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Late Quaternary vegetation and climate change in the Panama Basin: Palynological evidence from marine cores ODP 677B and TR 163-38

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Abstract

The Late Quaternary paleoenvironmental history from Pacific slopes of the western Andes is reconstructed by pollen analysis of 32 samples from two marine sediment cores from the Panama Basin, eastern equatorial Pacific: core ODP 677B (83°44.2200′ W, 1°12.1440′ N, 3473 m water depth) is 185 cm long and spans the last 39,410 years, core TR 163-38 (81.583° W, 1.337° N, 2200 m water depth) is 103 cm long and covers the last 17,380 years. Six ecological groups were established: mangrove, brackish and fresh water swamps, terra firma lowland forests, broad range taxa, Andean forests, and open vegetation. A good correspondence was found between the changes of these ecological groups in the two cores. The records evidence the continuous presence of all vegetation types during the last 39,410 years and specially the uninterrupted occurrence of tropical rain forest. They record a development from: (1) a cold and humid phase (39,410–28,120 yr cal BP) with moderately high sea levels, (2) the coldest and driest phase in the record (28,120–14,500 yr cal BP) accompanied by the lowest sea levels, (3) a transitional phase when sea level rose and humid conditions dominated, (4) a stage (11,300–5600 yr cal BP) of the highest sea levels and moisture conditions including a drier period ~7000 yr BP, to (5) a final period (5600 yr cal BP–Present) when sea level reached its present height, humidity persisted, and indicators of disturbance expanded. Peaks in pollen and spore concentration, associated with high river discharge periods, indicate periods of higher precipitation around 33,500, 28,000 and 12,000–9000 yr cal BP. Although main vegetation responses seem to reflect rainfall and moisture variations, a good correspondence was found between $\delta^{18}O$ values and percentages of Andean and lowland pollen, suggesting that vegetation also responded to tempearture changes.
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1. Introduction

Tropical lowland vegetation change during the last glacial–interglacial cycle has remained the subject of intense controversy. Palynological records from the Amazon Basin are interpreted either as evidence of decreased extent of the rain forest during last glacial maximum (LGM) when tree taxa were forced into small refugia (Van der Hammen and Absy, 1994; Hooghiemstra and Van der Hammen, 1998; Van der Hammen and Hooghiemstra, 2000), or as a reassortment of plant species as a response to climate change while maintaining forest extent (Colinvaux et al., 1996, 2000). The latter interpretation implies that tropical forests were widespread during the LGM but varied in composition due to changes in moisture, temperature and atmospher-

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ic CO_2. Despite almost 30 years of research, considerable debate still continues regarding the amount of precipitation reduction and the distribution of vegetation types at the LGM. The Chocó rain forest, on the Pacific coast of Colombia, has been considered as a target ecosystem for the study of the response of the tropical forests to climate change due to its extremely wet conditions, its high endemism and biological diversity (Gentry, 1986, 1993). As the Amazon forest, it has also been proposed as a neotropical refuge during glacial times (Gentry, 1982). This study contributes to elucidate how stable the Choco rain forest was and how vegetation responded during the last glacial–interglacial cycle.

When studying global climate change in the tropical Pacific, the Panama Basin is a key area. This is due to its unique oceanographic and climatic features, especially the Caribbean–Pacific moisture transference through the Panama Isthmus and its salinity difference, and the episodic influence of the ENSO phenomenon. Furthermore, the great number of continental studies of paleoclimate from the northern Andes makes the Panama Basin a very attractive area to establish ocean–continent correlations. Despite the importance of the Panama Basin in the understanding of oceanographic and continental vegetation dynamics, there have been very few paleoecological studies. In a marine core from the Carnegie Ridge, south of the Panama Basin, Heusser and Shackleton (1994) found a good correlation between the oxygen isotope stratigraphy and the arboreal pollen record. However, the specific responses of plant communities to climate change were not explored. Other palynological reconstructions from lacustrine and swampy environments in the Pacific slope of the western Andes provide more detailed reconstructions of the plant responses to the environmental changes, but these mostly reflect local signals and are restricted to the middle-late Holocene, e.g., Puisbi Lake (Behling et al., 1998b), Popayán plain (Behling et al., 1998a), El Caimito Lake (Vélez et al., 2001), Jotaordó Lake (Berrío et al., 2000), Tribuga Gulf (Jaramillo and Bayona, 2000), San Juan River Delta (Ramírez and Urrego, 2001), and Patía River Delta (Urrego and Del Valle, 2002). Due to the lack of long and continuous terrestrial palynological records that would provide a regional vegetation history for the Pacific slopes of the western Andes, the palynological reconstruction from marine sediments adjacent to the continent appears as the most appropriate approach.

This report adds to the multiproxy study of the Panama Basin that intends to reconstruct paleoceanographic conditions of the Basin for the past 40,000 years, with emphasis on the LGM (e.g., Martínez et al., 2003). In this study we present palynological analyses of two marine cores, Ocean Drilling Program (ODP) 677B and Trident (TR) 163-38; we reconstruct regional vegetation and climate, compare proxies for an ocean–continent correlation, and discuss the extent of forest cover and the intensity of aridity along the Pacific slopes of the northern Andes for the last glacial period.

2. Environmental setting

2.1. Location

The Panama Basin is located between the Panama Isthmus (5° N) and the Punta Santa Elena in Ecuador (2° S) and extends from the shorelines of Panama, Colombia and Ecuador to the Cocos Ridge (90° W). The Carnegie Ridge and the Cocos Ridge limit the Basin in the south and west, respectively (Fig. 1).

The Panama Basin is infilled by pelagic and mud-rich terrigenous sediments supplied by the coastal rivers and some eolian input from arid coastal regions of Ecuador and Peru. Biological productivity is very high (Moore et al., 1973) and is locally reflected in the sediments by high organic carbon concentrations and suboxic characteristics (Pedersen and Price, 1982).

2.2. Climate and ocean circulation

The Colombian Pacific coast is probably the wettest continental region on Earth, receiving average yearly precipitation of 8000 mm to over 13,000 mm (e.g., Eslava, 1993; Mesa et al., 1997). Rainfall is higher in the central part and diminishes southward and northward. More marked seasonality occurs in the north toward Panama and the Caribbean Sea, and in the south toward the Ecuadorian border. Precipitation is bimodal, with the greatest peak in the first half of the year. The rainy season is related to the annual migration of the Intertropical Convergence Zone (ITCZ), which reaches its southernmost position close to the equator in March and its northern limit along 9°–10° N in August (e.g. Vuille et al., 2000). The mean annual temperature is about 25–27 °C.

The atmospheric circulation over the Panama Basin is dominated by the confluence of the NE and SE trade winds at the ITCZ. Eastward winds, at the core of the ITCZ, are more intense in the second part of the year and result in intense mesoscale convective cells driven by orographic uplift over the Western Cordillera (Mesa et al., 1997).

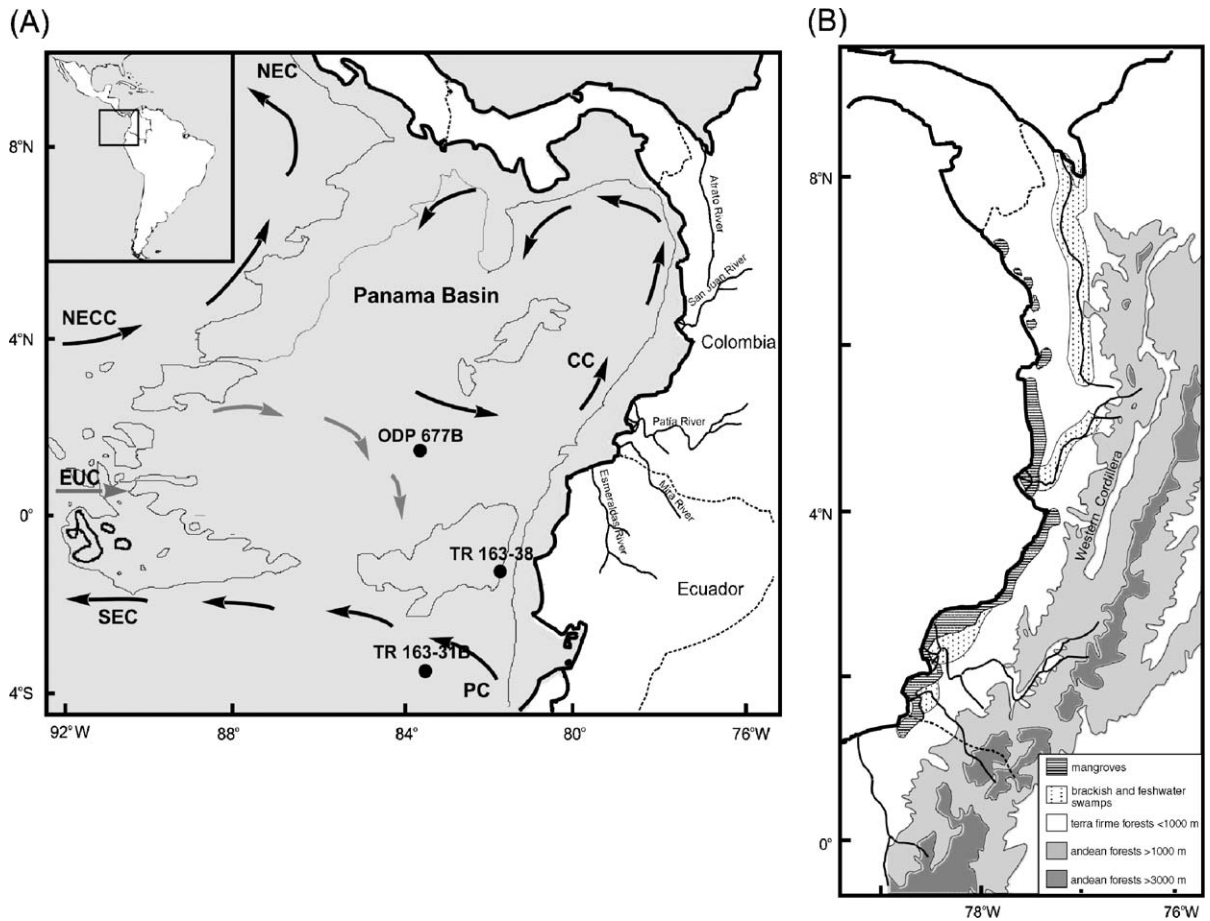The Panama Basin is located in the eastern extreme of the equatorial current system in the Pacific Ocean.

Fig. 1. (A) Map of the Panama Basin, eastern equatorial Pacific, showing sea surface currents (in black), the Equatorial Undercurrent (in gray) and core locations (black circles). NEC and SEC, North and South Equatorial Currents; EUC, Equatorial Undercurrent; NECC, North Equatorial Countercurrent; CC, Colombian Current; and PC, Peru Current. Main rivers that drain to the Panama Basin are also shown. (B) Present-day distribution of main vegetation types on the pacific side of the northern Andes.

Surface currents in the region include the west-flowing North and South Equatorial Currents (NEC and SEC) and their corresponding east-flowing countercurrents (NECC and SECC) (e.g., Tomczak and Godfrey, 1994), plus the Colombia Current, a small branch of the Peru–Chile Current. Both, the NEC and SEC, are driven by the trade winds. (Fig. 1A).

2.3. Modern vegetation and pollen source areas

To provide some basis for interpretation of the palynological deep-sea records, it is valuable to examine the major present-day distribution of selected plant communities. Major vegetation types of the Colombian and Ecuadorian Pacific coast range from lowland rainforest and mangroves through montane forest and paramo in the 4000 m high Western Cordillera. The Chocó biogeographic region broadly includes the eastern margin of Panama, and the coastal lowlands of western Colombia and north-western Ecuador, which are mainly covered by wet forest and pluvial forest. Several vegetation types are recognized based on the altitudinal gradient, the variation of soil water content and the influence of the sea (e.g., Cuatrecasas, 1958; Acosta-Solís, 1970; Von Prahl et al., 1979, 1990; Aguirre and Rangel, 1990; Rangel and Lowy, 1993; Velásquez et al., 1999).

Mangroves occupy large expanses along the Pacific coast, especially around the Patía River (Fig. 1B). Species that are characteristic belong to the genera *Rhizophora*, *Pelliciera*, *Avicennia*, *Laguncularia* and *Conocarpus*. They are frequently accompanied by tree and palm species including *Ardisia granatensis*, *Tabebuia palustris, Pachira aquatica, Euterpe oleracea*, and the fern *Acrostichum aureum* (Von Prahl et al., 1990; Del Valle, 1996). Behind the mangroves, a narrow strip of brackish water swamps dominated by *Mora megistosperma* communities occurs, where scattered indivi-

duals of *T. palustris*, *P. aquatica* and *E. oleracea* can be found (Del Valle, 1996).

In the hinterland, different fresh water swamp communities are established and receive the broad name of "guandal". They can be distinguished according to their dominant species: 1) homogeneous forests dominated by *Campnosperma panamensis* that can be associated with *Socratea exorrhiza*, *Otoba gracilipes* and *Mauritiella macroclada*; 2) communities dominated by *Otoba gracilipes* that colonize better drained areas and can be mixed with individuals of *Pterocarpus officinalis*, *Hyeronima* sp., *Symphonia* sp., *Virola* sp., and the palms *Euterpe oleracea* and *Oenocarpus bataua*; 3) forests dominated by the palm *Euterpe oleracea* (Rangel and Lowy, 1993; Del Valle, 1996).

According to Gentry (1986), the lowland pluvial forest or Pacific terra firma forest is floristically one of the most diverse in the world, and comprises high trees with stilty and tabular roots, with abundant hemiepiphytes. Important elements of this forest belong to the families Anacardiaceae, Araceae, Arecaceae (*Wettinia* sp., *Iriartea* sp., *Socratea* sp., *Phytelephas* sp., *Astrocarium* sp.), Bignoniaceae (*Jacaranda* sp.), Bombacaceae (*Ochroma* sp.), Cecropiaceae, Euphorbiaceae (*Alchornea* sp.), Leguminosae (*Machaerium* sp., *Inga* sp., *Pterocarpus* sp.), Melastomataceae, Moraceae (*Brosimum* sp., *Ficus* sp.), Meliaceae (*Cedrela* sp.), Rubiaceae and Piperaceae (Gentry, 1986, 1993; Rangel and Lowy, 1993). An interesting peculiarity of the Chocó lowlands is that taxa, usually restricted to the Andean uplands, also occur there (Gentry, 1986). Typical montane taxa with lowland representatives are *Podocarpus*, *Talauma*, *Hedyosmum*, *Brunellia*, *Panopsis* and *Ilex*. The presence of these montane taxa indicates the cloud-forest-like nature of the Chocó lowland forests (Gentry, 1986, 1993).

Andean forest of the Western Cordillera holds montane communities mainly dominated by *Alnus*, *Quercus*, Clusiaceae, *Brunellia*, *Hedyosmum*, *Podocarpus*, *Hyeronima*, *Ilex*, *Symplocos*, *Clethra*, *Myrsine*, Melastomataceae, Ericaceae, *Weinmannia* and *Vallea* (Van der Hammen, 1992; Velásquez et al., 1999).

2.4. Transport of palynomorphs to the Panama Basin

Heusser and Shackleton (1994) suggested that wind was the main transport mechanism of pollen grains from the continent to the sea floor in the southern Panama Basin. However, the large fluvial supply of water and sediment yield from the San Juan, Patía, Mira and Esmeraldas Rivers (Fig. 1), should be considered as an important source of pollen grains. It has been estimated that these rivers supply $\sim35 \times 0^6$ tons/year of suspended sediments to the Panama Basin (Van Andel, 1973; Restrepo and Kjerfve, 2000). The basin bathymetry and the deep current dynamics determine the distribution of terrigenous sediments, along with palynomorphs. Important transport mechanisms include mid-water flows, marine snow and packing of organic matter in fecal pellets (e.g., Martínez, 2001). The Carnegie and Cocos Ridges restrict the interchange of sediments with the Peru Basin and the Central Pacific, respectively. The high rates of orographic precipitation that characterize the Pacific coast also prevent high transportation rates of palynomorphs by the wind, because pollen grains remain in the atmosphere only for a short time before being washed down by the rain. Furthermore, prevailing westerly trade winds blowing from the ocean to the continent, i.e., the Chocó jet (Poveda and Mesa, 1997), prevent wind transport to the sea. Nevertheless, a minor percentage of palynomorphs can also be blown offshore by south-east trade winds and contribute directly to the fossil assemblage found in marine sediments.

3. Methods

Samples were taken from marine cores *Ocean Drilling Program* (ODP) 677B (83°44.2200′ W, 1°12.14′ N, 3473 m water depth) and *Trident* (TR) 163-38 (81.58° W, 1.34° N, 2200 m water depth), located 400 and 100 km offshore, respectively.

Thirty-two silty clay samples (3 cm^3) from cores ODP 677B and TR 163-38 were taken at 10 cm intervals for pollen analysis. Samples were treated with the standard acetolysis method, using sodium pyrophosphate (10%) to disaggregate the sediments and sieving through a 10 μm mesh to separate the palynomorphs. When quartz contents were high, samples were processed with hydrochloric acid (33%) and hydrofluoric acid (30%; cf. Herngreen method, 1983). Pollen concentrations were calculated by adding exotic *Lycopodium* tablets (± 14,542 spores/tablet) to samples before pollen extraction. Five to 20 slides per sample were mounted in a glycerin gelatin medium. A minimum pollen sum of 200 grains including herbs, shrubs and trees was reached in most samples. In cases where pollen concentrations were very low, <200 grains were counted. Spores and marine microfossils were also counted but not included in the pollen sum. For identification of palynomorphs, a recent pollen reference collection held at the Laboratorio de Ecología y Conservación Ambiental (Universidad Nacional, Sede Medellín), and published morphological descriptions

were used (e.g., Murillo and Bless, 1974; Murillo, 1978; Absy, 1979; Hooghiemstra, 1984; Roubik and Moreno, 1991; Hoorn, 1994; Herrera and Urrego, 1996; Velásquez et al., 1999). The zonation of the diagrams was based on CONISS dendrograms and visual inspection of the pollen percentage curves.

Principal Component Analysis (R-mode) was performed with the software MVSP version 3.1 (Kovach Computing Services, 1985–2001) in order to examine the consistency of the time scales, zonations and ecological grouping between cores. The ordination was carried out for the cumulative percentages of the groups, and data were transposed, centered and standardized before analysis.

The detailed chronostratigraphic control, obtained by comparing oxygen isotopes on planktonic foraminifera with the SPECMAP global isotopic scale, and complete AMS ^{14}C analyses are provided elsewhere (Martínez et al., 2003; Table 1).

4. Results

Some 220 palynomorphs types were recognized in the pollen preparations. Taxa obtained from the sites include ca. 140 terrestrial pollen types (90% of which were identified), 30 marine and aquatic microfossil types and 32 fern spore types. Identified pollen taxa were grouped into six main groups according to ecological affinities: a) mangrove, b) brackish-fresh water swamps, c) terra firma lowland forests, c) Andean forests, d) open vegetation and e) broad range taxa (Table 2). The last group includes typical Andean elements that are found in the Pacific lowlands. These six ecological groups represent different vegetation types of the Chocó Biogeographic region and the adjacent mountains that have been previously described by various authors (e.g., Hooghiemstra, 1984; Van der Hammen, 1992, Rangel and Lowy, 1993; Van't Veer et al., 1995; Del Valle, 1996; Velásquez et al., 1999; Ramírez and Urrego, 2001; Urrego and Del Valle, 2002).

4.1. Stratigraphy and chronology

The uppermost 185 cm of ODP core 677B is continuous and spans the time interval from ~39,410 yr cal BP to the present (Martínez et al., 2003). They consist of olive gray, olive green and light gray green clayey ooze, where clay, foraminifera, radiolarians and diatoms are all present in excess of 10%. Sponge spicules and silicoflagellates are minor components. Open burrows and *Zoophycos* occur in this core (Shipboard Scientific Party, 1988). Similarly, the uppermost 103 cm of core TR 163-38 is mainly composed of calcareous and biogenic ooze and covers the interval from ~17,450 yr cal BP to 1200 yr cal BP (Martínez et al., 2003; and Fig. 2).

4.2. Description of the pollen records

Species with abundances <1% (60 pollen taxa) were excluded from the interpretation. Downcore changes in the pollen percentages of core ODP 677B are shown in Fig. 3. Four different zones, ODP-I to ODP-IV, can be recognized based on 20 samples. For core TR 163-38 three zones were established: TR-I to TR-III based on 13 samples (Fig. 4). To facilitate comparisons between cores and with other published records, pollen diagrams were drawn as a function of time instead of depth. Main results of principal component analysis are summarized in Fig. 6.

4.2.1. Marine pollen record ODP 677B

Accumulation rates of terrestrial pollen and spores in core ODP 677B were very low for statistical treatment in three samples (90, 80, 30 cm depth), and in sample 110 cm no pollen grains were found. Pollen zones (Fig. 3) are characterized as follows:

Pollen zone ODP-I (185–130 cm: 39,410–28,120 yr cal BP, 4 samples). This zone is characterized by high values of Andean forest (16%) and broad range taxa (40%). *Hedyosmum*, *Podocarpus*, and Caryophyllaceae

Table 1

AMS ^{14}C ages of samples from cores ODP 677B and TR 163-38, Panama Basin, eastern equatorial Pacific (Martínez et al., 2003)

ID#	Sample; Size; cm	Depth (cmbsf)	^{14}C Age	Calendar Age (yr cal BP)
AA41922	ODP677B; 1–1:93–95	94	$15,910 \pm 130$	$18,410 \pm 280$
CAMS70909	ODP677B; 1–1:124–125	124	$21,710 \pm 180$	$25,110 \pm 210$
CAMS 70910	ODP677B; 1–2:3–4	153	$25,200 \pm 220$	$29,120 \pm 250$
CAMS 70911	ODP677B; 1–2:31–32	181	$32,240 \pm 960$	$37,000 \pm 1050$
AA41919	TR163–38; 120–122	121	$16,510 \pm 150$	$19,100 \pm 340$
AA41920	TR163-38; 142–144	143	$21,170 \pm 220$	$24,480 \pm 260$

CAMS: Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, University of California; AA: NSF Arizona AMS Facility, The University of Arizona; cmsbsf: centimeters below sea floor.

Table 2
List of the pollen taxa included in the ecological groups from the upper Quaternary sediments of the Panama Basin, marine cores ODP 677B and TR-163-38, eastern equatorial Pacific

Mangroves	Brackish and fresh water swamps	Terra firma lowland forests		Broad range taxa	Andean forests		Open vegetation
Rhizophora	Annonaceae	Acanthaceae	*Forsteronia*	Ericaceae	Alnus		*Acalypha*
	Apeiba	*Alchornea*	*Guettarda*	*Hedyosmum*	Caryophyllaceae		*Aeschynomene*
	Ardisia	*Protium*	*Alibertia*	Lauraceae	*Ilex*	*Clethra*		*Alternathera*
	Astronium	*Pterocarpus*	*Amanoa*	Loranthaceae	Melastomataceae	Dennstaedtiaceae		Amaranth./Chenpod.
	Attalea	*Sapium*	*Andira*	Meliaceae	*Podocarpus*	Escallonia		*Arrabidea*
	Bactris	*Spondias*	Apocynaceae	Menispermaceae	Rubiaceae	*Jamesonia* (Adiantaceae)	*Cestrum*
	Bromeliaceae	*Tabebuia*	Araceae	Mimosaceae		*Juglans*		*Chamaesyce*
	Campnosperma	*Thelypteris*	Arecaceae	Moraceae / Urticaceae		*Myrica*		Compositae
	Cassipourea	*Vantanea*	Bignoniaceae			*Myriophyllum*		Cyperaceae
	Croton	*Zanthoxylum*	Bombacaceae	*Odontadenia*		*Myrsine*		*Desmodium*
	Dalbergia		Burseraceae	*Paullinia*		*Pinus*		Poaceae
	Erythrina		*Casearia*	*Piper*		Proteaceae		Solanaceae
	Euterpe		*Cecropia*	*Rheedia*		*Quercus*		*Spermacoce*
	Gustavia		*Cedrela*	Rubiaceae		*Rapanea*		*Urera*
	Humiriaceae		*Celtis*	Sapindaceae		Scrophulariaceae		
	Hyeronima		*Cissampelos*	*Swartzia*		*Symplocos*		
	Lecythidaceae		*Cissus*	*Syzygium*		*Vallea*		
	Mabea		*Cordia*	*Teramnus*		*Weinmannia*		
	Machaerium		Cucurbitaceae	*Trema*				
	Marantaceae		*Cupania*	*Trichilia*				
	Mauritiella		Cyclanthaceae	*Trichospermum*				
	Ochroma		*Eugenia*	*Virola*				
			Euphorbiaceae	*Voyria*				
			Fabaceae	*Warczewiczia*				
			Flacourtiaceae					

reach their highest percentages in the core, and are accompanied by *Quercus* and *Alnus* mixed with some taxa from open vegetation (26%). Simultaneously, swamp forest elements reach their maximum abundance (15%) accompanied by a slight increment of mangrove in the upper part of the zone. Terra firma lowland forest elements are present (10–23%). This interval shows low representation of Compositae, Amaranthaceae/Chenopodiaceae and the lowest percentage in the core of Poaceae. Fern trilete and mono-
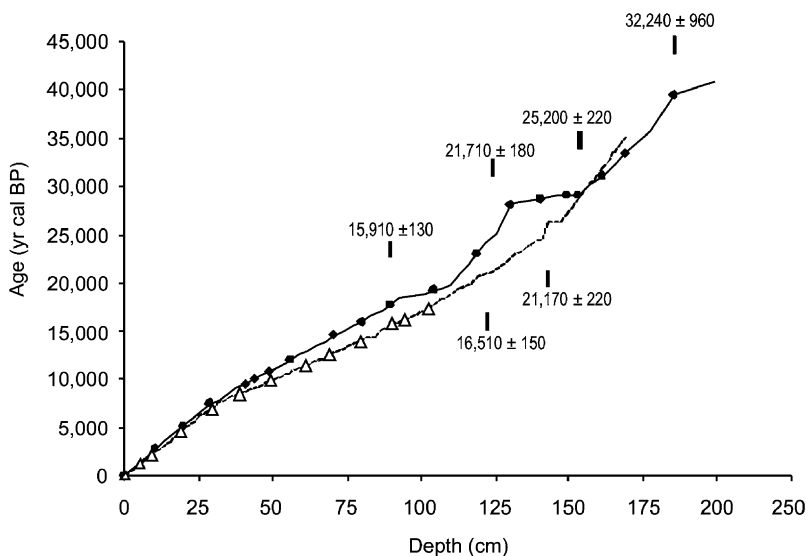

Fig. 2. Age against depth graph for marine cores ODP 677B (circles) and TR 163-38 (triangles), Panama Basin, eastern equatorial Pacific. Samples counted for pollen analysis are indicated with markers (circles and triangles). AMS ^{14}C dates are also indicated (vertical bars).

Marine Core ODP 677B
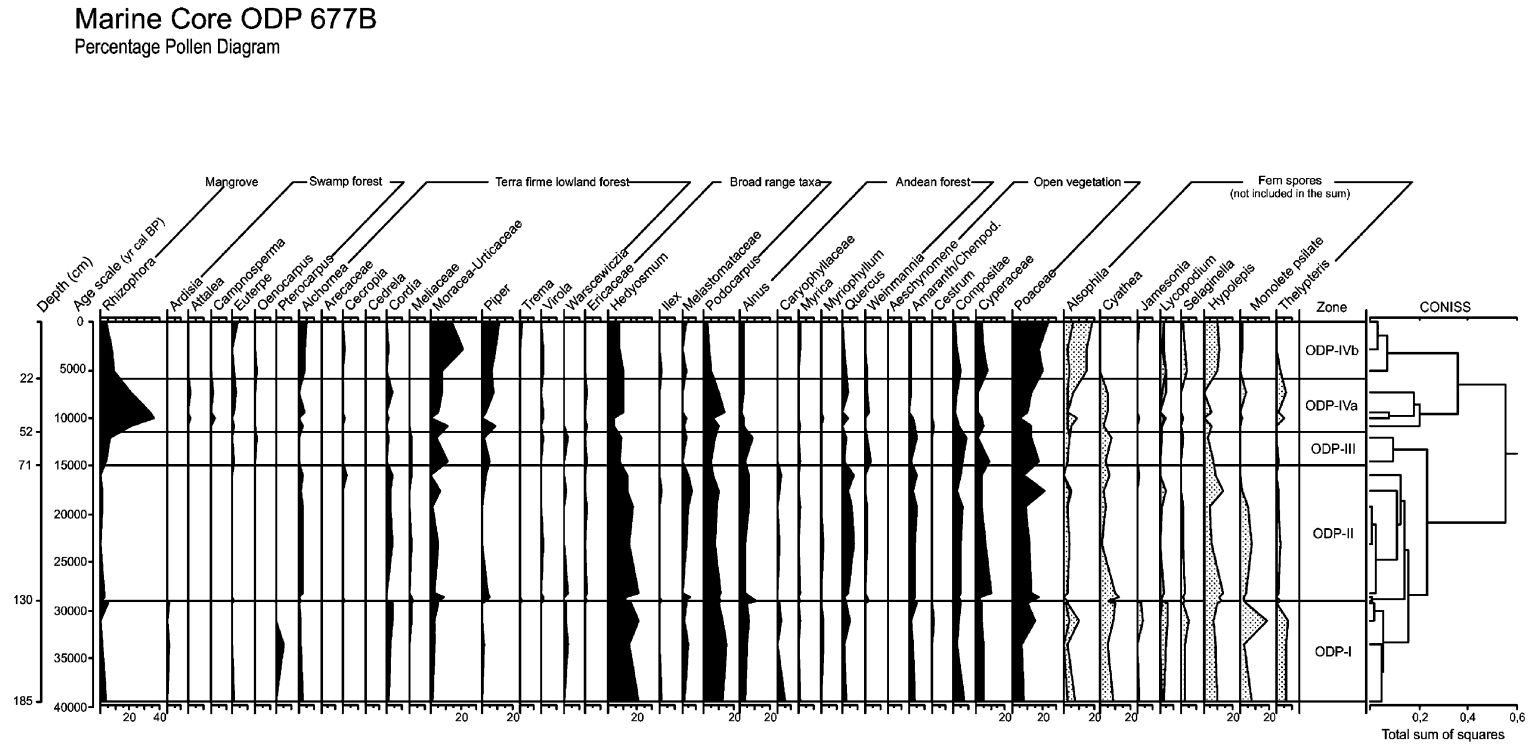## Percentage Pollen Diagram

Fig. 3. Percentage pollen diagram against time of main diagnostic taxa of the marine core ODP 677B, Panama Basin, eastern equatorial Pacific. Zones I to IVb are derived from the CONISS analysis and visual inspection.
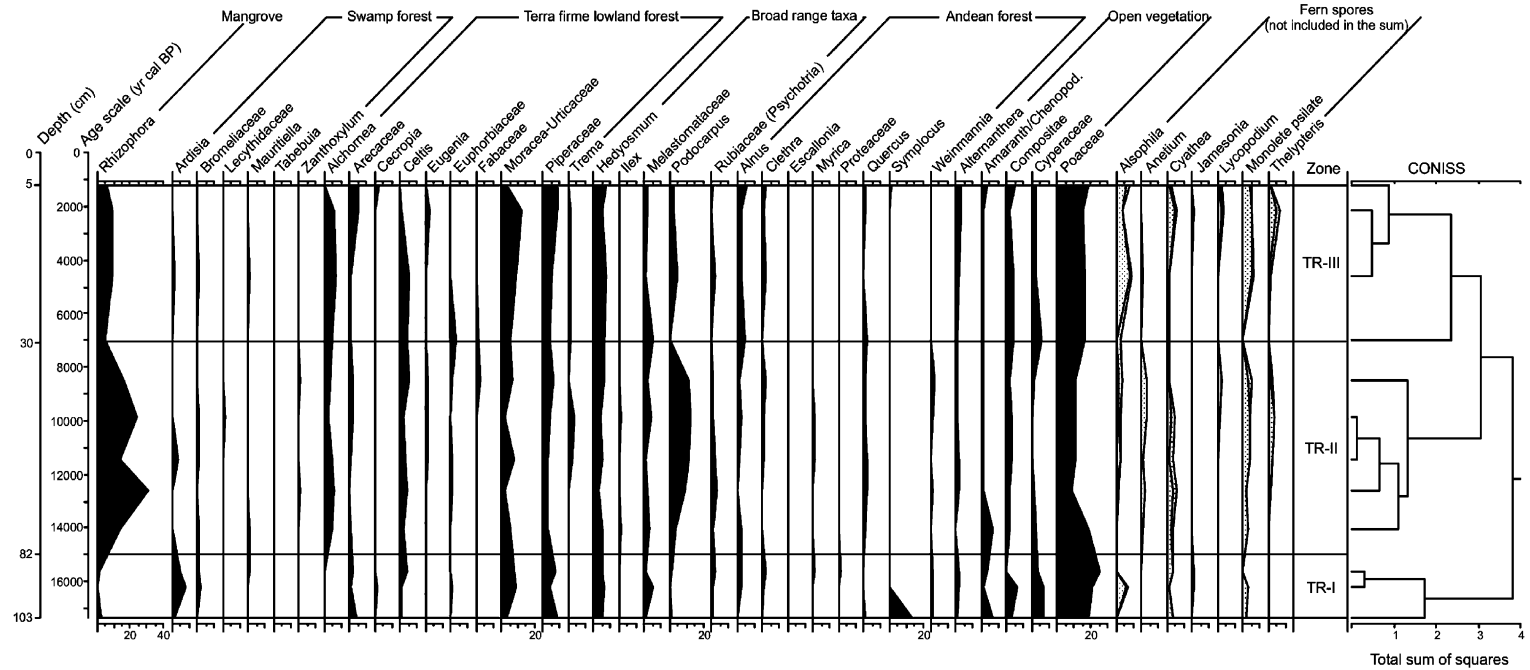
Fig. 4. Percentage pollen diagram against time of main diagnostic taxa of the marine core TR 163-38, Panama Basin, eastern equatorial Pacific. Zones I to II are derived from the CONISS analysis and visual inspection.

lete spores show their maximum values, whereas fungi spores show a slight increment. Pollen and spores concentrations are low, except for the latter part of the zone where there is a small increase at ~31,000 yr cal BP (Fig. 5).

Pollen zone ODP-II (130–71 cm: 28,120–14,470 yr cal BP, 7 samples). In this zone, taxa from Andean forest (21%) and open vegetation (36%) dominate: these are mainly Poaceae, *Alnus*, Cyperaceae, *Quercus*, Amaranthaceae/Chenopodiaceae, and *Weinmannia*; broad range taxa are also well represented (38%) as well as terra firma lowland vegetation (17–20%), although individual taxa like *Alchornea*, Moraceae/Urticaceae and *Piper* diminished to <1%. *Cordia* (<5%) values do not differ significantly from the values of the previous zone. A small *Cecropia* peak appears in the upper part of the zone. Mangrove taxa show their lowest percentages along the core, disappearing at ~16,000 yr cal BP. Fern spores have relatively high and constant values along the core and diminish to their minimum at the end of the zone. Fungi spores are minimal in this zone. Spore and pollen concentrations are low though the latter increase rapidly at the end of the zone.

Pollen zone ODP-III (71–52 cm: 14,470–11,300 yr cal BP, 2 samples). Elements of all ecological groups are present in this zone: open vegetation elements (36%), broad range taxa (28%), terra firma lowland forest (22%), mangrove (7%), and swamp forest elements (4%). Andean forest elements are also present but decrease to 13%. This zone is characterized by increasing percentages of *Rhizophora*, Moraceae/Urticaceae, *Piper*, *Alnus*, Compositae, and Cyperaceae. *Hedyosmum* and Poaceae are also well represented in this zone. Other taxa, like *Alchornea*, *Cordia*, *Paullinia*, *Trema*, Caryophyllaceae, and *Quercus*, drop to <1%. Trilete spores peak (33%) after their minimum value at ~14,400 yr cal BP (70 cm), whereas monolete and fungi spores are low. Pollen and spores concentration show maximum values at the end of this zone.

Pollen zone ODP-IV(52–0 cm: 11,300 yr cal BP– present, 7 samples). This zone is characterized by increasing percentages of mangrove forest (37%) and tropical lowland forest taxa (42%). Based on differences in the *Rhizophora* and swamp forest percentages, two subzones were recognized.

Subzone ODP-IVa (52–22 cm: 11,300–5600 yr cal BP, 5 samples) is characterized by the maximum representation in the diagram of *Rhizophora* (37%) and swamp forest taxa (11%) at ~45 cm (10,000 yr cal BP), with a simultaneous peak of *Podocarpus*. Poaceae and Moraceae/Urticaceae decrease markedly to their mini-

mum in the core as do the Andean taxa, *Quercus*, *Alnus*, *Hedyosmum*, Melastomataceae, *Myriophyllum*, and *Weimannia*, whereas trilete fern spores and fungi reach their maximum in this zone. Pollen and spore concentrations drop sharply (Fig. 5).

Subzone ODP-IVb (22–0 cm: 5600 yr cal BP– present, 2 samples) is characterized by a marked decrease of *Rhizophora* and swamp elements, and a simultaneous increase of terra firma lowland forest elements (42%) and open vegetation elements (35%). Poaceae, Moraceae/Urticaceae, *Piper* and *Alchornea* are the most important taxa, accompanied by low but maximum values in the core of *Euterpe*, *Trema*, *Acalypha* and *Cecropia*. Andean forest elements and broad range taxa show the lowest representations in the core (2% and 16%, respectively). Fern spores continue with high values and fungi spores decrease. Pollen and spores concentrations increase simultaneously along this subzone (Fig. 5).

4.2.2. Marine pollen record TR 163-38

Pollen zone TR-I (103–82 cm: 17,450–14,400 yr cal BP, 3 samples). This zone (Fig. 4) is characterized by the highest percentages of open vegetation (39%) and Andean forest elements (19%); terra firma lowland forest is also well represented (25%). The zone is characterized by the highest percentages of Poaceae, Cyperaceae, Compositae and Amaranthaceae/Chenopodiaceae. Andean forest decreases to <9% after its maximum (20%) at the base of the zone. There is an important contribution of *Symplocos*, *Ardisia*, *Hedyosmum*, Moraceae/Urticaceae, Arecaceae, and peaks of *Piper*, *Croton*, and *Cecropia. Rhizophora* shows its lowest percentages in the core. Fern and fungi spores percentages are low. Pollen and spore concentrations have a small peak in this zone (Fig. 5).

Pollen zone TR-II (82–30 cm: 14,400–6960 yr cal BP, 5 samples). This zone is characterized by a high representation of *Rhizophora* (31%) and swamp elements (8%). Terra firma lowland elements increase gradually from 20% to 32%, open vegetation contribution decreases to 16%, and Andean forest elements continue with similar low values. Broad range taxa, specifically *Podocarpus* and Melastomataceae, have maximum values peaking together with *Rhizophora*. Fern spores and fungi also show a similar trend to the mangrove curve. Poaceae, Amaranthaceae/Chenopodiaceae, Cyperaceae, and *Alnus* reach their minimum percentages in the middle part of the zone. Pollen and spore concentrations reach their highest values in the middle part of the zone and decrease toward the upper part.
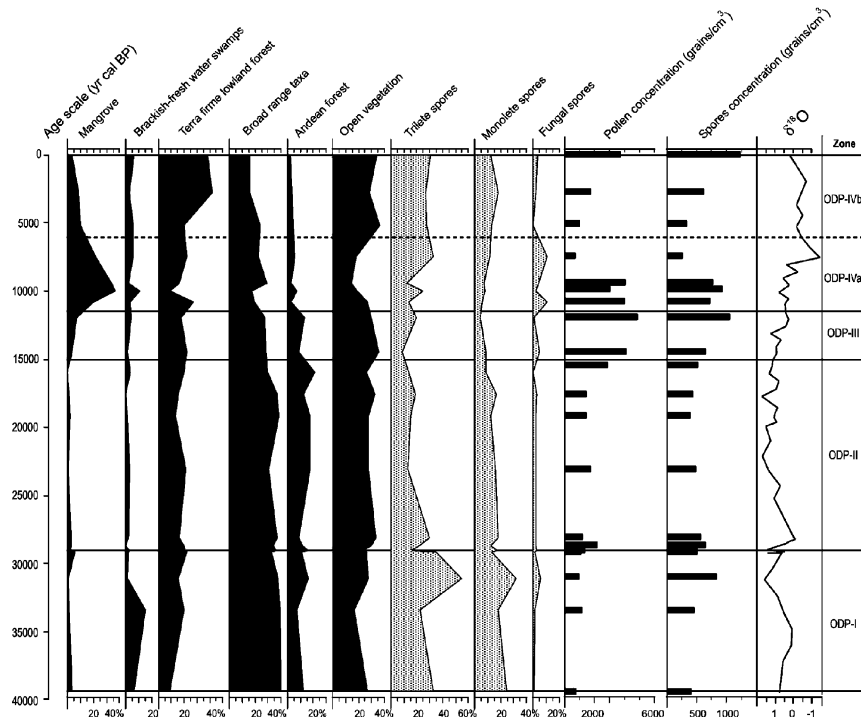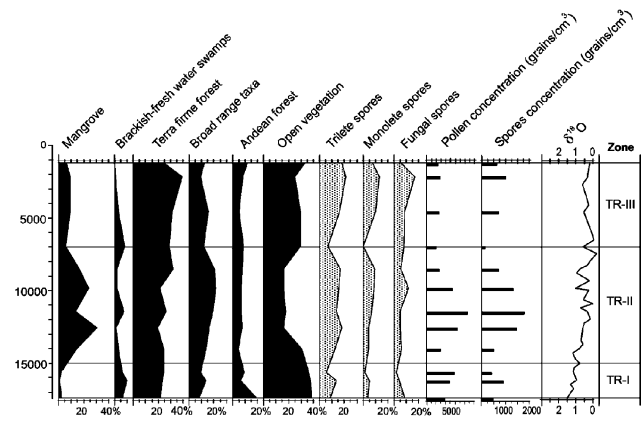
Fig. 5. Comparison of ecological groups from marine cores ODP 677B and TR 163-38, Panama Basin, eastern equatorial Pacific, including pollen and spores concentration, pollen zones and $\delta^{18}O$ values on the planktonic foraminifer *Neogloboquadrina dutertrei* (data in Martínez et al., 2003). Note that the two diagrams have the same vertical (age) scale.

Pollen zone TR-III (30–5.5 cm: 6960–1200 yr cal BP, 4 samples). This zone is characterized by the dominance of terra firma lowland elements, with the highest values of Moraceae/Urticaceae, *Piper*, *Alchornea*, Arecaceae, *Cecropia* and *Aeschynomene*. Open vegetation elements, mainly Poaceae, Cyperaceae and Compositae increase, especially in the upper part of the zone. *Rhizophora* values drop at the beginning of the zone and maintain low values (5–9%) along the zone, whereas fern and fungal spores increase to their maximum percentages. Pollen and spores concentrations are at minimum values in this zone (Fig. 5).

5. Discussion

5.1. Regional vegetation and environmental changes from the marine pollen records

According to the oxygen isotope record and radiocarbon dates, cores ODP 677B and TR 163-38 represent a continuous and undisturbed sequence of marine sediments for the Late Pleistocene/Holocene interval. Based on changes in the composition of the pollen assemblages in both cores and the relative contributions from individual taxa, the main environmental conditions of the Chocó biogeographic region and adjacent mountains can be inferred. A good correspondence between the two cores is evident from a side-by-side comparison (Fig. 5) the principal components analysis (Fig. 6). Differences might be due to age-model uncertainties, regional variations, pollen rain differences, and transport mechanisms.

Both pollen records show that all vegetation groups persisted throughout the whole time interval without any major ecological upheaval. This pattern reflects the regional and summarizing nature of the marine palynological records, which provide information of various vegetation types occurring along diverse ecological gradients—mainly moisture and temperature. It is worth noting that the very wet climatic conditions of Pacific slopes of the Western Cordillera have promoted the establishment of a peculiar assemblage of Andean, lowland and dry forest (hydric-stress resistant) taxa. This unusual assemblage makes it difficult to establish clear separations among vegetation types.

High percentages of Andean and lowland taxa, and the relatively low percentages of herb pollen (<40%) in the two cores suggest the dominance of forests and the absence of open grasslands as it has been previously pointed out by Bush (2002) for other tropical records in Central and South America during the late Pleistocene. Thus, our herb pollen percentages are insufficient to infer drastic drought conditions and could support the idea that changes in climate were never enough to disrupt the forest.

5.1.1. The Middle Pleniglacial: a cold and humid phase

During the 39,410–28,120 yr cal BP period (zone ODP-I), the dominance of Andean forest and broad range taxa was accompanied by peaks of *Rhizophora* and brackish and fresh water swamp elements, suggesting the presence of cool and humid environments. Higher sea levels have been previously reported for this period (Lambeck and Chappell, 2001), showing a good correspondence with high percentages of mangrove. Although high percentages of *Hedyosmum* and *Podocarpus* have been mostly interpreted as cold-temperature indicators, it is well known that these taxa can be frequently found in the very wet Pacific lowlands (Gentry, 1986; Torres, 1988). Due to the summarizing character of the marine palynological reconstructions, it is impossible to elucidate the provenance of these taxa: they could reflect either a decrease in temperature and the corresponding geographic expansion of Andean species, or the predominance of very wet conditions which would have favored their establishment in the lowlands. In any case, high values of *Podocarpus* and *Hedyosmum* are related to humid conditions. The high values of other exclusive cold-indicators such as Caryophyllaceae, *Quercus* and *Jamesonia*, reinforce the notion of cooler climates during this period, especially after 33,500 yr BP. Peaks of *Rhizophora*, swamp forest elements, and other moisture-indicators like *Myriophyllum*, and ferns (Cyatheaceae, *Thelypteris*, *Selaginella*) suggest highly wet environments associated with high fresh water discharge to the ocean. An increase in concentration of pollen and spores at ~31,060 yr BP point to a conspicuous event of increased precipitation and riverine discharge.

5.1.2. Was the Last Glacial Maximum truly dry?

A drop of Andean forest values characterizes the beginning of the 28,120–14,500 yr cal BP period, followed by a slight increment of broad range taxa, open vegetation and fern spores. This coincides with a simultaneous decrease in $\delta^{18}O$ values in both cores (Martínez et al., 2003), and the beginning of a high organic carbon mass accumulation rate (C_{org} MAR) event in core P7 (Pedersen et al., 1991) suggesting a possible regional link at ~28,000 yr BP. An increment in pollen concentration at this time supports the interpretation of higher fluvial inputs, and probably nutrients that would have favored the high C_{org} MAR values in core P7. However, modern analog sea surface tem-
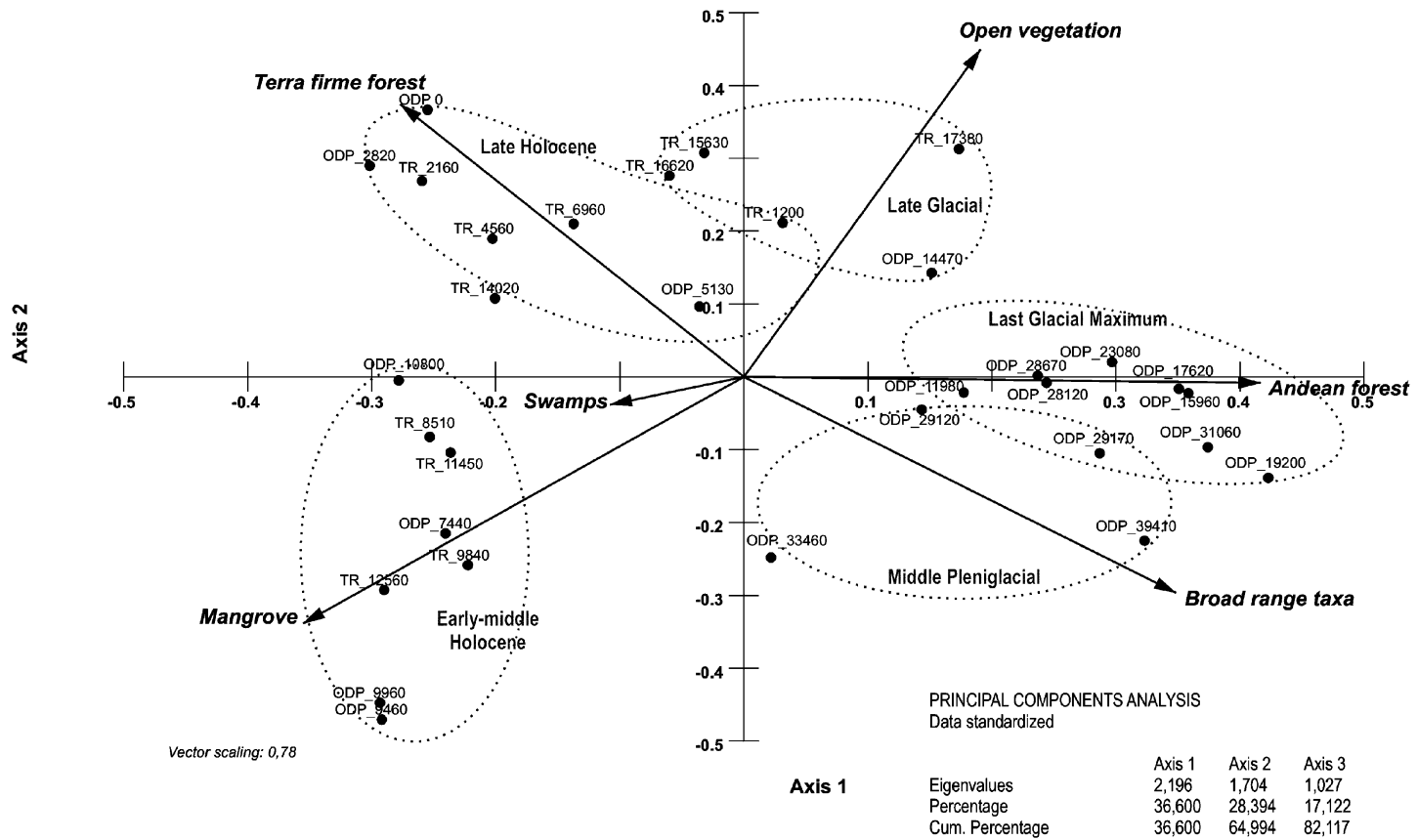
Fig. 6. Principal component analysis of ecological groups percentages for all the samples from marine cores ODP 677B and TR 163-38, Panama Basin, eastern equatorial Pacific. Zonation and correspondence between the two cores through time arise when examining axes 1 and 2.

perature reconstructions (Martínez et al., 2003) do not show any conspicuous and generalized increment of temperature for the entire Basin around 28,000 yr BP.

After 28,000 yr cal BP, the period is typified by the highest values of Andean forest and open vegetation elements, which suggest a cool climate episode. Although indicator taxa of flooded environments disappear in this zone, typical cloud and wet forests taxa such as *Podocarpus*, Melastomataceae, *Hedyosmum*, *Alnus*, *Quercus* and Cyperaceae are still present. Moisture conditions must have changed little to be in agreement with the presence of these taxa. Changes in Poaceae and Compositae percentages are minor and do not suggest great variations in herb presence during this period.

After 16,000 yr cal BP, pollen and spore concentrations start to rise dramatically in both records (Fig. 5), suggesting a change in the transport mechanism of palynomorphs. This change is, perhaps, related to changes in ENSO frequencies and increases of fluvial inputs. The upper limits of the pollen zones ODP-II and TR-I show a good correspondence, indicating that the recorded changes have regional extent.

5.1.3. The Pleistocene–Holocene transition: a scene dominated by water discharge

The 14,500–11,310 yr cal BP period is characterized by increments in mangrove and swamp forest elements. In core TR 163-38 maximum percentages of *Rhizophora* occur. Andean forest elements like *Quercus* and Caryophyllaceae diminish abruptly, and *Alnus* presents a small peak in the ODP 677B record. *Rhizophora* expansion is frequently associated with the infilling of the accommodation space by prograding fluvial sediments following a significant sea level rise (e.g., Poumot, 1989). Higher water inputs through rain and fluvial systems are also necessary for the establishment of swamp forest. This, added to the fact that the concentration of palynomorphs reaches its maximum during this period in both cores, supports the idea of high temperatures and moisture, and a corresponding high fluvial discharge. The *Alnus* percentage peak is in good correspondence with this idea, because this species establishes on marshy flat areas and along streams in the Andes (Hooghiemstra, 1984; Van't Veer and Hooghiemstra, 2000). Discrepancies in the timing of mangrove peaks between the two cores could be reflecting: a) timing displacements due to differences between age models, b) uncertainties due to sampling resolution, or c) latitudinal differences in the responses of vegetation, due to the climatic and seasonality gradient related to the position of the

Equatorial Front directly affecting core TR 163-38 site location (Martínez et al., 2003).

5.1.4. The Holocene: a humid phase with dry spots

During the 11,300–5600 yr cal BP period, the maximum marine transgression is recorded by simultaneous peaks in mangrove, especially at ~10,000 yr cal BP. Synchronously, peaks of swamp forest and other flood indicators such as *Myriophyllum* and *Thelypteris* occur together with high fungal spore levels, suggestive of high rainfall levels. Warmer climate is inferred by the rise of terra firma lowland elements and the decline to minimum values of Andean forest. It is worth noting that *Podocarpus* shows an analogous trend to mangrove in both cores. This could reflect *Podocarpus* affinity to humid environments, even in lowland regions. After 9000 yr cal BP mangrove drops significantly followed by an increase of lowland taxa, which could be related to the stabilization of sea level at ~7000–6000 yr BP (Lambeck and Chappell, 2001; Clark et al., 2001; Siddal et al., 2003), and the associated deltas formation (Stanley and Warne, 1994). Significant is the expansion and diversification of palms only after 10,000 yr cal BP that are an important component of today's Pacific vegetation (e.g., simultaneous occurrence of *Euterpe, Mauritiella, Attalea, Oenocarpus, Bactris*, and unidentified taxa). In a similar way to mangrove curves, the concentration of palynomorphs shows a dramatic decrease at ~7000 yr cal BP, which could be indicating a drier period and the consequent weakening of fluvial systems. In both cores, grasses and secondary forest taxa, like Compositae, Poaceae and *Piper*, increase, thus supporting the idea of drier climates at ~7000 yr BP. Given time model uncertainties, this dry event might correspond to the 8200 yr BP cold event recently reported in Costa Rica (Lachniet et al., 2004). The upper limits of the zones TR-II and ODP-IVa are well correlated in the two records (Fig. 5).

5.1.5. The late Holocene: human or climatic disturbances?

The period from 5640 yr BP to the present is characterized by the displacement of mangroves by terra firma forests, probably due to a natural process of succession–competition. This could be possible due to the prior stabilization of sea level and the consequent sedimentary progradation (Stanley and Warne, 1994). The period is characterized by the simultaneous occurrence of terra firma and open vegetation elements. Humidity indicators like *Euterpe, Oenocarpus, Ardisia,* Cyperaceae and ferns are still present, and pollen con-

centration rates increase again, suggesting a persistent wet climate. Open vegetation, as well as *Cecropia*, *Piper* and *Alchornea*, suggests disturbance processes of a different nature, probably related to the effects of more intense fluvial dynamics and human occupation, documented to start at ~10,000 yr BP in the Colombian Pacific (Cardale de Schrimpff et al., 1989).

5.2. Comparison between marine and continental paleoclimatic records

As shown in the previous section, the pollen records from marine cores ODP 677B and TR 163-38 describe a development from: (1) a cold and humid phase (39,410–28,120 yr cal BP) with moderately high sea levels, (2) the coldest and driest phase in the record (28,120–14,500 yr cal BP) accompanied by the lowest sea levels, (3) a transitional phase (14,500–11,300) when sea level rose, and humid conditions dominated, (4) a stage (11,300–5600 yr cal BP) of the highest sea levels and moisture conditions including a drier period at ~7000 yr cal BP, to (5) a final period (5600 yr cal BP–Present) when sea reached its present level, humidity persisted, and indicators of disturbance expanded.

The period corresponding to the Middle Pleniglacial (60,000–28,000 yr BP) has been described as a stage of cold and humid conditions with maximum advance of glaciers in the northern Colombian Andes (Van der Hammen and Hooghiemstra, 2000). Higher moisture than present has been reported for the cores Fúquene III and Tenjo V in the Eastern Cordillera of Colombia (Van der Hammen, 1995; González et al., 2002), and the Eastern Cordillera of Bolivia (Mourgiart and Ledru, 2003). Our palynological records support rapid increments in fluvial discharge at ~31,500 and 28,000 yr cal BP that are also reported for the Cariaco Basin in northern Venezuela (Peterson et al., 2000) and for marine core TR 163-31B in the Equatorial Pacific (Heusser and Shackleton, 1994). This event roughly corresponds to an increase in hemipelagic quartz in core TR 163-31B (northern Peru Basin) and lies within the 35,000–16,000 years BP interval of sea-surface temperature (SST) reduction documented for core ODP 846B (south the Galapagos Islands; Boven and Rea, 1998; Martínez et al., 2003).

SST estimates for the Panama Basin (Martínez et al., 2003) show that a cold period, between 28,000 and 14,000 yr BP, is enclosed between two warmer stages that coincide with deflections in the δ^{18}O curve of the ODP 677B core. This coincides with the phase described in the pollen zones ODP-I and ODP-II. When the δ^{18}O signal is compared to the Andean percentage

curve and the lowland forests (terra firma + swamp forests) inverse curve, a striking similarity appears (Fig. 7). This similarity was already reported for the whole Quaternary period when comparing the Andean forest curve of Funza II record in the Eastern Cordillera of Colombia and marine core ODP 677 (Hooghiemstra and Sarmiento, 1991). A similar correspondence was found in marine core TR 163-31B between arboreal elements and the isotopic curve (Heusser and Shackleton, 1994). These similar trends support the idea that, although the vegetation of the Pacific slope of the Andes is more sensitive to changes in precipitation, in a broad scale, it is responding to temperature shifts.

The interpretation of drier conditions accompanying temperature descent for the LGM (Heusser and Shackleton, 1994; Van der Hammen and Absy, 1994; Hooghiemstra and Van der Hammen, 1998; Van der Hammen and Hooghiemstra, 2000) is not obvious for the LGM from our pollen record. Although there is a clear decrease in flood indicators, lowland and Andean wet forest elements were still persistent. The extreme
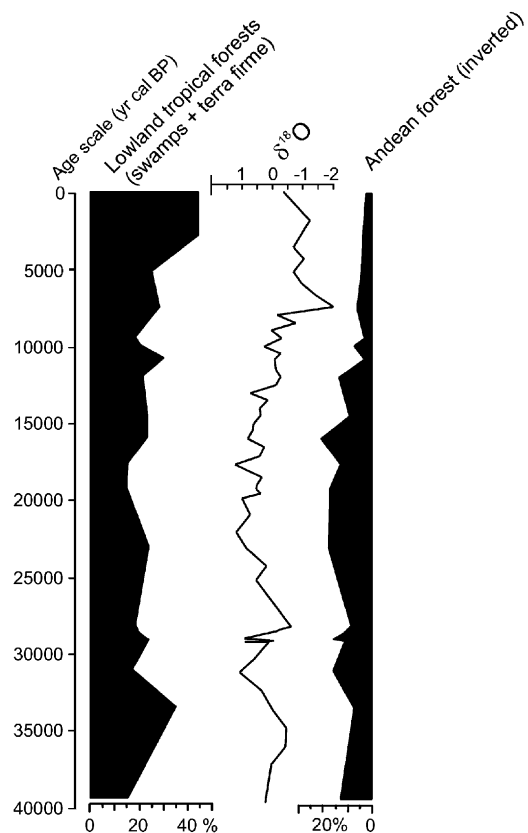

Fig. 7. Comparison among Andean and lowland forest pollen percentages, and δ^{18}O values on the planktonic foraminifer *Neogloboquadrina dutertrei* (data in Martínez et al., 2003), for the marine core ODP 677B, Panama Basin, eastern equatorial Pacific.

wet conditions characteristic of the Pacific flank of the Western Cordillera of Colombia imply that, even in cases of decline in precipitation, wet conditions can persist with no great changes in forest coverage. Perhaps in this case, changes are reflected more on plant composition than in forest density, an idea that is supported by the arrival of deciduous or dry forest species (<2%) (Mimosaceae, Bombacaceae, *Croton*, *Erythrina*, *Desmodium*). Better indicators of reduced precipitation during the LGM (18,000–21,000 yr cal BP) are the low values of pollen and spore concentrations that imply minor fluvial discharges. Furthermore, the absence of pollen at ~110 cm in core ODP 677B (~19,800 yr cal BP) can be interpreted as a hiatus due to weaken riverine discharges. Consequently, our records are more in agreement with the hypothesis of El Niño-like conditions during LGM (Stott et al., 2002; Visser et al., 2003). The latter would not be in complete discrepancy with Martínez et al. (2003), who interpreted LGM climates to be more akin to La Niña-like conditions implying stronger westerlies, i.e., the Chocó jet, but not necessarily wetter conditions because of the lower moisture carrying capacity of the atmosphere under lower temperatures.

El Niño-like conditions for the Panama Basin would be in agreement with the data of wet climates during LGM for Peru and Bolivia (Baker et al., 2001), as present El Niño conditions in the zone south of the Equatorial Front are manifested by high precipitation events (Díaz and Markgraf, 1993), while in the northwestern part of the Andes, El Niño-phase conditions are associated with below-average precipitation (Mesa et al., 1997; Vuille et al., 2000).

The period corresponding to the late glacial is a transitional stage, when more humid and warmer conditions prevailed. This is the period with maximum pollen concentration values in cores ODP 677B and TR 163-38 (~15,000 yr cal BP). For northeastern Brazil, Behling et al. (2000) also report maximum pollen concentration values between 15,500 and 11,800 yr BP as a response to more humid environments.

There is a good correlation with other marine cores for the timing of initial (16,000 yr cal BP), maximum (~13,000–~9000 yr cal BP) and final (~7000 yr cal BP) stages of mangrove development. Heusser and Shackleton (1994) report similar results for the eastern equatorial Pacific, core TR 163-31B, which are comparable to the Australian cores ODP 820 and SHI-9014 (Grindrod et al., 1999). This expansion of mangroves describes accurately the rise of sea level, linked to melting and deglaciation processes that in the tropical Pacific began after 18,000 yr BP (Lambeck and Chap-

pell, 2001; Clark et al., 2001; Siddal et al., 2003). This mangrove signal seems to be common to deep-ocean records thus reflecting sea level rising and the availability of estuarine environments suitable for the establishment of mangroves. It is important to consider the role that precipitation plays in the formation of these estuarine environments by fluvial discharge and terrigenous sediment yield. In the Panama Basin, maximum values of mangrove coincide with peaks of swamp forests. Since large areas of swamp forests in the Pacific lowlands do not depend on marine influence, but on seasonal river floods, these synchronized events must involve high sea levels as well as high precipitation rates. La Niña-like dominant state during the early Holocene in the Ecuadorian Andes (Moy et al., 2002) supports our interpretation.

Similarly, the weakening of the mangrove signal occurs simultaneously with periods of relative sea level stability (i.e., marine stillstands) and sea level lowering, as it has been previously reported by Grindrod et al. (1999). The decline of mangroves is related to the terrigenous sediment infilling of estuaries which favors natural succession–competition processes within plant communities, and displaces mangroves to restricted coastal and river fringes (Mulrennan and Woodroffe, 1998; Grindrod et al., 1999). Stanley and Warne (1994) give worldwide evidence of simultaneous timing of delta formation after sea level stabilization at ~8500–6000 yr BP. The mangrove-diminishing phase in the Panama Basin starts at ~6500 yr BP. During this period, tropical rain forest increases, which supports the idea of competitive success, but also coincides with a widely recorded dry phase for northern South America, i.e. northern Peru, Lake Titicaca (Baker et al., 2001), El Pinal and Carimagua lakes in Colombia (Behling and Hooghiemstra, 1999), Amazonia (Absy, 1979; Urrego, 1997) and southern Brazil (Ledru et al., 1996). At ~7000 yr BP the onset of a phase of more frequent and intense El Niño events has also been reported (Moy et al., 2002). This changes in frequency and amplitude of El Niño activity could have favored the expansion of grasses and secondary forests. The expansion of *Podocarpus* and palms during the Holocene coincides with an increased precipitation and the conformation of drainage systems after sea level stabilization. Likewise, marine core TR 163-31B shows the highest percentages of *Podocarpus* during the early Holocene (Heusser and Shackleton, 1994). For the Caquetá River (Colombian Amazonia), Urrego (1997) associates *Mauritia* expansions around 6000–5000 yr cal BP with the subsequent humid phase after a dry period. Colinvaux et al. (1996) found for the Lake Pata

(Brazilian Amazonia), that *Mauritia* was present in the record only during the Holocene with a significant increase after 7000 yr BP. This change was related to a higher precipitation or to an elevation of the water table due to the raise of sea level.

For the Holocene, evidence of human disturbance on the surroundings of the Panama Basin has been reported. According to Cardale de Schrimpff et al. (1989), the first evidence of human occupation in the western slope of the Western Cordillera dates from 9670 ^{14}C yr BP and first agricultural activities in the zone are reported around 7500 yr BP. Pollen of maize was first evidenced in the El Dorado pollen record (Western Cordillera of Colombia, 1200 m.a.s.l.) at ~7000 yr BP (Bray, 1991), but the most intensive use of the forest is registered at ~2000 yr BP, when forest diminished significantly and herbaceous pollen expanded. This coincides with the flourishing of the Ilama (Cardale de Schrimpff et al., 1989) and Tumaco–La Tolita cultures, the latter occupying areas of mangroves, swamps and streams extending from the Esmeraldas Province in Ecuador to the southern Pacific coast in Colombia since 2500 yr BP (Patiño, 1988). Other records from Panama show the presence of early hunters and gatherers since 11,050 ^{14}C yr BP, and slash-and-burn cultivation since 7000 ^{14}C yr BP (Piperno et al., 1990; Piperno and Jones, 2003; Bush et al., 1992). All this evidence can be related to the expansion of open vegetation as recorded in the uppermost part of the ODP 677B and TR 163-38 marine records, strengthened by the fact that swamp forest and wet forest elements persist. Probably the late Holocene changes in plant cover are the result of the interaction between human disturbance and high frequency climate fluctuations.

6. Conclusions

Pollen analysis of marine cores ODP 677B and TR 163-38 from the Panama Basin, eastern equatorial Pacific, led to conclusions that contribute to the understanding of regional vegetation and climate changes on northern South America, especially on the Pacific slopes of the northern Andes.

The continuous presence of all vegetation types during the last 39,410 yr and specially the uninterrupted occurrence of tropical rain forest in the two records is noteworthy. This is important when trying to explain regional diversity and endemism patterns of the Chocó Biogeographic region. On the other hand, there is multiple evidence that locally these forests are less than stable, and instead respond to local environmental changes like fluvial dynamics, tectonics, and human

disturbances (Behling et al., 1998b; Berrío et al., 2000; Vélez et al., 2001; Ramírez and Urrego, 2001; Urrego and Del Valle, 2002), which makes it more necessary to implement broader-scale studies in terms of climate change understanding.

A good correspondence was found between the two records in terms of main changes of ecological groups and the timing of those changes. Pollen data from marine records ODP 677B and TR 163-38 suggest the occurrence of cold and humid conditions between 39,410 and 28,120 yr cal BP and moderately high sea levels. Then, during the 28,120–14,500 yr cal BP period, coldest and driest conditions are recorded by the expansion of Andean forest and open vegetation, and the simultaneous diminishment of lowland taxa. During this period, sea level reached its minimum. A subsequent transitional phase is recorded, when sea level rose, and humid conditions dominated. Sea level reached its highest position during the 11,300–5600 yr cal BP period, and general humid conditions persisted, except at ~7000 yr cal BP, when drier conditions occurred. During the late Holocene (5600 yr cal BP–Present), sea level reached its present position, humidity persisted, and the tropical forest and indicators of disturbance expanded. The increase in terrigenous material transported to the ocean, containing high concentration of pollen and spores, indicates periods of higher precipitation around 33,500, 28,000 and 12,000–9000 yr cal BP, which agrees with Behling et al. (2000) and Peterson et al. (2000) results for northeastern Brazil and the Cariaco Basin, respectively. Although main vegetational responses seem to reflect rainfall and moisture variations, a good correspondence was found between $\delta^{18}O$ values and percentages of Andean and lowland pollen. This implies that even in cases like the forest of the Chocó Biogeographic region, where moisture seems to be the main climatic driving factor, temperature plays an important role on the composition and distribution of vegetation.

In order to improve our knowledge on the environmental history of this region, future studies should include higher resolution sampling, a better understanding of vegetation responses to diverse scale disturbances, a broader knowledge of pollen dispersion and transport patterns, and multiproxy approaches to permit more accurate interpretations.

Acknowledgements

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