling and Lima da Costa, 2001). This environmental signal is similarly recorded in south-central Brazil where from 4000 ^{14}C BP, tree-dominated vegetation communities developed in areas previously characterised by savanna (Alexandre et al., 1999). At the present southern boundary of the Amazonian rain forest, pollen evidence indicates a marked southerly expansion in rainforest at about 3500 ^{14}C BP when there was a sharp increase in the presence of *Isöetes*, an indicator of permanent lakes (Mayle et al., 2000). However, not all sites show a uniform environmental signal around 4000 ^{14}C BP. A dry, rather than wet, period is suggested from Ecuadorian Amazonia between 4200 and 3150 ^{14}C BP (Bush and Colinvaux, 1988; Liu and Colinvaux, 1985). After about 4000 ^{14}C BP the climate of equatorial South America became moister, essentially resembling modern conditions (Ledru et al., 1998; Marchant and Hooghiemstra, 2004).

One of the main climatic systems to influence the relatively recent climate dynamic in north-eastern South America is a change in the character of ENSO that is known to have evolved markedly over time (Markgraf et al., 2000). One recent record documenting long-term variability in the behaviour of ENSO comes from the Galapagos Island where a well-dated sedimentary record indicates minimal El Niño activity during the mid Holocene with a rapid increase in the frequency of events at about 4200 ^{14}C BP (Riedinger et al., 2002). These records from the Pacific Islands are also consistent with evidence from western South America where marine molluscan remains indicate a population structure change at about 3450 ^{14}C BP which may be associated with a change in flooding frequency driven by El Niño events around 3600 ^{14}C BP (Wells, 1990). Records from continental South America also support these oceanic records. Laminated sediments from a lake situated in the Ecuadorian Andes show a clear increase in El Niño activity about 5000 ^{14}C BP (Rodbell et al., 1999). Given the dynamic series of events about this period (Marchant and Hooghiemstra, 2004), it seems unlikely that any single climate mechanism was responsible for driving the shift in climate around 4000 ^{14}C BP. Changes in different components of the earth–atmosphere–ocean system have a magnifying, or buffering, effect on underlying climatic change. Changes, direct or resonant, in ENSO, solar activity, volcanic activity, ice-sheet dynamics and Atlantic circulation, and how they impacted on the vegetation locally would have been buffered by local environmental conditions and atmosphere–ocean–land feedbacks. As ENSO is shown to be particularly active from the mid-Holocene, and the sphere of influence is primarily within the tropics, this appears to be a major factor driving change about 4000 ^{14}C BP. The establishment of this major ocean circulation system had a direct impact on Atlantic SST and associated circulation. As an additional layer to these climate mechanisms, the relatively local impacts of increased dust loading (volcanic or terrestrial), changed albedo and CH_4 would have contributed to the climate shift, resulting in increased rate or magnitude of change that was manifested locally. The period around 4000 ^{14}C BP is characterised by high variability in all these factors (Marchant and Hooghiemstra, 2004). Added complexity is caused by steep environmental gradients associated with non-climatic factors (Marchant and Hooghiemstra, 2004). For example, the presence of the tropical dry forest biome in lowland Colombia, e.g. the catchment of El Piñal results from a combination of strongly seasonal conditions at present and locally strong edaphic influence (Behling and Hooghiemstra, 1999).

There are still numerous questions that remain regarding environmental variability in the Llanos Orientales, providing answers to these will allow a better understanding on how Neotropical areas reflect, and in turn respond, to changes in major climate-forcing factors. Moreover, processes should not be investigated in isolation but possible combinations need to be investigated in terms of enhanced impacts or resonances that may lead to particularly rapid, unidirectional, and relatively long lived periods of change. To develop such an understanding, high resolution, multiproxy data are required that target particular periods with increased temporal and spatial resolution. Inherent in this is the need for closer connections between climate/vegetation model development and palaeo data generation in a way that is mutually beneficial to data producers and users.

4.5. Anthropogenic influence

The majority of the sites record a reduction in forest in the uppermost samples, primarily dating to the last 2000–3000 years. A previous investigation indicating the presence and spread of degraded vegetation indicates an expansion in this type since the mid Holocene, (Marchant et al., submitted for publication). Separating out human-induced and climate-induced changes can be problematic as the environmental signals from both forcing factors are often similar and can be easily confused. Indeed, there can be a danger in over-interpreting such records, particularly when aiming to deduce a regional reconstruction when only the local conditions are recorded. The relevance of Holocene climatic shifts, however difficult to separate out, are paramount to understanding cultural change; climatic events resulting in ecosystem changes have an important bearing in the evolution of culture (Gnécco, 1999). Notwithstanding doubts about unidirectional 'cause and effect' relationships between environmental and cultural change, there are strong synchronicities between archeo-historical and palaeoenvironmental data (Proctor, 1998). This synthesis has indicated areas, and periods, where our interpretations are particularly contentious due either to a lack of information or conflicting data sets that should be targets for new initiatives. To develop some tantalising links that combine theories of climate change and environmental and cultural response, there is a strong need to work more closely with the archaeological community.

There is a growing amount of evidence against the suggestion that lowland tropical forests were unable to support substantial human populations due to humid climates, poor soils and profusion of pests (Pringle, 1998). Palaeoindians probably lived in the Chocó Rain forest since at least 3460 ^{14}C BP (Behling et al., 1999b). Indeed, Holden (1998) suggests that farming in the Americas may have begun within tropical forests. Direct archaeological evidence indicates that human occupation of lowland tropical rain forest that dates back to approximately 10,000 ^{14}C BP (Gnécco, 1999; Gnécco and Mohammed, 1994). Barse (1990) documented a centralised population in the middle Orinoco Basin (a forest/savanna transitional environment) that used unifacial stone tools dating to the early Holocene. Charcoal dated before approximately 4000 ^{14}C BP within the Rio Buritaca catchment provides direct evidence to support the suggestion that Amerindians were frequently using fires for clearing lands, probably for the cultivation of *Zea mays* (Hérrera, 1985). Cavelier et al. (1998) suggest such impact was able to transform moist forest ecosystems to secondary growth and eventually savanna. Archaeological evidence indicates human impact from the middle Holocene at several sites on the Colombian savanna where Pre-Colombians were living close to the rivers cultivating *Zea mays* and other plants from the gallery forest (Berrío et al., 2000a,b).

Interestingly, a number of lowland sites record the earlier increase in mesic vegetation as a marked increase in palms (*Mauritia* and *Mauritella*) that began from approximately 3800 ^{14}C BP in response. The mid Holocene onset of wetter environment, and the associated impact of increase climatic variability on resources, may be manifested as a concerted migration or establishment of a trade connection to another location. Such a situation would make the relatively dry areas of Colombia; such as the Llanos Orientales and the dry inter Andean valleys, more attractive for habitation. The widespread occurrence of this signal in tropical Latin America, and the opposite shift to a relatively arid environment in Africa, is highly interesting and its characterisation and possible cultural interconnections should be a target of future investigation (Marchant and Hooghiemstra, 2004). At approximately 2000 ^{14}C BP the concentration of degraded vegetation at lowland sites extends to the higher altitudes in Colombia (Marchant et al., submitted for publication) although there was no significant collapse in lowland agricultural systems as widely documented for Peruvian cultures (Kolata, 1986; Bray, 1990; Chepstow-Lusty et al., 1996; Moore, 1991) and more recently the Maya (Hodell et al., 1995). Start of forest recovery at Timbio is thought to occur slightly before the arrival of the Spanish conquistadors (Wille et al., 2000) when agricultural practices changed. Although Behling et al. (1999a) suggested that some tropical landscapes reverted to forest following the arrival of the Spanish, our analysis does not show this to be the case although the resolution in the uppermost sections of the cores needs to be increased to substantiate this claim.

5. Conclusions

The standard treatment of primary pollen data from Llanos Orientales permits a spatial and temporal perspective on the response of dry–moist vegetation types to climatic forcing since last glacial period. Combining these data with a vegetation model has allowed us to determine the factors driving vegetation change and how these vary over space and time. The application of a vegetation model is shown to be a useful tool with which to test ideas that result from these data analysis. Moisture dynamics are shown to be key in forcing vegetation change in the Llanos Orientales, particularly due to the link with WUE under conditions of low $[CO_2]_{atm}$.

Tropical South America experienced a major synchronous change to higher precipitation and/or a shorter dry season about 4000 ^{14}C BP. Whatever mechanism is invoked to explain the vegetation changes, increasingly it is shown that tropical palaeoecology is highly responsive.

There is a need to develop a better understanding between the tropical signals of environmental change, how these correspond to those of temperate latitudes, and what are the mechanisms, both atmospheric and oceanographic that transmit these signals. This could be the first a step in developing a better understanding of past environmental variability *and* the mechanisms responsible for driving the change. Given the strength of this relationship there is a real need to incorporate tropical research within research programs that have a predominately temperate focus.

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