

## Pollen-based biome reconstructions for Latin America at 0, 6000 and 18 000 radiocarbon years ago

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**Abstract.** The biomisation method is used to reconstruct Latin American vegetation at  $6000\pm 500$  and  $18\,000\pm 1000$  radiocarbon years before present ( $^{14}\text{C}$  yr BP) from pollen data. Tests using modern pollen data from 381 samples derived from 287 locations broadly reproduce potential natural vegetation. The strong temperature gradient associated with the Andes is recorded by a transition from high altitude cool grass/shrubland and cool mixed forest to mid-altitude cool temperate rain forest, to tropical dry, seasonal and rain forest at low altitudes. Reconstructed biomes from a number of sites do not match the potential vegetation due to local factors such as human impact, methodological artefacts and mechanisms of pollen representivity of the parent vegetation.

At  $6000\pm 500$   $^{14}\text{C}$  yr BP 255 samples are analysed from 127 sites. Differences between the modern and the  $6000\pm 500$   $^{14}\text{C}$  yr BP reconstruction are comparatively small; change relative to the modern reconstruction are mainly to biomes characteristic of drier climate in the north of the region with a slight more mesic shift in the south. Cool temperate rain forest remains dominant in western South America. In northwestern South America a number of sites record transitions from tropical seasonal forest to tropical dry forest and tropical rain forest to tropical seasonal forest. Sites in Central America show a change in biome assignment, but to more mesic vegetation, indicative of greater plant available moisture, e.g. on the Yucatán peninsula sites record warm evergreen forest, replacing tropical dry forest and warm mixed forest presently recorded.

At  $18\,000\pm 1000$   $^{14}\text{C}$  yr BP 61 samples from 34 sites record vegetation reflecting a generally cool and dry environment. Cool grass/shrubland is prevalent in southeast Brazil whereas Amazonian sites record tropical dry forest, warm temperate rain forest and tropical seasonal forest. Southernmost South America is dominated by cool grass/shrubland, a single site retains cool temperate rain forest indicating that forest was present at some locations at the LGM. Some sites in Central Mexico and lowland Colombia remain unchanged in the biome assignments of warm mixed forest and tropical dry forest respectively, although the affinities that these sites have to different biomes do change between  $18\,000\pm 1000$

$^{14}\text{C}$  yr BP and present. The “unresponsive” nature of these sites results from their location and the impact of local edaphic influence.

## 1 Introduction

Biomisation is an objective method to reconstruct broad vegetation types based on the assignment of pollen taxa to one or more plant functional types (PFTs) (Prentice et al., 1996a). The method is based on the assumption that a pollen spectrum will have different degrees of affinity to different biomes that can be quantified by a simple algorithm. Biome reconstructions from pollen data at  $6000\pm 500$   $^{14}\text{C}$  yr BP and the last glacial maximum (LGM) at  $18\,000\pm 1000$   $^{14}\text{C}$  yr BP have been produced for most regions of the world under the auspices of the BIOME 6000 project (Prentice et al., 1998, 2000). The validity of the method in reconstructing biomes at different time intervals has been demonstrated for Africa (Jolly et al., 1998a; Elenga et al., 2000), Australia (Pickett et al., 2004) Beringia (Bigelow et al., 2003; Edwards et al., 2000), China (Yu et al., 1998, 2001), Eastern North America (Williams et al., 2000), Eurasia (Tarasov et al., 1998a), Europe (Prentice et al., 1996a, b; Tarasov et al., 1998a, b; Elenga et al., 2000), Japan (Takahara et al., 2001) and Western North America (Thompson and Anderson, 2000). Results from Latin America, presented here, represent the last geographically large area to undergo this process. Within Latin America the biomisation method has been previously applied to Colombian and Mexican pollen data at a range of spatial and temporal scales; from the middle Holocene (Marchant et al., 2001a; Ortega-Rosas et al., 2008a, b), the LGM (Marchant et al., 2002a), to investigate modern-pollen vegetation relationships (Marchant et al., 2001b), impact of human societies on vegetation (Marchant et al., 2004a) and as a basis for comparisons with output from a vegetation model run under different climatic and environmental scenarios (Marchant et al., 2004b, 2006). In addition to these spatial investigations, the method has been applied down-core down to a 450 000 year pollen record from the high plain of Bogotá (Marchant et al., 2002b). As Colombia is biogeographically complex, encompasses high altitude, temperate and tropical floras reflecting a range of environmental space including transitions from hyper-humid to semi-arid climates, these analyses provided a suitable test-bed for the wider geographical focus presented here.

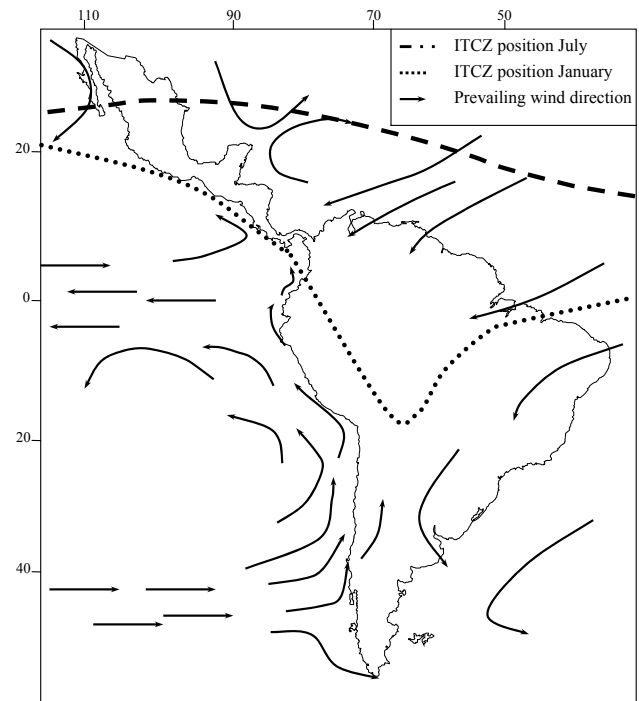


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In addition to reconstructing vegetation patterns, and investigating factors that can explain observed changes, data on past biomes contributes to testing of climate and vegetation models (Prentice et al., 1992; Haxeltine and Prentice, 1996; Peng et al., 1998; Marchant et al., 2006; Braconnot et al., 2007). Vegetation models can be used to portray output from Global Circulation Models (GCMs) as maps of potential vegetation (Claussen and Esh, 1994; Foley et al., 1996; Prentice et al., 1996b; Williams et al., 1998) that can be used in the development of models that couple biosphere, atmosphere and oceanic components (Braconnot et al., 2007; Claussen, 1994; Harrison et al., 2003; Texier et al., 1997) and testing of biogeochemical dynamics (Peng et al., 1998). There has been growing interest how atmosphere-biosphere interactions have operated under the changing environmental conditions since the LGM, particularly in trying to understand the response of ecosystems to different types of environmental forcing (Jolly and Haxeltine, 1997). Transformed pollen data can further be used in conjunction with other data types, such as on lake status (Jolly et al., 1998b) and archaeological evidence (Piperno et al., 1990, 1991a, b), to better understand the causal factors driving vegetation change over the recent geological past.

### 1.1 Latin American region

Latin America comprises the area from 35° N to 65° S, and from 35° W to 120° W extending from México to islands off southernmost South America from Eastern Brazil to the Galapagos Islands. Latin America is characterised by strong environmental gradients associated with 100° of latitude, approximately 7000 m of altitude and the transition from oceanic- to continentally-dominated climate systems (Fig. 1). Despite this great extent there has been permanent contact between the tropical and temperate domains throughout geological time. Physiographically, Latin America is characterised by stable cratons associated with the interior and areas of active mountain building, particularly associated with the Andes. This environmental variability is reflected by an incredibly diverse biogeography, ranging from the highly diverse rain forest of the Chocó Pacific (Colombia) to the cold deserts of the high Andes, from the hot semi-desert areas of México to the cold moorlands of Tierra del Fuego (Fig. 2). Descending an altitudinal gradient there is a transition from páramo (cool grass/shrubland) to high Andean forests (cool mixed and cool temperate rain forests) and lower Andean forest (warm evergreen forest) (Fig. 3). Complicating this potential vegetation distribution is the factor of human impact with the majority of the vegetation in Latin America being impacted on by the vegetation (Ellis and Ramanakuty, 2008). The timing of early human settlement in Latin America is a contentious subject, although it seems from the early Holocene there was considerable cultural diversity and adaptation to a series of different environments (Gnécco, 1999). Human-induced impact has had a direct in-



**Fig. 1.** Map of Latin America depicting the present-day summer and winter position of the ITCZ and the macro-scale wind (and hence moisture) patterns over Latin America.

fluence on vegetation composition and distribution through land-use practices and the introduction of alien taxa and cultivars to the Latin American flora. For example, in excess of 100 plants were under cultivation prior to the European conquests in the 15th century (Piperno et al., 2000).

### 1.2 Latin America climate

Cerveny (1998), Eidt (1968) and Metcalfe et al. (2000) have reviewed Latin American climate. Given the broad geographical scope, Latin America is characterised by a variety of climates that relates to its global position, shape of the landmass, location and height of the Andes, offshore currents, general hemisphere air flow and proximity of large water bodies (Fig. 1). Four dominant circulation regimes influence Latin America: the Inter-Tropical Convergence Zone (ITCZ), the prevailing westerlies, the semi-permanent high pressure cells located over the South Pacific and South Atlantic Oceans and the trade winds. Perhaps most dominant is the annual oscillation of the meteorological equator (ITCZ), this migrating some 10–15° latitude about the equator (Fig. 1). The ITCZ reaches its northernmost location in June, this bringing high rainfall for northern South America and the Caribbean, with January and February recording the dry season (Cerveny, 1998). However, due to the influence of the westerlies from the Pacific, and the sharply rising topography of the Andes, the ITCZ has a sinusoidal

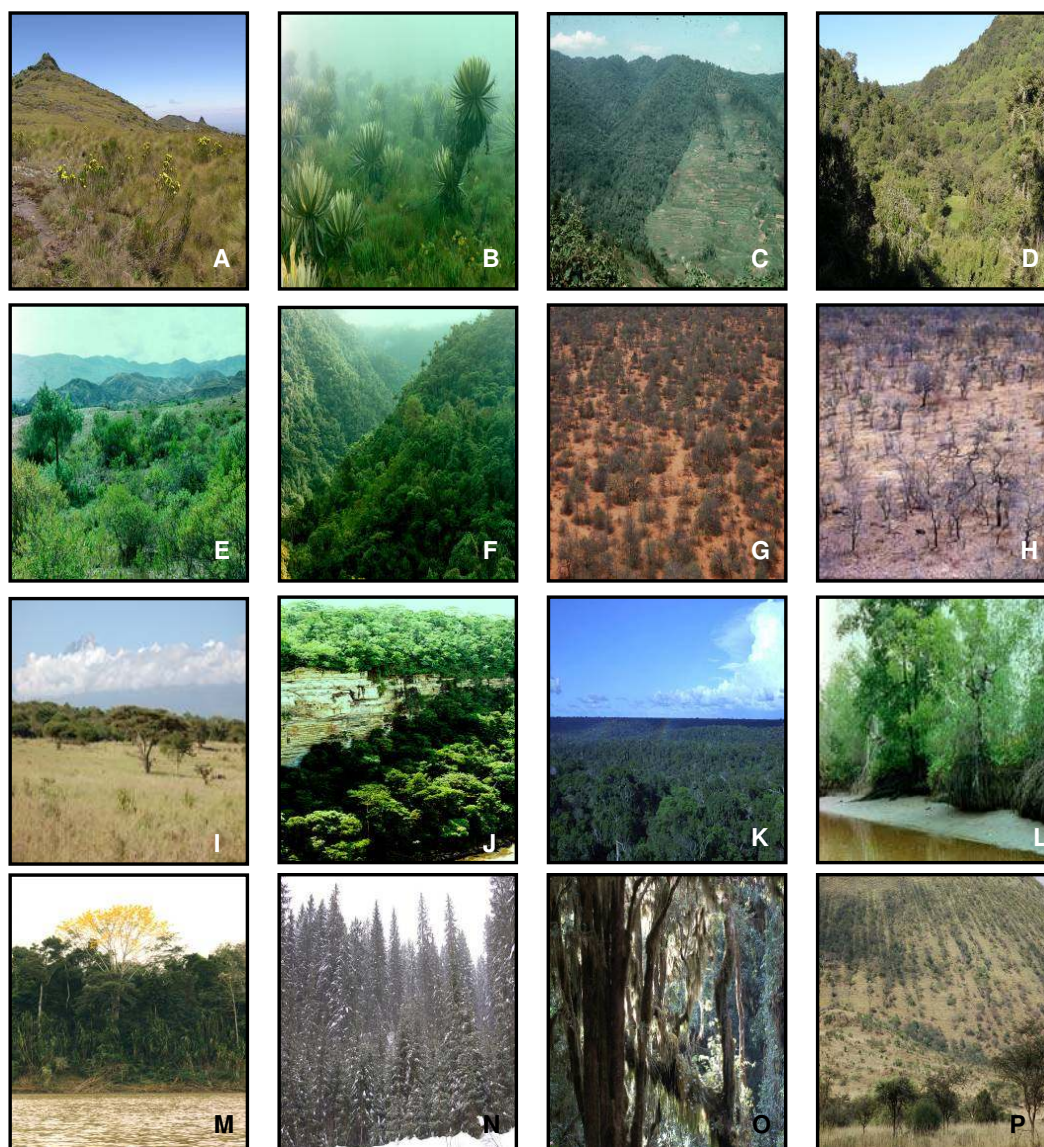


**Fig. 2.** Map of the modern potential vegetation as derived from Schmithüsen (1976) and Hück (1960). For example, the various divisions of seasonally dry forest such as cerrado, caatinga, campo rupstre, savanna, are combined to the biome of tropical dry forest. Acronyms are explained in Table 1.

profile over northwestern South America (Fig. 1). In southern South America the prevailing westerlies south of  $40^{\circ}$  S are particularly important in controlling the moisture regime. The topographic barrier of the Andes contributes to the creation of two large semi-present anticyclones, one over the South Pacific and one over the South Atlantic, the southeast trade winds associated with this latter system brings abundant moisture to the Amazon Basin (Cerveny, 1998). Due to the large size of South America, and the highland ranges that fringe much of the continent there is often a rapid transition from relatively moist coastal areas to a dry interior reflecting the transition from oceanic- to continental-dominated climate systems. For example, due to the proximal location of the Pacific-based moisture source and steeply rising ground,

precipitation is highest ( $>15\,000\text{ mm yr}^{-1}$ ) in the Chocó Pacific region. Exceptions to this scenario are areas located between the anticyclones, e.g. the Peruvian coast, where relatively arid conditions prevail.

One of the main environmental gradients in Latin America is associated with the Andes. The Andes are characterised by a diurnal climate (Kuhry, 1988); at a given location differences in monthly temperature are small ( $<3^{\circ}\text{C}$ ) although daily fluctuations may be large ( $20^{\circ}\text{C}$ ), especially during the dry seasons. Climatic changes with altitude can be summarised as a lapse rate (Barry and Chorley, 1990). Applying a lapse rate of  $6.6^{\circ}\text{C }1000\text{ m}^{-1}$  (Van der Hammen and González, 1965; Wille et al., 2001), this altitudinal rise equates to a temperature change of more than  $30^{\circ}\text{C}$ . Also



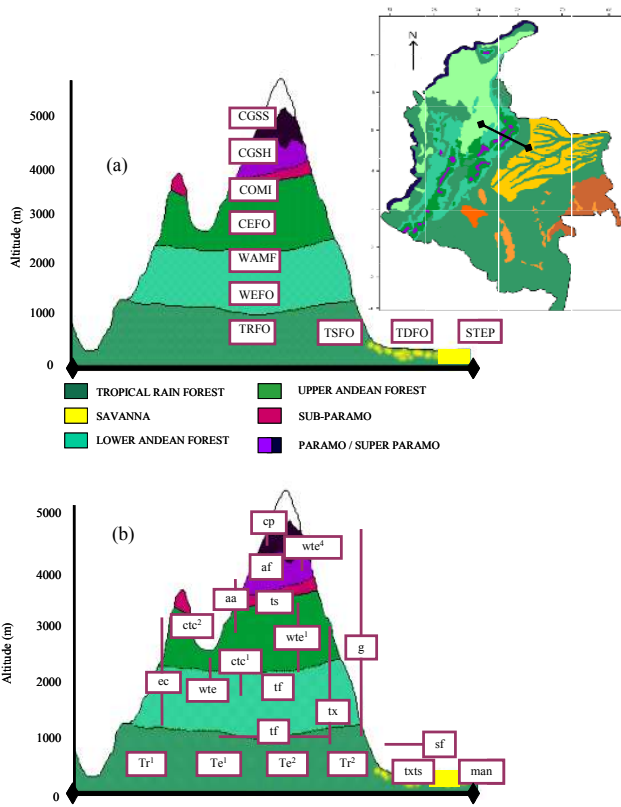
**Fig. 3.** Examples of Latin America biomes from cool grass shrubland with *Scenecio* and *Espeletia* (a, b) to cool mixed forest (c, d, e, f), tropical dry forest that can be dominated by *Bauhinia* (g, h) with dominance of open steppe grasslands (i) tropical rain forest (j, k), dominated by mangrove in areas fringing saline water (l), tropical seasonal forest (m), cool temperate forest (n, o). The bottom plate (p) shows the importance of edaphic factors on controlling vegetation, in this case local hydrology where rill channels allow trees to grow in areas that would be dominated by grassland.

associated with the Andes are steep gradients of moisture availability. Rainfall is high on the eastern slopes of the Andes; the concave nature acting as a receptacle for moisture transferred by the southeast trade winds from the Atlantic Ocean, in part receiving moisture generated by the Amazonian forest (Fjelds , 1993). Low rainfall is recorded within rain shadow areas, such as on the lower slopes of the Magdalena Valley and the inter-Andean plains (Kuhry, 1988). These climate gradients result in rapid transitions from mesic to xeric vegetation types, e.g., cool high-altitude grasslands change to “temperate” forests at mid-altitudes and diverse

tropical rain forests within a few kilometres (Fig. 3). In the southern part of Latin America rainfall is largely controlled by the persistence and strength of the westerly winds (Gilli et al., 2005). There has been increased interest in large-scale temperature-driven surface pressure oscillations in the Pacific Ocean termed the Southern Oscillation, and its assimilated oceanic aspects, El Ni o and its antithesis La Ni a (Cerveny, 1998; God nez-Dom nguez et al., 2000; Metcalfe et al., 2000), however, given the temporal foci of the vegetation reconstructions here this is not so relevant.

**Table 1.** Range of plant functional types identified within the Latin American region giving bioclimatic range and physiological adaptation.

Code	Plant functional type	Bioclimatic range and plant physiological adaptation
g	Graminoid	Ecologically broad category that occurs in a number of biomes, a highly adaptive PFT with a ubiquitous distribution and little diagnostic value.
man	Mangrove	Constituent of lowland tropical vegetation, control on distribution is mainly hydrological
tx	Tree fern	Can be locally dominant. Occupying a broad bioclimatic range, particularly common in temperate moist areas.
Te <sub>1</sub>	Tropical broad-leaved evergreen tree	MTCO > 15.5°C, $\alpha > 0.7$ , short dry season (1 month), GDD > 5000.
Te <sub>2</sub>	Tropical xeric broad-leaved evergreen tree	MTCO > 15.5°C, $\alpha > 0.6-0.8$ , longer dry season (2–4 months), GDD > 5000, withstands longer dry season by shedding leaves.
Tr <sub>1</sub>	Tropical rain green tree	MTCO > 15.5°C, $\alpha > 0.9$ , GDD > 5000, present in wettest tropical rain forest.
Tr <sub>2</sub>	Dry tropical rain green tree	MTCO > 15.5°C, $\alpha 0.8-0.9$ , GDD > 5000, present in range of tropical seasonal forest types.
ctc	Cold temperate conifer	MTCO 5°C–15°C, $\alpha > 0.7$ , GDD > 4500, common in the Brazilian highlands.
ctc <sub>1</sub>	Cool temperate conifer	MTCO –5°C–10°C, $\alpha 0.95-0.75$ , GDD > 900, common along the western coast of southern South America.
ctc <sub>2</sub>	Maritime evergreen conifer	MTCO –10°C–5°C, $\alpha > 0.65$ , GDD > 1000, common along the western coast of southern South America.
ec	Eurythermic conifer	MTCO > 5°C, $\alpha 0.4-0.6$ , GDD > 5000, common within dry forest of South America and Mexico.
txts	Tropical xerophytic tree/shrub	MTCO > 20°C, $\alpha 0.2-0.35$ , GDD > 5000, woody shrubs common in dry forest.
ds	Desert shrub	MTCO > 20°C, $\alpha 0.2-0.35$ , GDD > 5000, woody shrub and cacti in Mexico and coastal Peru
df	Xerophytic forb	MTCO > 20°C, $\alpha 0.2-0.35$ , GDD > 5000, woody shrub and cacti in Mexico and coastal Peru
tf	Tropical forb	MTCO > 15.5°C, $\alpha > 0.6$ , GDD > 5000, frost intolerant
tef	Temperate forb	MTCO > 5°C–15°C, $\alpha > 0.6$ , GDD > 1000, frost tolerant
sf	Eurythermic forb	MTCO 5°C–10°C, $\alpha 0.65-0.7$ , GDD 2500–4000, requires a seasonal moist environment
af	Arctic forb	MTCO –5°C–0°C, $\alpha 0.05-0.1$ , GDD < 500, frost tolerant
cp	Cushion forb	MTCO < –5°C, $\alpha < 0.2$ , GDD < 500, specific growth form, frost tolerant.
wte	Warm temperate evergreen broad-leaved tree	MTCO 5°C–15°C, $\alpha > 0.65$ , GDD > 3000, frost tolerant mesophyllous trees
ts	Temperate summer green tree	MTCO 0°C–5°C, $\alpha > 0.65$ , GDD > 2000, frost tolerant micro and mesophyllous trees
ts <sub>1</sub>	Temperate evergreen broad-leaved tree	MTCO –5°C–5°C, $\alpha > 0.5$ , GDD > 1000, sclerophyllous, usually evergreen
wte <sub>1</sub>	Temperate cool deciduous broad-leaved tree	MTCO 0°C–15°C, $\alpha > 0.6$ , GDD > 3000, winter deciduous, requires warm growing season.
wte <sub>4</sub>	Temperate cold-deciduous broad-leaved tree	MTCO –5°C–5°C, $\alpha 0.55$ , GDD is > 2500, winter deciduous, requires warm growing season but this can be short.
aa	Arctic shrub	MTCO –5°C–0°C, $\alpha 0.2-0.4$ , GDD 500–1000, frost tolerant



**Fig. 4.** Cross an altitudinal cross section across the northern Andes in Colombia showing the standard vegetation units and their relationship to Biomes (a) and plant functional types (b). Acronyms are explained in Tables 1 and 2.

### 1.3 Latin America vegetation

For the purpose of this investigation the potential vegetation composition and distribution Latin America is classified at a coarse resolution with twelve biomes being identified (Fig. 2) that summarise the 57 categories mapped by Hück (1960) and 45 by Schmithüsen (1976). This process of reclassifying the vegetation was carried out in consultation with a number of the co-authors, particularly those with good ecological knowledge and a range of geographical expertise. Reducing the number of vegetation categories results in a significant smoothing of the ecosystem transitions, particularly when these are very sharp or specific biomes are quite isolated. A good example are the relatively small deserts of north-western Mexico that get mapped as tropical dry forest rather than desert. The vegetation composition and distribution generally reflects the main climatic and topographic gradients described above. However, a series of caveats to this must be stressed. Firstly, the actual and potential vegetation can be quite different, the former reflecting a long history of human interaction that has been particularly pronounced since the colonial period but has been influencing the vegetation for at least the last 5000 years (Marchant et

al., 2004). In numerous areas this interaction has completely transformed the potential vegetation to an agricultural landscape. Another factor complicating the relationship between climate and vegetation is the locally strong edaphic influence by substrate, topography or geographic character (Fig. 3). The strength of this influence is demonstrated by areas of tropical dry forest that form on free-draining sandstones, e.g. the Llanos Orientales (Colombia); these are located in areas where the climate regime would support tropical seasonal forest, or even tropical rain forest.

Broad types of vegetation with similar composition and distribution (biomes) result from a combination of plant functional types (PFTs). PFTs and biomes, which lie at the heart of the biomisation technique, allow the high floristic diversity within the Latin America pollen flora to link with the relatively coarse vegetation classification (Fig. 4). PFTs group together species that have common character (Prentice et al., 1992). This grouping is based on common life form and phenology, combined with the geographic distribution that is in part determined by climate (Woodward, 1987). An indication of the bioclimatic range of each PFT and plant physiological adaptation, to the given environmental condition, is presented in Table 1. The range of biomes identified within the Latin America, floristic description, main location and equivalent floristic units is portrayed in Table 2. The cool grass/shrubland biome incorporates a relatively wide range of vegetation dominated by grasses, heath, cool temperate sclerophyll shrubs and cushion plants (Fig. 3). This biome is present in southern South America and at high altitudes along the Andes. In addition to the cool grassland a warm grassland (steppe) is identified. Steppe is found predominately under the warm, dry climates of southeast and northeast Brazil, northwestern Argentina and coastal northern South America. Warm temperate rain forest represents a mix of warm conifers such as *Araucaria*, Andean and Atlantic rain forest elements, whereas cool temperate rain forest contains cool conifers, such as *Fitzroya*, Andean and Valdivian rain forest elements. Dry forests are extensive in Latin America, specifically associated with areas located between the two semi-permanent anticyclones and influenced by the high seasonality of rainfall imposed by the annual migration of the ITCZ. For our classification we characterise the diverse dry vegetation formations (Fig. 4) as the tropical dry forest biome. Xerophytic trees and shrubs is widespread in the interior of South America, along the southwestern Pacific coast and northeast Brazil where it grades into steppe, additionally, there are patches in Colombia, on the Yucatán peninsula and in México (Fig. 2). Tropical dry forest is predominantly recorded in two main swaths either side of the Amazon basin, with an extension through Central America. The tropical seasonal forest biome is predominantly recorded to the north of Amazonia where it is interspersed with patches of dry forest; this reflecting a strong edaphic influence. A large area of tropical seasonal forest is recorded away from the hyper-humid area of Brazil along the Atlantic coast. The tropical

**Table 2.** Biomes identified within the Latin American region as portrayed in the vegetation map (Fig. 2) indicating a floristic description, the main location and equivalent floristic units found in a macro scale analysis of the Latin American vegetation.

Code	Biome	Definition	Main locations	Equivalent	Floristic characteristics
TRFO	Tropical rainforest	Closed canopy lowland evergreen forests. Canopy broken by emergent trees (>40 m). MTCO>18°C, precipitation >1500 mm yr <sup>-1</sup> , frost-intolerant.	Characterise much of the Amazon catchment. Can form a relatively thin band along tropical coastal areas, e.g. Atlantic rain forest of Brazil, Chocó pluvial forest of Colombia, maintained by high moisture derived from close proximity of oceanic influence.	Amazonian forest, Tropical moist forest, Atlantic rain forest, Terra firme forest, Várzea, Gallery forest, Chocó pluvial forest.	Generally characterised by plants with mesophyll leaf, although some sclerophyllous plants are present, often tree ferns and palms.
TSFO	Tropical seasonal forest	Relatively tall (20–30 m) closed canopy forest with occasionally tall (>40 m) emergent trees. Canopy opens in a mosaic as deciduous elements loose leaves. Seasonally dry from 1–4 months.	Dominant to the north of Amazonian tropical rainforest, in central America and formerly extensive in the interior of Brazil prior to extensive clearance.	Marsh forests, savanna gallery forest, Seasonal swamp forest with palms.	A mix of mesophyllous and sclerophyllous taxa. The structure of the forest is dependent on moisture demand and length of dry season – this determines the amount of deciduous taxa. Palms can be locally common.
TDFO	Tropical dry forest	Relatively low (5–10 m), occasionally tall (20 m) trees. Mixed forest, forming where the dry season leads to drought and plant water stress.	Extensive in central Brazil and central South America adjacent tropical rainforest. More fragmented in northwestern South America where free draining substrate leads to water-stress. Extends to mid altitudes, particularly within rain shadow areas. Extensive in western Central America and Mexico. Present on the Galápagos Islands.	Andean xerophytic bush, Cerrado, Campo rupestres, Campo cerrado (“campo” is more associated with grasslands). Cactus forest, Matorral, Deciduous xerophytic forest, Andean xerophytic bush, Espinar, Restinga dune forests, Thorn forest, Chaco.	Xeromorphic characteristic, particularly fire tolerant. For example, microphyllous leaves, thorns, deciduous leaves, thick bark, stomata often present along lines. Drought adapted taxa are common, e.g. tree cacti ( <i>Opuntia</i> and <i>Jasminocerus</i> ) with dense undergrowth of shrubs and herbs.
WTRF	Warm temperate rainforest	Evergreen closed forest, of relatively low stature (<20 m) with tall emergent trees (>25 m). Not tolerant of freezing. A transitional forest type between lowland and higher altitude forms (1000–2500 m).	Extending along the Andes at mid to low elevations (500–2000 m). Present at slightly lower elevations in eastern Brazilian highlands (<1000 m).	Lower montane forest, Moist lower montane forest, Submontane forest and <i>Araucaria</i> -dominated forest also with <i>Podocarpus</i> .	A mix of mesophyllous and sclerophyllous taxa constrained by altitude and length of dry season. Palms and tree ferns can be locally common.
WEFO	Warm-temperate evergreen broadleaf forest	Evergreen semi-closed forest with tall emergent trees (>30 m). Not tolerant of freezing.	Present within a relatively restricted range and along the Andes, particularly present from 1000–2000 m.	Andean forest, Transitional Andean forest, Upper Andean forest.	A mix of mesophyllous and sclerophyllous taxa. Tree ferns can be locally common.



**Table 2.** Continued.

Code	Biome	Definition	Main locations	Equivalent	Floristic characteristics
CTRF	Cool temperate rainforest	Medium height (<15 m) closed canopy forest with a dense under-story. Can tolerate freezing.	Predominant along western coast of southern South America extending to Patagonian steppe. Also present along the Andes at mid to high altitudes.	Patagonian rain forest, Temperate rain forest, Valdivian rain forest, Magallenic rain forest.	A mix of mesophyllous and sclerophyllous taxa. The structure can be quite variable depending on location – from dense forest to scrubby heath.
WAMF	Warm temperate mixed forest	Medium height (<15 m) open canopy with open under-story. Drought tolerant, semi fire-tolerant.	Mid to high altitudes of north Central America, in particular Mexico.	<i>Pinus</i> and <i>Quercus</i> -dominated forest.	Mixed evergreen forest dominated by sclerophyllous taxa that require warm for budburst.
COMI	Cool mixed forest	Short stature woodlands (<5 m) open canopy, open under-story forest. Frost tolerant.	High Andean shrub/dwarf tree forests, present close to the forest line	Upper montane forests, High Andean forest, Cloud forest.	Predominantly evergreen taxa with physiological adaptation to night frost, e.g. retaining old leaves for insulation.
CGSS	Cool grasslands	Common above the forest line of the Andes, dominated by tussock grasses and cushion plants.	Present only at the highest altitudes of the Andes	Puna, Heath, Cushion heath.	Poaceae-dominated cool grasslands with occasional cushion plants
STEP	Steppe	Dominated by grasses, occasional shrubs and steppe herbs. Profuse flowering during the wet season	Extensive in eastern Argentina, present in lowland Central America and northeast Brazil.	Steppe grasslands, Campo limpo, Pampa.	Grasses and chenopods forming low altitude warm grasslands.
DESE	Desert	Open semi-arid to arid vegetation.	Coastal Peru and Chile and western Mexico.	Coastal desert.	Occurrence of CAM-plants, cacti and succulents.
CGSH	Cool grass shrublands	Tropic-alpine environments, common above the forest line of the Andes. A mixture of tussock grasses and cold-adapted shrubs.	Present from extreme southern South America, on Tierra del Fuego above the forest line of Andes (2800–4000 m).	Páramo, Subpáramo, Magallenic moorland, Paramillo, Vegas.	Poaceae-dominated cool grasslands with numerous tussock forming grass. Also present are shrubs, e.g. <i>Empetrum</i> , <i>Espeletia</i> and <i>Puya</i> .

rain forest biome is present in three main areas: Amazonia, linear strips along the Atlantic coast and northeast South America extending into Central America. Forest associated with highland areas is divided into three biomes: warm evergreen forest, cool temperate rain forest and cool mixed forest (Fig. 4). Warm evergreen forest is most extensive along the lowland Andes, adjacent to the tropical rain forest. Cool mixed forest has a more restricted distribution, occupying a highland position until temperature becomes limiting for a number of taxa. Warm mixed forest is characterised by a mix of *Pinus* and *Quercus* species and is mainly restricted

to Central America. The desert biome is restricted to coastal Peru, due to the Pacific Ocean anticyclone, this area receives very little moisture.

## 2 Methods

### 2.1 Data sources

Over the past five decades researchers have collected numerous pollen-based records from lakes and bogs (Table 3)



Table 3. Continued.

Site	Country	Long.	Latitude	Alt.	Age range	Present biome	Sample type	RC	DC at 6000 yr BP	DC at 18 000 yr BP	Data type	Analyst	Site publications
Pedro Luro	Argentina	-62.53	-39.50	20	Modern	STEP	Soil	-	-	-	Raw	Schäbitz, F.	Schäbitz (1994)
Origone	Argentina	-62.43	-39.08	20	Modern	STEP	Soil	-	-	-	Raw	Schäbitz, F.	Schäbitz (1994)
Gaviotas	Argentina	-63.65	-39.07	90	Modern	TDFO	Soil	-	-	-	Raw	Schäbitz, F.	Schäbitz (1994)
Salina Anzotegui	Argentina	-63.77	-39.06	-5	0–10 360	STEP	Playa	5	3D	-	Raw	Schäbitz, F.	Schäbitz (1994)
Cueva Haichol	Argentina	-70.66	-38.58	1050	200–6890	STEP	Cave	2	1C	-	Raw	Markgraf, V.	Markgraf (1988)
Arroyo Sauce Chico	Argentina	-62.23	-38.07	85	Modern	STEP	Soil	-	-	-	Raw	Prieto, A. R.	Prieto (1996)
Cerro La China	Argentina	-58.64	-37.84	200	0–10 500	STEP	Soil	2	4C	-	Raw	Prieto, A. R.	Prieto and Páez (1989); Páez and Prieto (1993)
Empalme Querandíes	Argentina	-60.65	-37.00	105	0–15 000	STEP	Lake	8	2C	-	Raw	Prieto, A. R.	Prieto (1996)
Veranada Pelan	Argentina	-70.38	-36.88	1860	0–10 890	CGSH	Mire	3	3C	-	Raw	Schäbitz, F.	Schäbitz (1989)
Vaca Lauquen	Argentina	-71.08	-36.83	1450	0–11 260	CTRF	Mire	3	1C	-	Raw	Markgraf, V.	Markgraf (1987)
Veranada Vulkanpíckel	Argentina	-70.41	-36.68	2800	0–7790	CGSH	Mire	1	7D	-	Raw	Schäbitz, F.	Schäbitz (1989)
Salado	Argentina	-69.75	-35.33	3200	20–4330	CGSH	Mire	2	-	-	Raw	Markgraf, V.	Markgraf (1983)
Salina 2	Argentina	-69.33	-32.25	2000	100–6510	CGSH	Mire	2	1C	-	Raw	Markgraf, V.	Markgraf (1983)
Serra do Rio Rastro	Brazil	-49.55	-28.55	1420	800–11 180	WTRF	Mire	3	2C	-	Raw	Behling, H.	Behling (1993); Behling (1997a, b)
Morro da Igreja	Brazil	-49.86	-28.18	1800	0–10 390	WTRF	Mire	2	-	-	Raw	Behling, H.	Behling (1993); Behling (1997a, b)
Serra da Boa Vista	Brazil	-49.15	-27.70	1160	0–14 000	WTRF	Mire	4	2C	-	Raw	Behling, H.	Behling (1993); Behling (1997a, b)
Rano Kao	Chile	-109.43	-27.18	110	0–1360	TDFO	Lake	2	-	-	Raw	Flenley, J.	Flenley and King (1984); Flenley et al. (1991)
Rano Raraku Bore 3	Chile	-109.28	-27.16	75	0–35 260	TDFO	Lake	10	4C	4C	Raw	Flenley, J.	Flenley and King (1984); Flenley et al. (1991)
Rano Aroui	Chile	-109.40	-27.08	425	0–37 600	TDFO	Lake	11	2C	6C	Raw	Flenley, J.	Flenley and King (1984)
Poço Grande	Brazil	-48.86	-26.41	10	0–4840	WTRF	Section	4	-	-	Raw	Behling, H.	Behling (1993); Behling (1997a, b)
Reserva Volta Velha	Brazil	-48.38	-26.04	0	Modern	WTRF	Trap	-	-	-	Digi	Behling, H.	Behling et al. (1997)
Atlantic	Brazil	-48.35	-25.95	200	Modern	WTRF	Trap	-	-	-	Raw	Behling, H.	Behling et al. (1997)
Colombo	Brazil	-49.23	-25.33	920	Modern	TSFO	Trap	-	-	-	Raw	Behling, H.	Behling et al. (1997)
Serra Campos Gerais	Brazil	-50.21	-24.66	1200	0–12 480	WTRF	Mire	4	3C	-	Raw	Behling, H.	Behling (1997a)
Aguilar	Argentina	-65.75	-23.83	4000	0–9830	CGSH	Mire	3	2C	-	Raw	Markgraf, V.	Markgraf (1985)
Rio da Curuá	Brazil	-48.83	-23.83	800	0–7500	WTRF	Lake	4	-	-	Raw	Behling, H.	Behling et al. (1997)
Tumbre 2	Chile	-67.78	-23.31	3880	241–7500	CGSH	Lake	3	2C	-	Raw	Graf, K.	Graf (1992)
Agua Calientes	Chile	-67.42	-23.08	4210	0–6400	CGSH	Mire	1	7D	-	Raw	Graf, K.	Graf (1992)
Botucatu	Brazil	-48.00	-23.00	700	Modern	WTRF	Soil	-	-	-	Raw	Behling, H.	Behling (2009)
Curcuab	Brazil	-48.00	-23.00	700	Modern	WTRF	Soil	-	-	-	Raw	Behling, H.	Behling (2009)
Lagoa da Caço	Brazil	-43.43	-22.97	5	3000–20 000	TDFO	Lake	14	1C	-	Raw	Behling, H.	Ledru et al. (2001)
Morro de Itapeva	Brazil	-45.63	-22.78	1850	0–35 010	WTRF	Lake	9	4C	-	Raw	Behling, H.	Behling (1997b)
Assis	Brazil	-50.50	-22.68	540	Modern	TSFO	Soil	-	-	-	Raw	Behling, H.	Behling (2009)
Lagoa Santa	Brazil	-47.45	-22.36	630	Modern	WTRF	River	-	-	-	Digi	Parizzi, M. G.	Salgado-Labouriau et al. (1998)
Bauru	Brazil	-49.07	-22.32	570	Modern	TSFO	Soil	-	-	-	Raw	Behling, H.	Behling (2009)
Brotas	Brazil	-48.08	-22.29	700	Modern	WTRF	Soil	-	-	-	Raw	Behling, H.	Behling (2009)
Salitre	Brazil	-46.78	-19.00	1050	0–50 000	WTRF	Lake	14	1C	7C	Raw	Ledru, M.-P.	Ledru (1992, 1993); Ledru et al. (1994, 1996)
Ajata	Chile	-69.20	-18.25	4700	0–1460	CGSH	Mire	1	-	-	Raw	Graf, K.	Graf (1992)
Sajama	Bolivia	-68.88	-18.16	4250	0–4400	CGSH	Lake	9	-	-	Raw	Graf, K.	Graf (1992)
Lago do Pires	Brazil	-42.21	-17.95	390	0–9720	TSFO	Lake	7	1C	-	Raw	Behling, H.	Behling (1993); Behling (1997a, b)
Wasa Mayu	Bolivia	-65.91	-17.54	2720	1000–31 000	COMI	Lake	1	7D	7D	Raw	Graf, K.	Graf (1992)
Crominia	Brazil	-49.45	-17.28	200	0–32 200	TDFO	Palm swamp	5	2C	1D	Digi	Salgado-Labouriau, M. L.	Salgado-Labouriau et al. (1998)
Mt. Blanco	Bolivia	-67.35	-17.02	4780	1250–7500	CGSH	Lake	7	1C	-	Raw	Graf, K.	Graf (1992)
Lake Huinámimarca	Bolivia	-69.00	-16.50	3765	0–25 000	CSGH	Lake	48	1C	3C	Digi	Mourguiart, P. H.	Mourguiart et al. (1995); Argollo and Mourguiart (2000)
Cerro Calvario	Bolivia	-68.50	-16.50	3950	0–8360	CGSH	Mire	4	1C	-	Raw	Graf, K.	Graf (1992)
Rio Kaluyo	Bolivia	-68.13	-16.43	4070	130–9920	CGSH	Lake	3	3C	-	Raw	Graf, K.	Graf (1992)
Chacaltaya 1	Bolivia	-68.13	-16.36	4750	80–7400	CGSH	Mire	1	1C	-	Raw	Graf, K.	Graf (1992)
Cumre Unduavi	Bolivia	-68.03	-16.33	4620	0–9200	CGSH	Mire	6	3C	-	Raw	Graf, K.	Graf (1992)
Rio Jequitinhonha	Brazil	-38.92	-15.85	80	Modern	TDFO	River	-	-	-	Raw	Behling, H.	Behling et al. (2000)
Brasília 1	Brazil	-47.66	-15.59	1030	Modern	TDFO	Soil	-	-	-	Raw	Behling, H.	Behling (2009)
Aguads Emendadas	Brazil	-47.58	-15.56	200	0–28 000	TDFO	Palm swamp	6	7C	7D	Digi	Salgado-Labouriau, M. L.	Salgado-Labouriau et al. (1998)
Cuiaba	Brazil	-55.86	-15.35	350	Modern	TDFO	Soil	-	-	-	Raw	Behling, H.	Behling (2009)
Amarete	Bolivia	-68.98	-15.23	4000	0–9160	CGSH	Mire	2	5D	-	Raw	Graf, K.	Graf (1992)
Cotapampa	Bolivia	-69.11	-15.21	4450	0–9560	CGSH	Mire	5	2C	-	Raw	Graf, K.	Graf (1992)
Katantica	Bolivia	-69.18	-14.8	4820	50–7720	CGSH	Mire	3	1C	-	Raw	Graf, K.	Graf (1992)
Laguna Chaplin	Bolivia	-61.05	-14.50	750	0–40 000	TSFO	Lake	14	2C	1D	Digi	Mayle, F.	Mayle et al. (2000)
Rio de Contas	Brazil	-39.00	-14.28	80	Modern	TDFO	River	-	-	-	Raw	Behling, H.	Behling et al. (2000)
Laguna Bella Vista	Bolivia	-61.56	-13.58	750	0–55 000	TSFO	Lake	15	2C	1D	Digi	Mayle, F.	Mayle et al. (2000)
Laguna Jeronimo	Peru	-75.21	-11.78	4450	0–11 260	CGSH	Lake	4	4C	-	Raw	Hansen, B. C. S.	Hansen et al. (1994)

Table 3. Continued.

Site	Country	Long.	Latitude	Alt.	Age range	Present biome	Sample type	RC	DC at 6000 yr BP	DC at 18 000 yr BP	Data type	Analyst	Site publications
Laguna Pomacocha	Peru	-75.50	-11.75	4450	4100–10 220	CGSH	Lake	4	1C	–	Raw	Hansen, B. C. S.	Hansen et al. (1994)
Laguna Paca	Peru	-75.50	-11.71	3600	0–5410	CGSH	Lake	1	4D	–	Raw	Hansen, B. C. S.	Hansen and Rodbell (1995)
Laguna Tuctua	Peru	-75.00	-11.66	4250	0–11 390	CGSH	Lake	4	2C	–	Raw	Hansen, B. C. S.	Hansen et al. (1994)
Laguna Milloc	Peru	-76.35	-11.56	4325	280–11 050	CGSH	Lake	1	3C	–	Raw	Graf, K.	Graf (1992)
Laguna Junin2	Peru	-76.18	-11.00	4100	0–43 000	CGSH	Lake	11	6C	1C	Raw	Hansen, B. C. S.	Hansen and Rodbell (1995)
Laguna Huatacocha	Peru	-76.55	-10.76	4500	0–10 620	CGSH	Lake	5	2C	–	Raw	Hansen, B. C. S.	Hansen and Rodbell (1995)
Rio São Francisco	Brazil	-43.00	-10.46	400	0–11 500	TDFO	River	6	1C	–	Digi	De Oliveira, P. E.	De Oliveira et al. (1999)
Saquinho	Brazil	-43.23	-10.44	480	0–11 000	TSFO	Mire	6	1C	–	Digi	De Oliveira, P. E.	De Oliveira et al. (1999)
Rio São Francisco	Brazil	-36.50	-10.26	80	Modern	TDFO	River	–	–	–	Raw	Behling, H.	Behling et al. (2000)
Katira	Brazil	-63.00	-9.00	750	0–60 000	TDFO	Lake	4	7D	1D	Digi	van der Hammen, T.	van der Hammen and Absy (1994)
Campina Grande I	Brazil	-35.75	-7.23	70	Modern	TSFO	Soil	–	–	–	Raw	Behling, H.	Behling et al. (2000)
Lagoa Grande	Brazil	-47.45	-7.08	75	Modern	TDFO	Lake	–	–	–	Raw	Behling, H.	Behling et al. (2000)
Picos	Brazil	-41.40	-7.06	70	Modern	TDFO	Soil	–	1D	1D	Raw	Harbele, S.	Behling et al. (2000)
Lago Bolim	Brazil	-35.18	-6.04	90	Modern	TDFO	Lake	–	–	–	Raw	Behling, H.	Behling et al. (2000)
Rio Protengi	Brazil	-35.25	-5.78	80	Modern	TDFO	River	–	–	–	Raw	Behling, H.	Behling et al. (2000)
Mirim	Brazil	-35.30	-5.68	70	Modern	TDFO	Soil	–	1D	7D	Raw	Ledru, M.-P.	Behling et al. (2000)
Rio Mirim	Brazil	-35.40	-5.64	70	Modern	TDFO	River	–	–	–	Raw	Behling, H.	Behling et al. (2000)
Rio (unclear)	Brazil	-38.00	-5.50	50	Modern	TDFO	River	–	–	–	Raw	Behling, H.	Behling et al. (2000)
Carajas	Brazil	-48.00	-5.00	150	0–20 000	TSFO	Lake	8	2C	6C	Digi	Absy, M. L.	Absy et al. (1991)
Ciudad Universitaria X	Colombia	-74.18	-4.75	2560	0–>35 000	COMI	Lake	4	4C	7D	Raw	van der Hammen, T.	van der Hammen and González (1960)
Rio Jaguaribe II	Brazil	-37.76	-4.55	50	Modern	TDFO	River	–	–	–	Raw	Behling, H.	Behling et al. (2000)
Rio Jaguaribe I	Brazil	-37.75	-4.43	50	Modern	TDFO	River	–	–	–	Raw	Behling, H.	Behling et al. (2000)
Lake Surucucho	Ecuador	-78.95	-3.75	970	0–12 000	WTRF	Lake	9	4C	–	Digi	Colinvaux, P.	Colinvaux et al. (1997)
Ayauch	Ecuador	-78.13	-2.09	550	0–7500	WTRF	Lake	4	2C	–	Digi	Bush, M.	Bush et al. (1990); Bush and Colinvaux (1988); Colinvaux et al. (1988)
Llaviucu	Ecuador	-79.43	-1.83	3120	Modern	CTRF	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Kumpack	Ecuador	-78.51	-1.53	700	Modern	WTRF	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Indanza	Ecuador	-78.83	-1.53	2100	Modern	CTRF	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Comprida	Brazil	-53.15	-1.5	130	0–7200	TRFO	Lake	5	1C	–	Digi	Bush, M.	Bush et al. (2000)
Geral	Brazil	-53.00	-1.5	130	0–6000	TRFO	Lake	2	1C	–	Digi	Bush, M.	Bush et al. (2000)
Puyo Bog	Ecuador	-79.06	-1.43	953	Modern	WTRF	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Rum Tum	Ecuador	-79.03	-1.13	2392	Modern	CTRF	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Yambo	Ecuador	-79.03	-1.03	2600	Modern	CTRF	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Lago Crispim	Brazil	-48.00	-0.8	0	0–9000	TRFO	Lake	4	1C	–	Raw	Behling, H.	Behling et al. (1997)
Lagoa da Curuça2	Brazil	-47.85	-0.76	35	0–9440	TRFO	Lake	4	2C	–	Raw	Behling, H.	Behling (1996)
Maríname-II	Colombia	-72.03	-0.66	160	0–5000	TRFO	Lake	5	1C	–	Raw	Behling, H.	Behling et al. (1999)
Monica-1	Colombia	-72.50	-0.60	160	0–12 000	TRFO	Lake	3	2C	–	Raw	Behling, H.	Behling et al. (1999)
Añangucocha	Ecuador	-77.03	-0.53	280	Modern	TRFO	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Limoncococha	Ecuador	-76.66	-0.38	230	0–1300	TRFO	Lake	2	–	–	Digi	Colinvaux, P.	Colinvaux et al. (1988)
Cayambe	Ecuador	-78.03	-0.03	4350	0–5200	CGSH	Mire	6	4D	–	Raw	Graf, K.	Graf (1989, 1992)
Cuyabeno	Ecuador	-77.01	0	280	Modern	TRFO	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Lago Agrio	Ecuador	-77.03	0.03	330	Modern	TRFO	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990); Colinvaux et al. (1988)
San Marcos	Ecuador	-79.03	0.03	3400	Modern	CGSH	Mire	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Santa Cecilia	Ecuador	-77.03	0.04	330	Modern	TRFO	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Lake Santa Cecilia	Ecuador	-77.02	0.06	330	0–1000	TRFO	Lake	2	–	–	Digi	Colinvaux, P.	Colinvaux et al. (1988); Bush et al. (1990)
Cunro	Ecuador	-79.03	0.08	2800	Modern	CTRF	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Mera	Ecuador	-76.92	0.11	1100	Modern	WTRF	Lake	–	–	–	Digi	Bush, M.	Bush et al. (1990)
Yaguara cocha	Ecuador	-79.03	0.13	2210	Modern	CTRF	Lake	–	–	–	Raw	Bush, M.	Bush et al. (1990)
La Pata	Brazil	-66.66	0.25	300	0–45 000	TRFO	Lake	12	2C	1D	Digi	Colinvaux, P.	Colinvaux et al. (1996); Colinvaux et al. (2000)
Lagoa das Patas	Brazil	-66.68	0.26	300	0–42 210	TFFO	Lake	16	1D	1C	Raw	De Oliveira, P. E.	De Oliveira (1992)
Piusbi	Colombia	-77.89	1.66	200	0–10 400	TRFO	Lake	3	1C	–	Raw	Behling, H.	Behling and Hooghiemstra (1999)
Pitalito	Colombia	-76.50	1.75	1300	0–7350	WEFO	Mire	6	6D	–	Raw	Bakker, J. G. M.	van der Hammen et al. (1980)

Table 3. Continued.

Site	Country	Long.	Latitude	Alt.	Age range	Present biome	Sample type	RC	DC at 6000 yr BP	DC at 18 000 yr BP	Data type	Analyst	Site publications
Piagua	Colombia	-76.50	2.30	1700	0–14 000	WEFO	Lake	7	7D	–	Raw	Wille, M.	Wille et al. (2001); van der Hammen et al. (1980)
Pantano de Genagra	Colombia	-76.50	2.50	1750	0–9000	WEFO	Mire	7	4C	–	Raw	Behling, H.	Behling et al. (1999); van der Hammen et al. (1980)
Rio Timbio	Colombia	-76.50	2.50	1750	0–14 000	WEFO	Lake	6	2C	–	Raw	Wille, M.	van der Hammen et al. (1980)
El Caimito	Colombia	-76.60	2.53	50	0–4500	TRFO	Lake	4	–	–	Raw	Wille, M.	Wille et al. (1999)
Loma Linda	Colombia	-73.35	3.22	310	0–8720	TDFO	Lake	8	1C	–	Raw	Behling, H.	Behling et al. (1999)
Lago Agua Sucia	Colombia	-73.54	3.46	260	0–15 340	TDFO	Lake	4	7D	–	Raw	Wijnstra, T. A.	Wijnstra and van der Hammen (1966)
El Gobernador	Colombia	-75.00	3.95	3815	0–10 050	CTRF	Mire	2	2C	–	Raw	Melief, A. B. M.	Melief (1985)
La Guitarra	Colombia	-74.28	4.00	3450	0–15 300	COMI	Mire	3	4C	–	Raw	Melief, A. B. M.	Melief (1985)
La Primavera	Colombia	-74.13	4.00	3525	0–11 200	CGSH	Mire	6	1C	–	Raw	Melief, A. B. M.	Melief (1985)
Corazón Partido	Colombia	-74.25	4.00	4100	Modern	CGSH	Mire	–	–	–	Raw	Melief, A. B. M.	Melief (1985)
El Trinagulo	Colombia	-74.25	4.00	4100	Modern	CGSH	Mire	–	–	–	Raw	Melief, A. B. M.	Melief (1985)
Carimagua	Colombia	-74.14	4.04	180	0–8270	TDFO	Lake	6	2C	–	Raw	Behling, H.	Behling and Hooghiemstra (1999)
La Rabona	Colombia	-74.25	4.05	4000	0–5100	CGSH	Mire	1	4D	–	Raw	Melief, A. B. M.	Melief (1985)
El Piñal	Colombia	-70.40	4.09	185	0–19 000	TDFO	Lake	8	4C	2D	Raw	Behling, H.	Behling and Hooghiemstra (1999)
Alsacia	Colombia	-74.11	4.09	3100	0–13 700	COMI	Mire	3	6D	–	Raw	Melief, A. B. M.	Melief (1985)
Andabobos	Colombia	-74.15	4.09	3570	0–15 000	CGSH	Mire	2	7D	–	Raw	Melief, A. B. M.	Melief (1985)
Ubaqué	Colombia	-73.55	4.33	2000	Modern	WEFO	Lake	–	–	–	Raw	Jean-Jacob, K.	Wille et al. (2001); van der Hammen et al. (1980)
de la América	Colombia	-74.00	4.33	3550	0–9000	CGSH	Mire	1	1D	–	Raw	Kuhry, P.	Kuhry (1988); van der Hammen and González (1960)
Turbera de Calostros	Colombia	-73.48	4.41	3730	Modern	CGSH	Soil	1	–	–	Raw	Salomons, J. B.	van der Hammen et al. (1980)
Laguna Angel	Colombia	-70.54	4.45	205	0–10 026	TDFO	Lake	8	2C	–	Raw	Behling, H.	Behling and Hooghiemstra (1998)
Libano	Colombia	-75.50	4.50	1820	0–14 000	WEFO	Soil	1	7D	–	Raw	Salomons, J. B.	van der Hammen et al. (1980)
de Pedro Palo III	Colombia	-74.41	4.50	2000	0–5500	COMI	Lake	2	7D	–	Raw	van der Hammen, T.	van der Hammen (1974)
Paramo Palacio	Colombia	-73.88	4.76	3550	0–5500	CGSH	Mire	4	5D	–	Raw	van der Hammen, T.	van der Hammen and González (1960)
Greja	Colombia	-73.70	4.86	4000	0–12 000	CGSH	Lake	2	3C	–	Raw	van der Hammen, T.	van der Hammen (1962)
Sardinas	Colombia	-69.45	4.95	180	0–11 600	TDFO	Lake	6	2C	–	Raw	Behling, H.	Behling and Hooghiemstra (1998)
Herrera	Colombia	-73.91	5.00	2000	0–20 000	COMI	Lake	3	4D	–	Raw	van Geel, B.	van Geel and van der Hammen (1973)
Agua Blanca	Colombia	-74.45	5.0	3250	0–46 000	COMI	Mire	2	6D	7D	Raw	Kuhry, P.	Graf (1992); Kuhry (1988b); Kuhry et al. (1983)
El Abra II	Colombia	-73.96	5.02	2570	0–11 000	COMI	Cave	1	7D	–	Raw	Schreve-Brinkman, E. J.	Schreve-Brinkman (1978)
Paramo de Peña Negra	Colombia	-74.09	5.09	3625	0–12 500	CGSH	Mire	10	2C	–	Raw	Kuhry, P.	Kuhry et al. (1983)
ODP site 932	Brazil	-47.03	5.18	0	0–45 000	TRFO	Fan	2	2C	1D	Raw	Haberle, S.	Haberle and Maslin (1999)
Paramo de Laguna Verde	Colombia	-74.00	5.25	3625	0–5500	CGSH	Mire	2	4D	–	Raw	Kuhry, P.	Kuhry et al. (1983)
Fúquene II	Colombia	-73.87	5.50	2580	0–25 000	COMI	Lake	2	7D	7C	Raw	van Geel, B.	van Geel and van der Hammen (1973)
Jotaordó	Colombia	-76.66	5.66	50	0–4200	TRFO	Lake	7	–	–	Raw	Berrio, J. C. B.	Berrio et al. (2000)
Ciénaga del Visitador	Colombia	-72.83	6.13	3300	0–12 000	COMI	Mire	2	7D	–	Raw	van der Hammen, T.	van der Hammen and González (1965)
Bobos	Colombia	-72.85	6.13	3800	0–5000	CGSH	Lake	4	6D	–	Raw	van der Hammen, T.	van der Hammen (1962)
Ciega I	Colombia	-72.31	6.50	3510	0–2000	COMI	Lake	1	–	–	Raw	van der Hammen, T.	van der Hammen et al. (1980)
Valle de Lagunillas	Colombia	-72.34	6.50	3880	0–7100	CGSH	Lake	8	7D	–	Raw	van der Hammen, T.	van der Hammen et al. (1980)
Cana, Darien	Panama	-77.58	7.68	1000	Modern	TSFO	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Cana Swamp	Panama	-77.59	7.74	500	0–4600	TRFO	Swamp	5	–	–	Digi	Bush, M.	Bush and Colinvaux (1994)
Wodehouse Swamp	Panama	-77.58	7.75	500	0–4200	TRFO	Swamp	1	–	–	Digi	Bush, M.	Bush and Colinvaux (1994)
La Chonta	Costa Rica	-82.00	8.00	2310	0–80 000	CTRF	Lake	3	2C	7D	Digi	Islebe, G.	Hooghiemstra et al. (1992); Islebe and Hooghiemstra (1997); Islebe et al. (1995a, b)

Table 3. Continued.

Site	Country	Long.	Latitude	Alt.	Age range	Present biome	Sample type	RC	DC at 6000 yr BP	DC at 18 000 yr BP	Data type	Analyst	Site publications
El Valle	Panama	-79.78	8.43	500	0–20 000	TSFO	Lake	5	–	2C	Digi	Bush, M.	Bush (1995); Bush and Rivera (1998); Piperno et al. (1991a, b)
La Yeguada	Panama	-80.78	8.43	650	0–14 000	TSFO	Lake	11	1C	–	Digi	Bush, M.	Bush (1995); Bush et al. (1992); Bush and Rivera (1998); Piperno et al. (1991a, b)
Cerro Campana	Panama	-79.93	8.63	800	Modern	WTFO	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Quebrada Nelson	Panama	-82.31	8.66	1130	Modern	WTRF	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Laguna Volcán	Panama	-82.75	8.75	1500	0–2860	WTRF	Lake	4	–	–	Digi	Behling, H.	Behling (2000)
Valle Laguna Negra	Venezuela	-70.76	8.79	3450	0–3350	CGSH	Lake	1	–	–	Raw	Graf, K.	Rull et al. (1987)
Valle Laguna Victoria	Venezuela	-70.79	8.80	3250	0–12 210	CGSH	Lake	4	4C	–	Raw	Graf, K.	Rull et al. (1987)
Horsefly Ridge	Panama	-82.24	8.83	1150	Modern	WTRF	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
El Bosque	Colombia	-75.45	8.85	3650	0–4700	CGSH	Mire	4	–	–	Raw	Melief, A. B. M.	Kuhry (1988a); Melief (1985)
Volcan Baru	Panama	-82.52	8.85	2600	Modern	CTRF	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Finca Lerida	Panama	-82.45	8.87	1630	Modern	WTRF	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Volcan Irazu	Panama	-82.52	8.88	2300	Modern	CTRF	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Paramo de Miranda	Venezuela	-70.85	8.91	3290	310–11 470	CGSH	Mire	3	4C	–	Raw	Salgado-Labouriau, M. L.	Salgado-Labouriau (1988, 1991)
Panama	Panama	-80.87	9.00	100	0–7200	TSRO	Lake	8	1C	–	Raw	Leyden, B. W.	Leyden et al. (1995)
Ocelot Pond	Panama	-79.59	9.12	20	Modern	TSFO	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Soberania	Panama	-79.66	9.13	20	Modern	TSFO	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Paramo Piedras Blancas	Venezuela	-70.83	9.16	4080	0–1340	CGSH	Mire	2	–	–	Raw	Salgado-Labouriau, M. L.	Rull et al. (1987)
Pipeline Rd	Panama	-79.66	9.33	40	Modern	TSFO	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Barro Colorado Island	Panama	-79.75	9.35	50	Modern	TSFO	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Lago Chirripó	Costa Rica	-83.48	9.48	3520	Modern	CTRF	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Talamancas	Costa Rica	-83.72	9.5	2500	Modern	CTRF	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Lago de las Morrenas	Costa Rica	-83.49	9.50	3480	0–10 000	CTRF	Lake	6	2C	–	Digi	Horn, S. P.	Horn (1993)
Bog 70	Costa Rica	-83.85	9.61	2670	Modern	CTRF	Bog	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Tres de Junio	Costa Rica	-83.87	9.62	2670	Modern	CTRF	Bog	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Bog 68	Costa Rica	-83.85	9.64	2670	Modern	CTRF	Bog	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Asuncion	Costa Rica	-83.75	9.64	3340	Modern	CTRF	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Carara Biological Reserve	Costa Rica	-84.62	9.73	0	Modern	TSFO	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Quebrador	Costa Rica	-83.84	9.74	3040	Modern	CTRF	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Cataracta, Carara 1	Costa Rica	-84.63	9.83	270	Modern	TSFO	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Cataracta, Carara 2	Costa Rica	-84.63	9.85	270	Modern	TSFO	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Carara	Costa Rica	-84.60	9.88	35	Modern	TSFO	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Laguna Bonilla	Costa Rica	-83.61	9.99	380	Modern	TSFO	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Laguna Barva	Costa Rica	-84.11	10.14	2840	Modern	CTRF	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Laguna Palmita	Costa Rica	-84.95	10.18	60	Modern	TDFO	Soil	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Laguna Botos	Costa Rica	-84.18	10.18	2600	Modern	CTRF	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Bosque Alegre	Costa Rica	-84.21	10.21	740	Modern	WTRF	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Laguna González	Costa Rica	-84.45	10.25	710	Modern	WTRF	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Laguna Congo	Costa Rica	-84.29	10.27	740	Modern	WTRF	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Laguna Hule	Costa Rica	-84.19	10.27	740	Modern	WTRF	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Laguna María Aguilar	Costa Rica	-84.18	10.27	770	Modern	WTRF	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)
Brauillo Carillo, Heredia	Costa Rica	-83.94	10.3	630	Modern	WTRF	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Monteverde, Heredia	Costa Rica	-84.8	10.3	1500	Modern	WTRF	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Volcan Poas	Costa Rica	-84.19	10.3	2580	Modern	CTRF	Pollster	–	–	–	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Lake Valencia	Venezuela	-67.75	10.32	403	400–13 000	STEP	Lake	28	1C	–	Raw	Leyden, B. W.	Bradbury et al. (1981); Leyden (1985)
Laguna Río Cuarto	Costa Rica	-84.18	10.34	380	Modern	WTRF	Lake	–	–	–	Digi	Horn, S. P.	Rodgers and Horn (1996)

Table 3. Continued.

Site	Country	Long.	Latitude	Alt.	Age range	Present biome	Sample type	RC	DC at 6000 yr BP	DC at 18 000 yr BP	Data type	Analyst	Site publications
La Selva, Heredia	Costa Rica	-84.00	10.43	80	Modern	TSFO	Pollster	-	-	-	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Cantarrana Swamp	Costa Rica	-84.00	10.45	36	Modern	TRFO	Swamp	-	-	-	Digi	Horn, S. P.	Rodgers and Horn (1996)
La Pacifica, Guanacaste	Costa Rica	-85.11	10.45	110	Modern	TSFO	Pollster	-	-	-	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Sendro Sedro Swamp	Costa Rica	-84.00	10.46	40	Modern	TRFO	Swamp	-	-	-	Digi	Horn, S. P.	Rodgers and Horn (1996)
Laguna La Palma	Costa Rica	-84.73	10.49	570	Modern	WTRF	Lake	-	-	-	Digi	Horn, S. P.	Rodgers and Horn (1996)
Laguna Cedeño	Costa Rica	-84.71	10.49	610	Modern	WTRF	Lake	-	-	-	Digi	Horn, S. P.	Rodgers and Horn (1996)
Tortuguero	Costa Rica	-83.53	10.53	0	Modern	TSFO	Pollster	-	-	-	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Santa Rosa2	Costa Rica	-85.64	10.83	0	Modern	TSFO	Soil	-	-	-	Digi	Horn, S. P.	Rodgers and Horn (1996)
Santa Rosa1	Costa Rica	-85.66	10.84	0	Modern	TRFO	Soil	-	-	-	Digi	Horn, S. P.	Rodgers and Horn (1996)
Boca de Lopez	Colombia	-75.36	10.85	0	0–4000	TRFO	Coastal	5	-	-	Raw	van der Hammen, T.	Behling et al. (1999)
Cafetal, Guanacaste	Costa Rica	-85.65	10.85	300	Modern	TSFO	Pollster	-	-	-	Raw	Bush, M.	Bush (1995); Bush and Rivera (1998)
Santa Rosa3	Costa Rica	-85.62	10.86	280	Modern	TSFO	Soil	-	-	-	Digi	Horn, S. P.	Rodgers and Horn (1996)
Santa Rosa4	Costa Rica	-85.62	10.86	280	Modern	TSFO	Soil	-	-	-	Digi	Horn, S. P.	Rodgers and Horn (1996)
Escondido	Costa Rica	-85.61	10.87	280	Modern	TSFO	Lake	-	-	-	Digi	Horn, S. P.	Rodgers and Horn (1996)
Volcán Cacao	Costa Rica	-85.47	10.92	1000	Modern	WTRF	Soil	-	-	-	Digi	Horn, S. P.	Rodgers and Horn (1996)
Sierra de Cuchumatanes5	Guatemala	-91.00	15.75	2800	Modern	WAMF	Polster	-	-	-	Digi	Islebe, G.	Islebe and Hooghiemstra (1995)
Sierra de Cuchumatanes4	Guatemala	-91.25	15.75	3000	Modern	CTRF	Polster	-	-	-	Digi	Islebe, G.	Islebe and Hooghiemstra (1995)
Sierra de Cuchumatanes3	Guatemala	-91.5	15.75	3400	Modern	CTRF	Polster	-	-	-	Digi	Islebe, G.	Islebe and Hooghiemstra (1995)
Sierra de Cuchumatanes2	Guatemala	-91.75	15.75	3600	Modern	WAMF	Polster	-	-	-	Digi	Islebe, G.	Islebe and Hooghiemstra (1995)
Sierra de Cuchumatanes1	Guatemala	-92.00	15.75	4200	Modern	CGSH	Polster	-	-	-	Digi	Islebe, G.	Islebe and Hooghiemstra (1995)
Lago Quexil	Guatemala	-89.88	16.92	110	0–27 500	TSFO	Lake	4	7D	-	Raw	Leyden, B. W.	Leyden (1984); Leyden et al. (1993, 1994)
Lake Peten-Itza	Guatemala	-90.00	17.25	200	0–9000	TDFO	Lake	7	2C	-	Digi	Islebe, G.	Islebe et al. (1996)
Lago Catemaco	Mexico	-95.00	18.66	340	0–2230	TRFO	Lake	5	2C	-	Raw	Byrne, A. R.	Byrne and Horn (1989)
Zempoala	Mexico	-99.30	19.20	3100	0–4600	WAMF	Lake	5	-	-	Raw	Almeida, L.	Almeida (1997)
Quila	Mexico	-99.20	19.30	2800	0–10 000	WAMF	Lake	4	3C	-	Raw	Almeida, L.	Almeida (1997)
Lake Texcoco	Mexico	-99.12	19.44	2330	0–35 000	WAMF	Lake	7	3C	4C	Digi	Lozano-García, S.	Lozano-García and Ortega-Guerrero (2009)
Chalco Lake	Mexico	-99.00	19.50	2240	8000–27 500	WAMF	Lake	8	3C	1C	Raw	Lozano-García, M. S.	Lozano-García and Ortega-Guerrero (1994); Lozano-García et al. (1993); Ortega-Guerrero (1992)
Lake Pátzcuaro	Mexico	-101.58	19.58	2044	20–44 100	WAMF	Lake	24	2C	6C	Raw	Watts, W. A.	Saporito (1975), Watts and Bradbury (1982)
San Jose Chulchaca	Mexico	-90.13	20.86	1	0–7300	TDFO	Lake	8	2C	-	Raw	Leyden, B. W.	Leyden et al. (1995)
Lake Coba	Mexico	-87.55	20.86	100	5880–19 230	WAMF	Playa	8	7D	2C	Raw	Leyden, B. W.	Leyden et al. (1998)

that have been used to unravel past vegetation changes in Latin America with ecosystem reconstructions now existing from all major vegetation types over the late Quaternary period. The Latin American Pollen Database (LAPD) ([www.ncdc.noaa.gov/paleo/lapd.html](http://www.ncdc.noaa.gov/paleo/lapd.html)) is an online resource used to collate these data and facilitated the systematic inter-operation presented here; indeed the majority of the pollen

data used here are available through the LAPD. Additional data were obtained from researchers working in Latin America; all active palynologists being given the opportunity to contribute data not currently lodged in the LAPD. Indeed, data from a number of sites in Argentina, Brazil, Costa Rica, México and Panama were made available specifically for this work. The majority of data from Colombia were prepared for

this analysis directly from the original count sheets and are in preparation for uploading to the LAPD.

The majority of the data used in our analysis are complete raw pollen counts, this permitted all pollen taxa recorded by the original analyst to be allocated to PFTs and allowed the integrity of the data to be maintained throughout the analysis. Application of raw pollen data in other regions has been shown to help in differentiating between biomes (Tarasov et al., 1998b). However, numerous pollen records are either not submitted to the LAPD, or, were not made available for this analysis. Rather than omitting these data, the pollen counts were digitised from published pollen diagrams (Table 3): digitising such data provides a spatially more complete reconstruction than available from presented archived data. The process of digitisation involved either back calculation of the pollen counts if information on the pollen sum was present; if the pollen sum was not available the pollen percentage diagram was used as a count of 100 and values for the pollen taxa were abstracted at the time intervals used for our analysis. This scenario of combining data from different formats comes with a number of caveats that can have bearing on the results, and their interpretation (Marchant and Hooghiemstra, 2001). Firstly, the sub-set of pollen taxa in a count used to construct published pollen diagrams, and pollen sums that comprise it, often result from the bias of individual researchers', particularly on what are the reliable indicator taxa for a particular area and range of different vegetation types under investigation. This issue is particularly crucial in Latin America where the large numbers of pollen taxa encountered in the original counting are rarely depicted on published pollen diagrams. Furthermore, the level of identification achieved within pollen analysis, to a generic or family level, commonly comprises species that can be found in a range of different vegetation types, ecologies and growth forms (Marchant et al., 2002c). The majority of the samples for the biomisation presented here are derived from sites close to the Andean spine. Primarily, this concentration reflects the sensitive response of the vegetation to climate change on the steep altitudinal gradients (Marchant et al., 2001b); the area forming an ideal location for palaeoecological research. Additionally, the comparative lack of data from the lowlands is fuelled by problems of access, suitable sites and strong river dynamics that commonly result in sedimentary hiatuses (Ledru, 1998). Because of the steep environmental gradients associated with 7000 m of altitudinal change found along the Andes this spatial bias did not reduce the number of biomes we were able to reconstruct, (Fig. 4). However, the concentration of sites did result in numerous assignments being mapped overlapping each other and hence the changes between the different time periods difficult to detect. To rectify this problem in addition to presenting the results on the traditional biome dot maps (Figs. 7, 8 and 9) results are presented for all sites in a table (Table 6) that has been ordered by altitude so one can see which biome has been reconstructed for each site, how this compares to the

potential vegetation and how it changes at each time period.

Uncalibrated radiocarbon dates available from the original stratigraphic analysis were used to select samples representing the time period used here. On a site-by-site basis, a linear age-depth model was applied to the pollen data. The validity of this model was assessed at each site taking into account sedimentary hiatuses and dating problems such as age reversals and dates with large standard errors; a summary of this dating control is provided in Table 1 following the COHMAP scheme (Webb, 1995; Yu and Harrison, 1999). Multiple samples ( $\leq 3$ ) were selected when more than one sample fell within the age range allowed for each time period. These data were compiled, to produce a site *vs* taxa matrix that was then checked to standardise nomenclature, e.g., the combined file contained many synonyms such as Gramineae and Poaceae, and *Mysine* and *Rapanea*. Synonymous taxa were combined using the nomenclature of Kewensis (1997) and the International Plant Names Index (IPNI) (2008). Aquatic and non-tree fern taxa were removed from the matrix as they commonly reflect local hydrological conditions rather than local climate envelope. Marker additions and exotic spikes such as *Lycopodium* were also removed.

A total of 381 samples from 287 locations derived from core tops ( $< 500$   $^{14}\text{C}$  yr BP), surface samples, pollen traps and moss polsters comprise the modern data set (Table 3). For the time period  $6000 \pm 500$   $^{14}\text{C}$  yr BP, 255 samples derived from 127 pollen records comprise the data set (Table 3). For the time period  $18\,000 \pm 1000$   $^{14}\text{C}$  yr BP, 61 samples derived from 34 pollen records comprise the data set (Table 3). The data sets to undergo analysis comprised 515 pollen taxa for the modern calibration, 493 for the  $6000$   $^{14}\text{C}$  yr BP reconstruction and 232 for the  $18\,000$   $^{14}\text{C}$  yr BP reconstruction. The taxonomic diversity of the Neotropical phytogeographical realm is greater than Africa [364] (Jolly et al., 1998a), Europe [41] (Prentice et al., 1996b), Russia and Mongolia [98] (Tarasov et al., 1998a) and China [68] (Yu et al., 1998), however this number will be biased by sampling intensity and density and some of these previous applications only focuses on the numerically important taxa.

## 2.2 Biomisation

Prentice et al. (1996a) and Prentice and Webb (1998) have documented the steps involved in the biomisation technique. First, a conceptual framework for PFTs and biomes in Latin American vegetation was developed by investigating the relationship between potential biomes and three environmental gradients. The environmental gradients considered were moisture availability ( $\alpha$ : Priestley-Taylor coefficient of plant available moisture), temperature (MTCO: mean temperature of the coldest month) and seasonal warmth (GDD: growing degree-days). Similarly to the biomes, but at a finer ecological resolution, the spatial distribution of PFTs is determined by environmental controls on plant growth form and ecological tolerance (Woodward, 1987). In Latin America the



dominant environmental gradients are temperature, primarily associated with altitude, moisture availability and seasonality. PFT definitions were modified from the classification originally developed for the BIOME 1 model (Prentice et al., 1992, 1996a, b) taking into account schemes developed for other regions, particularly those that abut the Latin American region or contain similar floristic elements (Jolly et al., 1998a; Pickett et al., 2004; Takahara et al., 2001; Elenga et al., 2000; Thompson and Anderson, 2000; Yu et al., 2000). Five main groups of PFT were distinguished: these containing tropical (non-frost tolerant), coniferous (needle-leaved), temperate (frost tolerant), xerophytic (drought tolerant), and frost and drought tolerant taxa (Table 1, Fig. 6). This latter group is present in cold dry conditions of southern South America and the high Andes. A sixth “miscellaneous” group represents various life forms with restricted diagnostic value. The Latin American flora was divided into 25 PFTs (Table 1) that, although being of ecologically distinct, can be multiply assigned to the biomes (Table 2). The classification is based on the original scheme devised for the Biome-1 vegetation model (Prentice et al., 1992) and modification through regional applications to pollen data. Where possible the scheme devised for Latin America conforms to existing classification and definitions. However, some of the specific vegetation types in Latin America were not adequately covered by the existing range so two new PFTs (heath and cushion plants) were added. To aid in the separation of the African forest/savanna boundary, Jolly et al. (1998a) subdivided the tropical raingreen trees PFT (Tr) into three groups. In the case of Latin America, it was decided that the overlap (taxa being multiply assigned to the PFTs) between the PFTs would be too great, and the distinction somewhat minimal. Furthermore, the tropical xerophytic trees and shrubs PFT encompass many taxa that would be assigned to the driest tropical raingreen category. Therefore, the Tr PFT was subdivided into “wet” (Tr<sub>1</sub>) and “dry” (Tr<sub>2</sub>) tropical raingreen trees.

The cornerstone of research concerned with the composition and distribution of Latin American vegetation, be it in a contemporary time frame, or one that aims to work in the past, is a good understanding of the ecology and distribution of the taxa concerned. The Latin American pollen taxa were assigned to one or more PFTs depending on the modern ecological range of the most important (i.e. most abundant) taxa responsible for producing the pollen identifiable within the modern data set. These assignments were made following reference to the known biology of plants from several floras (Rzedowski, 1983; Schofield, 1984; Wingenroth and Suarez, 1984; Kahn and de Granville, 1992; Gentry, 1993; Maberly, 1993; Seibert, 1996), botanical and palynological studies (Beard, 1955; van der Hammen, 1963; 1972; Wijnstra and van der Hammen, 1966; Eiten, 1972; Cleef and Hooghiemstra, 1984; Hooghiemstra and Cleef, 1984; Pires and Prance, 1985; Prance, 1985; Cuatrecasas and Barreto, 1988; Brown and Lugo, 1990; Bush, 1991; Dov Par, 1992; Kappelle, 1993;

Duivenvoorden and Cleef, 1994; Witte, 1994; Armesto et al., 1995; Harley, 1995; Kappelle, 1995; Kershaw and McGlone, 1995; Veblen et al., 1995; Colinvaux, 1996; Grabherr, 1997; Hooghiemstra and van der Hammen, 1998) and personal communication with modern ecologists and palaeoecologists. Much of this information has been collated into a dictionary on the distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database (Marchant et al., 2002c). The resultant taxon vs. PFT assignments are presented in Table 4. Due to the high intra-generic diversity, and also the wide range of ecology's exhibited by the parent taxa present within some genera, a number of taxa were multiply assigned to a number of PFTs; where possible, pollen taxa were assigned to the PFTs within which the parent taxa are most common.

Thus, the identified PFTs from Latin America are described by the suite of pollen taxa assigned to them, in turn the biomes are distinguished by the suite of constituent PFTs (Table 5). A number of pollen taxa belong to more than one PFT (Table 4), and, as is the case with the potential vegetation, most PFTs contribute to more than one biome (Table 5). Two problems can arise here for our analysis that can be circumvented by manipulation of the input matrices and output biome affinity scores (the numerical sum computed for the pollen spectra for each sample this is equal to the sum of the square root of the percentages of the pollen types). First, pollen samples can have equal maximum affinity with more than one biome; this commonly occurs when the PFTs characteristic of one biome are a subset of another biome. Assigning the biomes so that subsets always come first in the analysis solves the problem. A second problem arises where multiple samples fall within the time window we are interested in. Multiple samples from a single site may have maximum affinity to a number of different biomes; the chance of this is high when the score of the “best” biome is close to that of the next “best” and the dominant biome switches between the top scoring biomes. In such cases, the “majority” biome is mapped. For example, site A contains eight samples within the time frame of  $6000 \pm 500$  <sup>14</sup>C yr BP, five samples have the greatest affinity to biome 1, two samples to biome 2 and one sample to biome 3. The result is that biome 1 is mapped for site A at  $6000 \pm 500$  <sup>14</sup>C yr BP. This situation is not ideal as it masks the transient nature of the ecosystem to environmental shifts, however, this is a problem with the biomisation technique and can be overcome at a single site or few sites by mapping the biome scores rather than the most dominant biome (Marchant et al 2002a, b).

To enable a definition of the biomes to be based on bioclimatic data the climate space encompassed by Latin America (as abstracted from the climate data set of Lemans and Cramer, 1991) was used to plot plant available moisture ( $\alpha$ ) against a temperature gradient (MTCO). This plot was used to map the locational range of the biomes and to identify the location of the sites used in the analysis where there are pollen data for each of the three time periods in

two-dimensional bioclimatic space (Fig. 5). Two immediate issues are apparent from this plot – firstly there is a bias of sites with an  $\alpha$  of 1 within Latin America and a potentially different measure of moisture could provide some definition in this area of the plot. Secondly, as would be expected, there is little desert bioclimatic space in Latin America and no pollen sites located in this area of the plot. The twelve biomes identified within Latin America (Table 2) are designed to incorporate the range of major vegetation types and ensure consistency with previous areas to undergo the process within the BIOME-6000 community. Biomes were reconstructed from pollen data at sites with surface sample, trap and radiocarbon-dated core-top data. The results were used to produce a modern pollen-derived biome dot map (Fig. 7); for each site a colour dot records the reconstructed biome with the highest affinity score. These were compared site by site, with the potential modern vegetation distribution (Fig. 2). The biomisation procedure was applied to the fossil datasets without modification. Results for all sites and periods are provided in Table 6 which allows a site-by-site comparison through time and a comparison between the modern reconstruction and potential vegetation.

### 3 Results

#### 3.1 Modern pollen vs. potential biome reconstruction

Visual comparison shows that the biomes reconstructed from modern pollen data (Fig. 7) reflect the broad features in the potential vegetation map (Fig. 2). In particular the modern reconstruction reproduces the transition from relatively mesic vegetation types, around the coastal areas of South America, to the more xeric biomes towards the interior. For example, in eastern Argentina there is a transition from steppe to xerophytic woods and scrub. Warm temperate rain forest is an important biome in the southern and southeastern Brazilian highlands, with tropical dry forest being reconstructed towards the interior. Notable from this region is the large number of different biomes being reconstructed in a relatively small area. In part this reflects the variability of potential vegetation, not portrayed in our relatively coarse resolution vegetation map (Fig. 2). For example, a site recording tropical rain forest reflects the sites' lowland position where it is characterised by moist gallery forest with a number of typical rain forest taxa present. Steppe is correctly reconstructed from the grasslands of south-eastern Argentina and dry forest in central Argentina, mirroring the transition to “drought-deciduous thorn forests” of central Argentina (Schmithüsen, 1976). Steppe is assigned farther west at approximately 1000 m in the Andes, southernmost South America and northeast Brazil. The vegetation of southern South America is dominated by cool temperate rain forest. The failure of the analysis to pick up the transition from cool temperate rain forest to cool grass/shrubland as

one progresses east along Tierra del Fuego stems from the pollen spectra having a relatively large amount of *Nothofagus* pollen. Moving northwards from southern South America there is a transition to cool mixed forest, cool grass/shrubland and steppe; these latter assignments are particularly associated with eastern flanks of the Cordillera de los Andes.

The concentration of sites along the Andes results in a wide range of reconstructed biomes being geographically adjacent to each other when mapped in two-dimensional space (Fig. 7). This phenomenon is most apparent in the northern Andes where the altitudinal, and therefore climatic gradients are at their steepest. Despite these rapid environmental changes, the biome assignments reflect the changing vegetation patterns (Table 6). There is an altitudinal transition with low altitudes (<300 m) being mainly assigned to the tropical rain forest, tropical dry forest, tropical seasonal forest and steppe. Sites located at mid altitudes are described by a number of different biomes including tropical seasonal forest, warm mixed forest, cool mixed forest and cool temperate rain forest. Within this wide range of warm temperate rain forest and tropical seasonal forest are commonly assigned at lower elevations (Fig. 7, Table 6). Many of the sites at high altitude have a high affinity to the cool grass/shrubland biome. The line of the Andes can be easily seen by the cool grass/shrubland biome assignments, these being commonly recorded at sites above 3800 m. The warm temperate rain forest is assigned at lower elevations and is analogous to Andean forest, being dominated by *Podocarpus*, *Quercus* and *Weinmannia* comprises a different forest type to that assigned in southern and southeast Brazil or southern South America. A mixture of biomes presently characterises the Amazon Basin with only four sites recording the tropical rain forest biome; two of these are in coastal locations. Tropical seasonal forest is recorded in four locations; this representing a slightly drier type of forest than tropical rain forest, containing some deciduous taxa. A number of “Amazonian” sites record warm temperate rain forest, these assignments responding to the presence of Andean floristic elements within lowland vegetation. There are a number of sites that record tropical dry forest, this being relatively widespread, e.g. on Easter Island, lowland Colombia and the Brazilian interior. Warm temperate rain forest describes the majority of the sites in the Panamanian and southern Costa Rican isthmus with warm mixed forest, being commonly at higher altitudes. This is an area where the comparison between the observed and predicted biomes shows a discrepancy; the possible reasons behind this will be discussed fully. Warm mixed forest is correctly assigned to the highlands of central and southern México as is tropical dry forest in southern México.

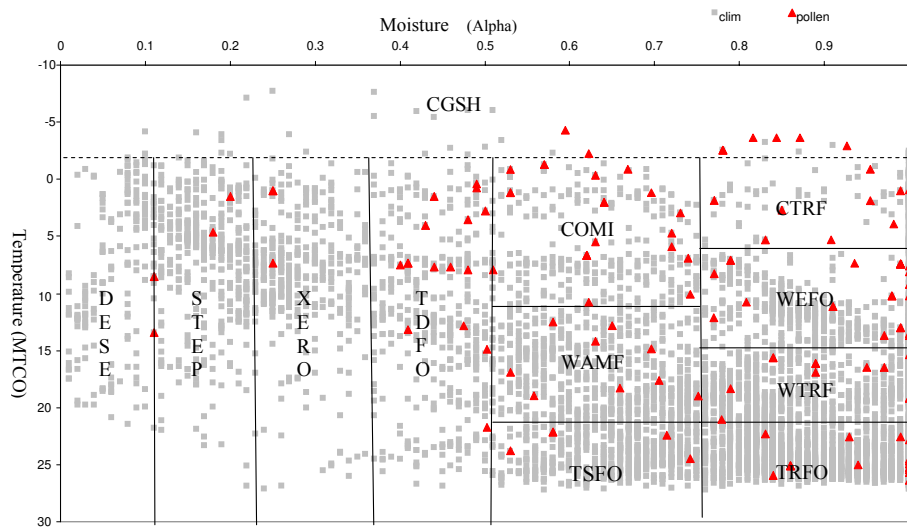
Investigating the correspondence between the pollen-based reconstruction and the potential vegetation for individual biomes provides a check on the methodology, particularly the construction of the matrices. The cool grass/shrubland biome is accurately reconstructed at the majority of sites. The sites that do not match the potential

**Table 4.** Latin American pollen taxa used in the biomisation analysis and their assignment to the plant functional types (PFTs).

PFT Codes	Pollen Taxa
g	Poaceae.
man	<i>Acrostichum</i> -type, <i>Avicennia</i> , <i>Laguncularia</i> , <i>Rhizophora</i> .
tx	<i>Alsophila</i> , <i>Alstroemeria</i> , <i>Cnemidaria</i> , <i>Cyathea</i> , <i>Dicksonia</i> , <i>Nephelea</i> .
Tr <sub>1</sub>	<i>Alibertia</i> , Anacardiaceae, <i>Andira</i> -type, <i>Astronium</i> , <i>Bauhinia</i> , Bombacaceae, <i>Bougainvillea</i> , Caesalpineae, <i>Casearia</i> -type, <i>Clematis</i> , <i>Coccoloba</i> , <i>Copaifera</i> , <i>Didymopanax</i> , <i>Eugenia</i> , <i>Euterpe</i> , <i>Goupia</i> -type, <i>Guapira</i> , <i>Heliocarpus</i> , <i>Hura</i> , <i>Hieronima</i> , Hippocrateaceae, <i>Ipomoea</i> , <i>Laplacea</i> , Lecythidaceae, Leguminoseae, Loranthaceae, <i>Macharium</i> , <i>Macrolobium</i> , Malpighiaceae, Malvaceae, <i>Maytenus</i> , <i>Ocotea</i> -type, <i>Pera</i> , <i>Phyllostylon</i> , <i>Piper</i> , <i>Pisonia</i> , <i>Psychotria</i> , Rubiaceae, Rutaceae, <i>Salix</i> , <i>Sapium</i> , <i>Simira</i> , <i>Siparuna</i> , <i>Spirotheca</i> , <i>Spondias</i> , <i>Symplocos</i> , <i>Tecoma</i> , <i>Trema</i> , <i>Xylosma</i> , <i>Zanthoxylum</i> .
Tr <sub>2</sub>	<i>Acacia</i> , <i>Alchornea</i> , <i>Alibertia</i> , <i>Andira</i> -type, Anacardiaceae, Apocynaceae, <i>Astronium</i> , <i>Banisteriopsis</i> , <i>Bauhinia</i> , Bombacaceae, <i>Bougainvillea</i> , <i>Brosimum</i> , <i>Brunellia</i> , <i>Bulnesia</i> , <i>Bumelia</i> -type, <i>Bursera</i> , <i>Byrsonima</i> , Caesalpineae, Celastraceae, <i>Chrysophyllum</i> , <i>Clematis</i> , Combretaceae, <i>Copaifera</i> , <i>Cordia</i> , <i>Coriaria</i> , <i>Cuphea</i> , <i>Curatella</i> , <i>Didymopanax</i> , Elaeocarpaceae, <i>Eryngium</i> , <i>Erythrina</i> , <i>Euterpe</i> , <i>Gallesia</i> , <i>Guapira</i> , <i>Hieronima</i> , <i>Hura</i> , Hymenophylleaceae, <i>Ipomoea</i> , Loranthaceae, Malvaceae, <i>Maytenus</i> , Melastomataceae, Meliaceae, <i>Mimosa</i> , <i>Passiflora</i> , <i>Pera</i> , <i>Phyllostylon</i> , <i>Piper</i> , <i>Pisonia</i> , <i>Protium</i> , <i>Pseudobombax</i> , Rhamnaceae, Rutaceae, <i>Salix</i> , <i>Sapium</i> , <i>Schinus</i> , <i>Simira</i> , <i>Siparuna</i> , <i>Spirotheca</i> , <i>Spondias</i> , <i>Styrax</i> , <i>Symplocos</i> , Tiliaceae, <i>Trema</i> , <i>Xylosma</i> , <i>Zanthoxylum</i> .
Te <sub>1</sub>	<i>Abutilon</i> , <i>Actinostemon concolor</i> , <i>Alchornea</i> , <i>Amanoa</i> , <i>Apeiba</i> , Apocynaceae, Araliaceae, Arecaceae, <i>Arrabidaea</i> , <i>Aspidosperma</i> , <i>Astrocarium</i> , Begoniaceae, Bignoniaceae, Bombacaceae, <i>Bonamia</i> , <i>Brosimum</i> , <i>Brunellia</i> , <i>Brownea</i> , <i>Calliandra</i> , <i>Campomanesia</i> , <i>Cardiospermum</i> , <i>Castilla</i> , <i>Cecropia</i> , <i>Cedrela</i> , <i>Celtis</i> , <i>Copaifera</i> , <i>Coprosma</i> , Cucurbitaceae, Cunoniaceae, <i>Dalbergia</i> , <i>Dioclea</i> , <i>Doliocarpus</i> , <i>Elaeagia</i> , <i>Euterpe</i> , <i>Ficus</i> , Flacourtiaceae, <i>Forsterania</i> , <i>Geonoma</i> , <i>Guapira</i> , <i>Guazuma</i> , <i>Guarea</i> , <i>Hura</i> , <i>Ilex</i> , <i>Inga</i> , <i>Iriartea</i> , <i>Iva xanthifolia</i> -type, Lecythidaceae, Leguminoseae, <i>Licania</i> , <i>Mabea</i> , <i>Macharium</i> , <i>Macrolobium</i> , <i>Macrocarpea</i> , Malpighiaceae, <i>Mauritia</i> , Marcgraviaceae, <i>Maripa</i> , <i>Marattia</i> , <i>Matayba</i> , Melastomataceae, Meliaceae, <i>Miconia</i> , Moraceae, <i>Myrsine</i> , Myrtaceae, <i>Mauritiella</i> , Nyctaginaceae, Ochnaceae, <i>Ocotea</i> -type, <i>Oenocarpus</i> , <i>Oreopanax</i> , Palmae, <i>Panopsis</i> , <i>Parahancornia</i> , <i>Passiflora</i> , <i>Plenckia</i> , <i>Protium</i> , <i>Pseudopanax laetevirens</i> , <i>Rauwolfia</i> , <i>Rhipsalis</i> , Rubiaceae, Sapotaceae, <i>Scheelea</i> , <i>Scleronema</i> , <i>Socratea</i> , <i>Sloanea</i> , Solanaceae, <i>Sophora</i> , <i>Strutanthus</i> , <i>Symphonia</i> , <i>Swartzia</i> , <i>Taperira</i> , <i>Ternstroemia</i> cf. <i>T. brasiliensis</i> , <i>Tetrochiduum</i> , <i>Tetraploa aristata</i> , Thymelaeaceae, Tiliaceae, <i>Trichilia</i> , <i>Trigonía</i> , <i>Vismia</i> , <i>Warsewiczia</i> .
Te <sub>2</sub>	<i>Abutilon</i> , <i>Acacia</i> , <i>Aegiphila</i> , <i>Alibertia</i> , <i>Apeiba</i> , Apocynaceae, <i>Aspidosperma</i> , Boraginaceae, <i>Bougainvillea</i> , <i>Brosimum</i> , <i>Brunellia</i> , <i>Calliandra</i> , <i>Cecropia</i> , <i>Cedrela</i> , <i>Celtis</i> , Combretaceae, <i>Croton</i> , Cucurbitaceae, <i>Dalbergia</i> , <i>Didymopanax</i> , <i>Dioclea</i> , <i>Forsterania</i> , Hippocrateaceae, <i>Humiria</i> , <i>Humulus</i> , <i>Ilex</i> , <i>Iriartea</i> , Leguminoseae, <i>Macrolobium</i> , <i>Mauritia</i> , Melastomataceae, <i>Miconia</i> , Moraceae, <i>Mysine</i> , Myrtaceae, Ochnaceae, <i>Ocotea</i> -type, Palmae, <i>Panopsis</i> , <i>Passiflora</i> , <i>Plenckia</i> , <i>Pseudopanax</i> , <i>Psychotria</i> , Sapotaceae, <i>Scleronema</i> , <i>Serjania</i> , <i>Sophora</i> , <i>Strutanthus</i> , <i>Swartzia</i> , <i>Taperira</i> , Tiliaceae, <i>Vismia</i> , <i>Warsewiczia</i> .
wtc	<i>Abies</i> , <i>Araucaria</i> , <i>Juniperus</i> , <i>Pinus</i> .
ctc <sub>2</sub>	<i>Abies</i> , <i>Araucaria</i> , <i>Araucaria augustifolia</i> , Cupressaceae, <i>Dacrydium</i> , <i>Juniperus</i> , <i>Pilgerodendron</i> , <i>Podocarpus</i> , <i>Prumnopitys andina</i> , <i>Saxegothaea conspicua</i> .
ctc <sub>1</sub>	<i>Austrocedrus chilensis</i> , Cupressaceae, <i>Dacrydium</i> , <i>Fitzroya cupressoides</i> -type, <i>Pilgerodendron</i> , <i>Pinus</i> , <i>Podocarpus</i> , <i>Prumnopitys andina</i> , <i>Saxegothaea conspicua</i> , <i>Taxodium</i> .
txts	<i>Acacia</i> , <i>Aeschynomene</i> , <i>Agave</i> , <i>Anthurium</i> , <i>Aphelandra</i> , <i>Arrabidaea</i> , <i>Atamisquea</i> , <i>Ayenia</i> , <i>Bursera</i> , <i>Byrsonima</i> , <i>Bytmeria</i> , <i>Cabomba</i> , Cactaceae, <i>Caryocar</i> , <i>Cayaponia</i> , <i>Cercidium</i> , <i>Chomelia</i> , <i>Chrysophyllum</i> , <i>Chuquiragua</i> , <i>Cissus</i> , <i>Clusia</i> , Combretaceae, Convolvulaceae, <i>Cordia</i> , <i>Cuphea</i> , <i>Curatella</i> , <i>Dodonaea</i> , <i>Echinodorus</i> , <i>Eichhornia</i> , <i>Evolvulus</i> , Hippocrateaceae, <i>Humulus</i> , <i>Hyptis</i> , <i>Ipomoea</i> , <i>Larrea</i> , <i>Lithraea</i> , Malpighiaceae, <i>Manihot</i> , <i>Maprounea</i> , Menispermaceae, <i>Metopium</i> , <i>Miconia</i> , <i>Mimosa</i> cf. <i>M. taimbensis</i> , <i>Palicourea</i> , <i>Peperomia</i> , <i>Phaseolus</i> , <i>Phyllanthus</i> , <i>Polygala</i> , <i>Polylepis-Acaena</i> , <i>Pouteria</i> , Portulaccaceae undiff., <i>Prosopis</i> , Rhamnaceae, <i>Sapium</i> , <i>Schefflera</i> , <i>Schinus</i> , <i>Sebastiania</i> , <i>Serjania</i> , Solanaceae, <i>Sloanea</i> , <i>Stryphnodendron</i> , <i>Tecoma</i> , <i>Trixis</i> , <i>Zornia</i> .
h	<i>Arenaria</i> , <i>Aristolelia</i> , Asteraceae, Berberidaceae, <i>Berberis</i> , <i>Empetrum</i> , Ericaceae, <i>Sisyrinchium</i> -type.
ds	<i>Agave</i> , <i>Atamisquea</i> , Cactaceae, <i>Ephedra</i> , <i>Monttea aphylla</i> .
df	<i>Alternanthera</i> , <i>Ephedra</i> , <i>Monttea aphylla</i> , <i>Xyris</i> .

Table 4. Continued.

PFT Codes	Pollen Taxa
tf	<i>Acalypha</i> , Acanthaceae, <i>Alchemilla</i> , Alismataceae, <i>Alsophila</i> , <i>Anemia</i> , <i>Antheroceros</i> , <i>Armeria</i> , <i>Artemisia</i> , <i>Assulina</i> , Asteraceae, <i>Astelia</i> , <i>Begonia</i> , <i>Bernardia</i> , Brassicaceae, <i>Bravaisia</i> , Bromeliaceae, Calyceraceae, <i>Caperonia</i> , Caryophyllaceae, <i>Cassia</i> , Cichoriaceae, <i>Cirsium</i> , Cruciferae, <i>Eriogonum</i> , Eriocaulaceae, <i>Euphorbia</i> , Euphorbiaceae, Fabaceae, Geraniaceae, <i>Gomphorena</i> , <i>Gunnera</i> , <i>Hebenaria</i> , <i>Iresine</i> , <i>Justicia</i> , Lamiaceae, <i>Laporteia</i> , <i>Liquidambar</i> , Liliaceae, <i>Lobelia</i> , Menispermaceae, <i>Muehlenbeckia</i> , <i>Nerthea</i> , Onagraceae, Orchidaceae, <i>Pilea</i> , <i>Polygala</i> , <i>Rhaphithamnus</i> , <i>Rhus</i> , Rubiaceae, <i>Smilax</i> , <i>Triumfetta</i> , Umbelliferae, Urticaceae, <i>Verbena</i> , Verbenaceae, <i>Vernonia</i> , <i>Viburnum</i> , <i>Vitis</i> .
tef	<i>Acalypha</i> , Acanthaceae, <i>Apiaceae</i> , <i>Apium</i> , <i>Artemisia</i> , <i>Astelia</i> , <i>Azara</i> , <i>Borreria</i> , Brassicaceae, <i>Bravaisia</i> , Bromeliaceae, <i>Cassia</i> , Cichoriaceae, Eriocaulaceae, <i>Eriogonum</i> , <i>Euphorbia</i> , Euphorbiaceae, Fabaceae, <i>Genipa</i> , <i>Gordonia</i> , <i>Gunnera</i> , <i>Hippeastrum</i> , <i>Hydrocotyle</i> , Iridaceae, <i>Jungia</i> , <i>Justicia</i> , <i>Lachemella</i> , <i>Lamanonia</i> , Lamiaceae, <i>Laporteia</i> , Liliaceae, <i>Lupinus</i> , Malvaceae, Marcgraviaceae, <i>Moritzia</i> -type, <i>Mutisia</i> , <i>Nerthea</i> , Onagraceae, Orchidaceae, <i>Pamphalea</i> , <i>Perezia</i> , <i>Phaseolus</i> , <i>Pilea</i> , <i>Piscidia</i> , <i>Plantago</i> , Polemoniaceae, <i>Polygala</i> , Portulacaceae undiff., <i>Pouteria</i> , Ranunculaceae, Rubiaceae, <i>Rumex</i> , <i>Satureja</i> , Scrophulariaceae, <i>Selaginella</i> , <i>Thalictrum</i> , <i>Triumfetta</i> , Umbelliferae, Urticaceae, Verbenaceae, <i>Vernonia</i> , <i>Vicia</i> , <i>Vitis</i> , <i>Wendtia</i> , <i>Xyris</i> .
sf	<i>Alternanthera</i> , Amaranthaceae/Chenopodiaceae, <i>Antheroceros</i> , <i>Armeria</i> , <i>Assulina</i> , Asteraceae, <i>Astelia</i> , <i>Borreria</i> , Calyceraceae, <i>Cardus</i> , Caryophyllaceae, <i>Cardus</i> , <i>Conarus</i> , Cruciferae, <i>Embothrium</i> , <i>Eriogonum</i> , <i>Eryngium</i> , <i>Euphorbia</i> , Euphorbiaceae, Fabaceae, Geraniaceae <i>Gomphorena</i> , <i>Gunnera</i> , <i>Hebenaria</i> , <i>Hippeastrum</i> , <i>Hydrocotyle</i> , Iridaceae, <i>Jungia</i> , <i>Justicia</i> , Liliaceae, Lamiaceae, <i>Liquidambar</i> , <i>Mutisia</i> , <i>Nanodea</i> , <i>Nassauvia</i> -type, Orchidaceae, <i>Oxalis</i> , <i>Phacelia</i> , <i>Physalis</i> , <i>Plantago</i> , Polemoniaceae, <i>Pouteria</i> , Ranunculaceae, Restionaceae, Rosaceae, Rubiaceae, <i>Satureja</i> , <i>Scutellaria</i> -type, Umbelliferae, Urticaceae, <i>Vicia</i> , <i>Vitis</i> , <i>Wendtia</i> , <i>Xyris</i> .
af	<i>Arenaria</i> , <i>Astragalus</i> , <i>Azorella</i> , <i>Bartsia</i> -type, <i>Borreria</i> , Bromeliaceae, <i>Bravaisia</i> , Campanulaceae, <i>Cardus</i> , Caryophyllaceae, <i>Deschampsia antarctica</i> , <i>Diphasiastrum complanatum</i> -type, <i>Donatia</i> , <i>Draba</i> , <i>Epilobium</i> , Eriocaulaceae <i>Eriocaulon</i> , <i>Eriogonum</i> , <i>Gaimardia</i> , <i>Gilia</i> , <i>Halenia</i> , <i>Hebenaria</i> , <i>Hippeastrum</i> , <i>Hydrocotyle</i> , Iridaceae, <i>Jamesonia</i> , Labiatae, <i>Lachemella</i> , Lamiaceae, <i>Liquidambar</i> , <i>Lupinus</i> , <i>Lysipomia</i> , <i>Montia</i> , <i>Moritzia</i> -type, <i>Muehlenbeckia</i> , <i>Nassauvia</i> -type, Orchidaceae, <i>Oxalis</i> , <i>Perezia</i> , <i>Plantago</i> , <i>Puya</i> , <i>Quinchamalium</i> , <i>Relbunium</i> , Rosaceae, Rubiaceae, <i>Rumex</i> , <i>Satureja</i> , Scrophulariaceae, <i>Scutellaria</i> -type, <i>Selaginella</i> , <i>Sisyrinchium</i> -type, Umbelliferae, <i>Valeriana</i> , <i>Viola</i> .
cp	<i>Apiaceae</i> , <i>Azorella</i> , <i>Gaimardia</i> , <i>Montia</i> , <i>Plantago</i> , <i>Saxifraga</i> .
wte	<i>Aegiphila</i> , <i>Allophylus</i> , <i>Aphelandra</i> , Araliaceae, <i>Azara</i> , <i>Baccharis</i> , <i>Bauhinia</i> , Begoniaceae, <i>Buddleja</i> , <i>Bumelia</i> -type, <i>Clusia</i> , <i>Croton</i> , <i>Daphnopsis</i> , <i>Desfontainia</i> , Elaeocarpaceae, <i>Embothrium</i> , <i>Eucryphia/Caldcluvia paniculata</i> , <i>Euterpe</i> , <i>Fuchsia</i> , <i>Geonoma</i> , Geraniaceae, <i>Griselinia</i> , <i>Guettardia</i> , <i>Gunnera</i> , Guttiferae, <i>Hedyosmum</i> , <i>Heliocarpus</i> , <i>Humiria</i> , Labiatae, <i>Lomatia/Gevuina</i> , Loranthaceae, <i>Ludwigia</i> , <i>Luehea</i> , Malpighiaceae, <i>Matayba</i> , Melastomataceae, Meliaceae, <i>Mimosa</i> , <i>Mimosa</i> cf. <i>M. scabrella</i> , <i>Mutisia</i> , <i>Myrica</i> , <i>Mysine</i> , <i>Nothofagus obliqua</i> -type, <i>Oreopanax</i> , <i>Palicourea</i> , Proteaceae, <i>Prunus</i> , <i>Pseudopanax laetevirens</i> , <i>Psychotria</i> , <i>Quercus</i> , <i>Roupala</i> , <i>Sambucus</i> , Solanaceae, <i>Stryphnodendron</i> , <i>Styloceras</i> , <i>Tepualia stipularis</i> , <i>Tetrochiduum</i> , Thymelaeaceae, <i>Trichilia</i> , Verbenaceae, <i>Viburnum</i> , <i>Warsewiczia</i> , <i>Weinmannia</i> .
wte <sub>1</sub>	<i>Aegiphila</i> , <i>Alnus</i> , Arecaceae, <i>Aragoa</i> , <i>Arctophyllum</i> , <i>Aristotelia</i> , <i>Azara</i> , <i>Banara</i> , <i>Banisteriopsis</i> , Begoniaceae, <i>Bocconia</i> , <i>Brunellia</i> , <i>Buddleja</i> , <i>Calandrinia</i> , Campanulaceae, Celastraceae, <i>Chuquiraga</i> , <i>Clethra</i> , <i>Daphnopsis</i> , <i>Desfontainia</i> , <i>Dodonaea</i> , <i>Drimys</i> , Epacridaceae, Ericaceae, <i>Fuchsia</i> , <i>Galium</i> , <i>Gaultheria ulei</i> , Geraniaceae, Gesneriaceae, <i>Hedyosmum</i> , <i>Hydrangea</i> , <i>Hypericum</i> , Labiatae, Loranthaceae, <i>Ludwigia</i> , <i>Maytenus</i> , Meliaceae, <i>Meliosma</i> , <i>Muehlenbeckia</i> , Myrtaceae, <i>Mysine</i> , <i>Nothofagus</i> , <i>Nothofagus antarctica</i> -type, <i>Ostrya</i> -type, Proteaceae, <i>Prunus</i> , <i>Pseudopanax laetevirens</i> , <i>Quercus</i> , <i>Ribes</i> , <i>Roupala</i> , <i>Sambucus</i> , Solanaceae, <i>Tepualia stipularis</i> , Verbenaceae, <i>Viburnum</i> , <i>Weinmannia</i> .
wte <sub>4</sub>	<i>Abatia</i> , <i>Adesmia</i> , <i>Alchemilla</i> , <i>Alfaroa</i> , <i>Arctophyllum</i> , <i>Assulina</i> , Asteraceae, <i>Clethra</i> , <i>Colignonia</i> , <i>Dodonaea</i> , Ericaceae, <i>Gaiadendron</i> , <i>Gaultheria ulei</i> , Guttifera, <i>Laurelia</i> , <i>Muehlenbeckia</i> , <i>Myrteola</i> , <i>Polylepis-Acaena</i> , <i>Ribes</i> , Rosaceae, <i>Tetrochiduum</i> , <i>Weinmannia</i> .
ts	<i>Alnus</i> , <i>Banksia</i> , <i>Carpinus</i> , <i>Cayaponia</i> , <i>Fagus</i> , <i>Fraxinus</i> , <i>Juglans</i> , Loranthaceae, <i>Luehea</i> , <i>Myrica</i> , <i>Populus</i> , <i>Styrax</i> , <i>Trema</i> , Ulmaceae, <i>Vallea</i> .
ts <sub>1</sub>	<i>Escallonia</i> , <i>Eugenia</i> , <i>Gordonia</i> , <i>Liquidambar</i> , <i>Luehea</i> , <i>Misodendrum</i> , <i>Myzodendron</i> , <i>Styrax</i> , <i>Ternstroemia</i> cf. <i>T. brasiliensis</i> , <i>Trema</i> , <i>Vallea</i> .
aa	<i>Aragoa</i> , <i>Arctophyllum</i> , <i>Arenaria</i> , Asteraceae, <i>Baccharis</i> , Cruciferae, <i>Draba</i> , <i>Empetrum</i> , <i>Ephedra</i> , Ericaceae, <i>Eriogonum</i> , <i>Escallonia</i> , <i>Gentiana</i> , Gentianaceae, <i>Hypericum</i> , <i>Nassauvia</i> -type, <i>Puya</i> , Rosaceae, <i>Senecio</i> .



**Fig. 5.** Theoretical biome scheme for Latin America portrayed on a grid of environmental space along the gradients of temperature (mean temperature of the coldest month) and plant available moisture (alpha). Grey fields reflect the climate space in 100×100 km grid cells from Mexico to Patagonia as derived from Leemans and Cramer (1991). The location of sites where pollen data is used for the reconstruction of biomes across Latin America are shown as red triangles.

**Table 5.** Assignment of Latin American plant functional types to Biomes.

CODES	Plant functional types
TRFO	man, tx, Te <sub>1</sub> , Te <sub>2</sub> , tf
TSFO	tx, Tr <sub>1</sub> , Tr <sub>2</sub> , Te <sub>2</sub> , tf
TDFO	Tr <sub>2</sub> , tf, txts, df
WTRF	tx, Tr <sub>1</sub> , Te <sub>1</sub> , wtc, ctc <sub>2</sub> , tef, wte
WEFO	tx, Tr <sub>2</sub> , wtc, ctc <sub>2</sub> , ec, tef, wte
CTRF	tx, h, ctc <sub>1</sub> , tef, wte, wte <sub>1</sub>
WAMF	Tr <sub>2</sub> , wtc, tef, wte, ts
COMI	ctc <sub>1</sub> , tef, wte <sub>1</sub> , wte <sub>4</sub> , ts <sub>1</sub>
STEP	sf
DESE	ds, df
CGSH	af, aa, wte <sub>4</sub> , h
CGSS	af, aa, cp

vegetation commonly result from the inclusion of high altitude arboreal pollen, this resulting in assignments of cool mixed forest and cool temperate rain forest. The other common assignment is towards steppe; the dominance of the pollen spectra by Poaceae, and lack of shrubby taxa, result in the assignment to the steppe biome. Indeed, the affinity scores to the cool grass/shrubland and steppe biome at most sites, where one of these biomes is dominant, is normally quite close. For the cool mixed forest biome 66% of sites accurately reconstruct the potential vegetation. The 34% of “wrong” assignments mainly result in either a reconstruction of cool grass/shrubland, thought to represent possible forest clearance, and the dominance of the vegetation by grassland,

or cool temperate rain forest biome due to the numerous shared taxa between these two biomes. 75% of cool temperate rain forest biome reconstructions match the potential vegetation at the site. The remaining 25% of the sites mainly show either warm mixed forest or warm temperate rain forest assignments. For the tropical dry forest biome some 90% of the sites accurately reflect the potential vegetation at the site. For the remaining 10% of “wrong” assignments the common result is towards a cool temperate rain forest or steppe. For the tropical rain forest biome 85% of the sites accurately reflect the potential vegetation. For the sites that do not match, a common reconstruction is warm temperate rain forest. This can be explained by the number of Andean elements being present within lowland tropical forests with a couple of sites reconstructing the closely related biome of tropical seasonal forest. This facet of the pollen data is also exemplified by a number (35%) of the tropical seasonal forest sites recording the warm temperate rain forest biome. Warm evergreen forest is correctly assigned at 80% of the sites. Warm temperate rain forest is assigned correctly at 78% of sites. 75% of the sites that do not reconstruct this biome “correctly” lead to assignments of tropical rainforest and tropical seasonal forest at low altitudes (<500 m) and cool mixed forest at high (>2000 m).

The generally correct biome assignments, in relation to a map of potential vegetation confirm the robustness of our application of the biomisation method to Latin America. Where the match between pollen and potential vegetation reconstructions is relatively low (tropical seasonal forest and warm temperate rain forest), then a common forcing factor, that of “high altitude” plants presently growing at low altitudes

**Table 6.** Site locations showing biome changes from the present, 6000±500 and 18 000±1000 <sup>14</sup>C yr BP. The relationship between the present observed biome and the biome reconstructed from the modern pollen data is also shown.

Site	Long.	Latitude	Alt.	Present biome	Modern	6000	18 000
Lake Ása3	-61.13	-62.62	35	CGSH	CGSH		
Harberton	-67.16	-54.88	20	STEP	STEP	STEP	
Puerto del Hambre	-70.92	-53.59	5	CTRF	CTRF	CTRF	
La Misión	-67.83	-53.5	5	STEP	STEP	STEP	
Punta Arenas	-70.97	-53.15	75	CTRF	CTRF	CTRF	CGSH
Meseta Latorre 1	-72.05	-51.52	980	CGSH	COMI	CTRF	
Meseta Latorre 2	-72.03	-51.44	1000	CGSH	COMI	CGSH	
Torres del Paine	-72.66	-50.98	100	CTRF	CTRF	TDFO	
Moreno Glacier Bog	-73.00	-50.46	200	CTRF	CTRF	COMI	
Patagonia	-72.90	-50.25	50	CTRF	CTRF		
Patagonia	-72.90	-50.20	20	CTRF	CTRF		
Patagonia	-72.70	-50.20	80	CTRF	CTRF		
Patagonia	-72.00	-50.15	150	CTRF	CTRF		
Patagonia	-71.70	-50.15	180	CTRF	CTRF		
Patagonia	-71.50	-50.15	180	CTRF	CTRF		
Patagonia	-71.10	-50.15	180	CTRF	CTRF		
Patagonia	-69.90	-50.15	180	CTRF	CTRF		
Patagonia	-69.30	-50.15	180	CTRF	CTRF		
Patagonia	-71.30	-50.15	190	CTRF	CTRF		
Patagonia	-70.90	-50.15	190	CTRF	CTRF		
Patagonia	-70.20	-50.15	190	CTRF	CTRF		
Patagonia	-69.60	-50.15	190	CTRF	CTRF		
Patagonia	-72.98	-50.15	20	CTRF	CTRF		
Patagonia	-70.50	-50.15	200	CTRF	CTRF		
Patagonia	-72.95	-50.15	50	CTRF	CTRF		
Patagonia	-72.90	-50.15	50	CTRF	CTRF		
Patagonia	-72.85	-50.15	60	CTRF	CTRF		
Patagonia	-72.75	-50.15	60	CTRF	CTRF		
Patagonia	-72.80	-50.15	70	CTRF	CTRF		
Patagonia	-72.55	-50.10	100	CTRF	CTRF		
Patagonia	-71.95	-50.10	180	CTRF	CTRF		
Patagonia	-69.00	-50.10	190	CTRF	CTRF		
Patagonia	-68.90	-50.05	100	CTRF	CTRF		
Patagonia	-72.00	-50.05	150	CTRF	CTRF		
Patagonia	-72.90	-50.05	50	CTRF	CTRF		
Patagonia	-68.60	-50.05	50	CTRF	CTRF		
Patagonia	-68.10	-50.00	0	CTRF	CTRF		
Patagonia	-68.30	-50.00	20	CTRF	CTRF		
Dichan	-73.88	-49.66	50	CTRF	CTRF	CTRF	
Puerto Eden	-74.41	-49.13	50	CTRF	CTRF	CTRF	
La Esperanza	-72.83	-46.63	330	CTRF	CTRF		
LagoBsAs	-71.45	-46.44	230	CTRF	WAMF		
Laguna Six Minutes	-74.33	-46.43	50	CTRF	CTRF	CTRF	CTRF
Laguna Stibnite	-74.43	-46.43	50	CTRF	CTRF	CGSH	
Laguna Stibnite	-74.38	-46.43	50	CTRF	CTRF	CTRF	CGSH
Pico Salam	-67.43	-45.42	637	STEP	STEP		
Laguna Lincoln	-74.07	-45.34	50	CTRF	CTRF	CTRF	CGSH
Laguna Lofel	-74.43	-44.85	50	CTRF	CTRF	CTRF	CGSH
Estero Huitanque	-73.82	-43.61	52	CTRF	CTRF	COMI	
AustroEsqu	-71.47	-42.66	1100	CTRF	CTRF		
Mayol	-73.75	-42.64	75	CTRF	CTRF	CTRF	
Puchilco	-73.62	-42.63	110	CTRF	CTRF	CTRF	
AlercesNor	-71.60	-42.56	800	CTRF	CGSH		
San Pedro	-73.95	-42.25	650	CTRF	CTRF		
Chepu	-73.66	-42.17	140	CTRF	CTRF		

Table 6. Continued.

Site	Long.	Latitude	Alt.	Present biome	Modern	6000	18 000
Mallin Book	-71.58	-41.33	800	CTRF	COMI	CTRF	
Comallo	-70.21	-41.01	815	CGSH	STEP		
Puerto Octay PM13	-72.90	-40.93	120	CTRF	CTRF	CTRF	COMI
Espuma	-63.25	-40.67	50	TDFO	TDFO		
Primavera	-71.18	-40.66	800	CTRF	CGSH	TDFO	
Encantado	-71.13	-40.66	960	CTRF	COMI		
Ruta 3.4	-62.79	-40.50	20	STEP	STEP		
Ruta 3.3	-62.59	-40.08	20	STEP	STEP		
Caunahue	-72.00	-40.00	500	CTRF		CTRF	
Ruta 250.19	-65.58	-39.54	117	STEP	STEP		
Pedro Luro	-62.53	-39.50	20	STEP	STEP		
Origone	-62.43	-39.08	20	STEP	STEP		
Gaviotas	-63.65	-39.07	90	TDFO	TDFO		
Salina Anzotegui	-63.77	-39.06	-5	STEP	STEP	STEP	
Cueva Haichol	-70.66	-38.58	1050	STEP	STEP	STEP	
Arroyo Sauce Chico	-62.23	-38.07	85	STEP	STEP		
Cerro La China	-58.64	-37.84	200	STEP	TDFO	TDFO	
Empalme Querandías	-60.65	-37.00	105	STEP	STEP	TDFO	
Veranada Pelan	-70.38	-36.88	1860	CGSH	CGSH	TDFO	
Vaca Lauquen	-71.08	-36.83	1450	CTRF	COMI	CGSH	
Veranada Vulkanpickel	-70.41	-36.68	2800	CGSH	STEP	TDFO	
Salado	-69.75	-35.33	3200	CGSH	CGSH		
Salina 2	-69.33	-32.25	2000	CGSH	STEP	STEP	
Serra do Rio Rastro	-49.55	-28.55	1420	WTRF	WTRF	CGSH	
Morro da Igreja	-49.86	-28.18	1800	WTRF	WTRF	WTRF	
Serra da Boa Vista	-49.15	-27.70	1160	WTRF	WTRF	CTRF	
Rano Kao	-109.43	-27.18	110	TDFO	TDFO		
Rano Raraku Bore 3	-109.28	-27.16	75	TDFO	TDFO	TDFO	TDFO
Rano Aroui	-109.40	-27.08	425	TDFO	TDFO	CGSH	WTRF
Poço Grande	-48.86	-26.41	10	WTRF	WTRF		
Reserva Volta Velha	-48.38	-26.04	0	WTRF	WTRF		
Atlantic	-48.35	-25.95	200	WTRF	WTRF		
Colombo	-49.23	-25.33	920	TSFO	TSFO		
Serra Campos Gerais	-50.21	-24.66	1200	WTRF	WAMF	TDFO	
Aguilar	-65.75	-23.83	4000	CGSH	CTRF	STEP	
Rio da Curuá	-48.83	-23.83	800	WTRF		TRFO	
Tumbre 2	-67.78	-23.31	3880	CGSH	CGSH	STEP	
Aguas Calientas	-67.42	-23.08	4210	CGSH	CGSH	CGSH	
Botucatu	-48.00	-23.00	700	WTRF	WTRF		
Curcuab	-48.00	-23.00	700	WTRF	WTRF		
Lagoa da Caço	-43.43	-22.97	5	TDFO		TDFO	STEP
Morro de Itapeva	-45.63	-22.78	1850	WTRF	WEFO	TDFO	CGSH
Assis	-50.50	-22.68	540	TSFO	TSFO		
Lagoa Santa	-47.45	-22.36	630	TDFO	TDFO		
Bauru	-49.07	-22.32	570	TSFO	TSFO		
Brotas	-48.08	-22.29	700	WTRF	WTRF		
Salitre	-46.78	-19.00	1050	WTRF	WTRF	TDFO	CGSH
Ajata	-69.20	-18.25	4700	CGSH	CGSH		
Sajama	-68.88	-18.16	4250	CGSH	CGSH		
Lago do Pires	-42.21	-17.95	390	TSFO	TSFO	TSFO	
Wasa Mayu	-65.91	-17.54	2720	COMI		CGSH	STEP
Crominia	-49.45	-17.28	200	TDFO	TDFO	TSFO	TDFO
Mt. Blanco	-67.35	-17.02	4780	CGSS		CGSS	
Lake Huinānimarca	-69.00	-16.50	3765	CGSH	CGSH	CGSH	CGSS
Cerro Calvario	-68.50	-16.50	3950	CGSH	CGSH	CGSH	

Table 6. Continued.

Site	Long.	Latitude	Alt.	Present biome	Modern	6000	18 000
Rio Kaluyo	-68.13	-16.43	4070	CGSH	CGSH	STEP	
Chacaltaya 1	-68.13	-16.36	4750	CGSH	CGSH	CGSH	
Cumre Unduavi	-68.03	-16.33	4620	CGSS	CGSS	CGSS	
Rio Jequitinhonha	-38.92	-15.85	80	TDFO	TDFO		
Brasilia 1	-47.66	-15.59	1030	TDFO	CTRF		
Aguads Emendadas	-47.58	-15.56	200	TDFO	CTRF	TSFO	CGSH
Cuiaba	-55.86	-15.35	350	TDFO	TDFO		
Amarete	-68.98	-15.23	4000	CGSH	CGSH	CGSH	
Cotapampa	-69.11	-15.21	4450	CGSH	CGSH	CGSH	
Katantica	-69.18	-14.8	4820	CGSH	CGSH	CGSH	
Laguna Chaplin	-61.05	-14.50	750	TSFO	TSFO	TDFO	TSFO
Rio de Contas	-39.00	-14.28	80	TDFO	STEP		
Laguna Bella Vista	-61.56	-13.58	750	TSFO	TSFO	TSFO	TDFO
Laguna Jeronimo	-75.21	-11.78	4450	CGSH	CGSH	CGSH	
Laguna Pomacocha	-75.50	-11.75	4450	CGSH	CGSH	CGSH	
Laguna Paca	-75.50	-11.71	3600	CGSH	CTRF		
Laguna Tuctua	-75.00	-11.66	4250	CGSH	COMI	WTRF	
Laguna Milloc	-76.35	-11.56	4325	CGSH	CGSH	CGSH	
Laguna Junin2	-76.18	-11.00	4100	CGSH	COMI	COMI	CGSH
Laguna Huatacocha	-76.55	-10.76	4500	CGSH	CGSH	CGSH	
Rio São Francisco	-43.00	-10.46	400	TDFO	TDFO	TSFO	
Saquinho	-43.23	-10.44	480	TSFO	TSFO	WEFO	
Rio São Francisco	-36.50	-10.26	80	TDFO	STEP		
Katira	-63.00	-9.00	750	TDFO	TDFO	TDFO	TDFO
Campina Grande I	-35.75	-7.23	70	TSFO	STEP		
Lagoa Grande	-47.45	-7.08	75	TDFO	CTRF		
Picos	-41.40	-7.06	70	TDFO	WTRF		
Lago Bolim	-35.18	-6.04	90	TDFO	STEP		
Rio Protengi	-35.25	-5.78	80	TDFO	CTRF		
Mirim	-35.30	-5.68	70	TDFO	STEP		
Rio Mirim	-35.40	-5.64	70	TDFO	WTRF		
Rio (unclear)	-38.00	-5.50	50	TDFO	CTRF		
Carajas	-48.00	-5.00	150	TSFO	TSFO	TSFO	TSFO
Ciudad Universitaria X	-74.18	-4.75	2560	COMI	COMI	WAMF	WAMF
Rio Jaguaribe II	-37.76	-4.55	50	TDFO	TDFO		
Rio Jaguaribe I	-37.75	-4.43	50	TDFO	STEP		
Lake Surucucho	-78.95	-3.75	970	WTRF	CTRF	WTRF	
Ayauch	-78.13	-2.09	550	WTRF	WTRF	TSFO	
Llaviucu	-79.43	-1.83	3120	CTRF	WTRF		
Indanza	-78.83	-1.53	2100	CTRF	WTRF		
Kumpack	-78.51	-1.53	700	WTRF	WTRF		
Puyo Bog	-79.06	-1.43	953	WTRF	WTRF		
Rum Tum	-79.03	-1.13	2392	CTRF	WTRF		
Yambo	-79.03	-1.03	2600	CTRF	WTRF		
Lago Crispim	-48.00	-0.8	0	TRFO	STEP	TSFO	
Lagoa da Curuça2	-47.85	-0.76	35	TRFO	TRFO	TRFO	
Mariñame-II	-72.03	-0.66	160	TRFO	TRFO	WTRF	
Monica-1	-72.50	-0.60	160	TRFO	TRFO	TRFO	
Añangucocha	-77.03	-0.53	280	TRFO	WTRF		
Limoncocha	-76.66	-0.38	230	TRFO	CTRF		
Cayambe	-78.03	-0.03	4350	CGSH	CGSH	CGSH	
Lago Agrio	-77.03	0.03	330	TRFO	WTRF		
San Marcos	-79.03	0.03	3400	CGSH	TDFO		
Santa Cecilia	-77.03	0.04	330	TRFO	WTRF		
Lake Santa Cecilia	-77.02	0.06	330	TRFO	TRFO		
Cuyabeno	-77.01	0.08	280	TRFO	WTRF		



Table 6. Continued.

Site	Long.	Latitude	Alt.	Present biome	Modern	6000	18 000
Cunro	-79.03	0.08	2800	CTRF	WTRF		
Mera	-76.92	0.11	1100	WTRF	WTRF		
Lake Agrio	-76.92	0.11	330	TRFO	TRFO		
Yaguara cocha	-79.03	0.13	2210	CTRF	WTRF		
La Pata	-66.66	0.25	300	TRFO	TSFO	WTRF	WTRF
Lagoa das Patas	-66.68	0.26	300	TRFO	WTRF	TSFO	WTRF
Piusbi	-77.89	1.66	200	TRFO	TRFO	TRFO	
Pitalito	-76.50	1.75	1300	WEFO	WEFO	TSFO	
Piagua	-76.50	2.30	1700	WEFO	WEFO	WEFO	
Pantano de Genagra	-76.50	2.50	1750	WEFO	TDFO	WEFO	
Rio Timbio	-76.50	2.50	1750	WEFO	WEFO	WEFO	
El Camito	-76.60	2.53	50	TRFO	TRFO		
Loma Linda	-73.35	3.22	310	TDFO	TDFO	TDFO	
Lago Agua Sucia	-73.54	3.46	260	TDFO	TDFO	STEP	
El Gobernador	-75.00	3.95	3815	CTRF	CTRF	WTRF	
La Guitarra	-74.28	4.00	3450	COMI	COMI	CTRF	
La Primavera	-74.13	4.00	3525	CGSH	CGSH	COMI	
Corazón Partido	-74.25	4.00	4100	CGSH	CGSH		
El Trinagulo	-74.25	4.00	4100	CGSH	CGSH		
Carimagua	-74.14	4.04	180	TDFO	TDFO	CGSS	
La Rabona	-74.25	4.05	4000	CGSH	CGSH	CTRF	
El Piñal	-70.40	4.09	185	TDFO	TDFO	TDFO	TDFO
Alsacia	-74.11	4.09	3100	COMI	WAMF	COMI	
Andabobos	-74.15	4.09	3570	CGSH	CGSH	CGSH	
Ubaqué	-73.55	4.33	2000	WEFO	WEFO		
De la América	-74.00	4.33	3550	CGSH	CGSH	CTRF	
Turbera de Calostros	-73.48	4.41	3730	CGSH	CGSH		
Laguna Angel	-70.54	4.45	205	TDFO	TSFO	TDFO	
Libano	-75.50	4.50	1820	WEFO	WEFO	COMI	
de Pedro Palo III	-74.41	4.50	2000	COMI	WTRF	WTRF	
Paramo Palacio	-73.88	4.76	3550	CGSH	CGSH	CGSH	
Greja	-73.70	4.86	4000	CGSH	CGSH	CGSH	
Sardinas	-69.45	4.95	180	TDFO	TDFO	TDFO	
Herrera	-73.91	5.00	2000	COMI	CGSH	COMI	CTRF
Agua Blanca	-74.45	5.0	3250	COMI	COMI	CTRF	CGSH
El Abra II	-73.96	5.02	2570	COMI	CTRF	CTRF	
Paramo de Peña Negra	-74.09	5.09	3625	CGSH	CGSH	COMI	
ODP site 932	-47.03	5.18	0	TRFO	WTRF	WTRF	TSFO
Comprida	-47.63	5.18	130	WTRF	WTRF	TRFO	
Geral	-47.53	5.18	130	WTRF	WTRF	TRFO	
Paramo de Laguna Verde	-74.00	5.25	3625	CGSH	CGSH	CGSH	
Fúquene II	-73.87	5.50	2580	COMI	CGSH	CTRF	CTRF
Jotaordo	-76.66	5.66	0	TRFO	TRFO		
Ciénaga del Visitador	-72.83	6.13	3300	COMI	COMI	CGSH	
Bobos	-72.85	6.13	3800	CGSH	CGSH		
Ciega I	-72.31	6.50	3510	COMI	CTRF		
Valle de Lagunillas	-72.34	6.50	3880	CGSH	CGSH	CTRF	
Cana, Darien	-77.58	7.68	1000	TSFO	TSFO		
Cana Swamp	-77.59	7.74	500	TRFO	TRFO		
Wodehouse Swamp	-77.58	7.75	500	TRFO	TRFO		
La Chonta	-82.00	8.00	2310	CTRF	CTRF	COMI	WAMF
El Valle	-79.78	8.43	500	TSFO	TSFO		TDFO
La Yeguada,	-80.78	8.43	650	TSFO	TSFO	TSFO	
Cerro Campana	-79.93	8.63	800	WTRF	WTRF		
Quebrada Nelson	-82.31	8.66	1130	WTRF	WTRF		
Laguna Volcán	-82.75	8.75	1500	WTRF	WAMF		

Table 6. Continued.

Site	Long.	Latitude	Alt.	Present biome	Modern	6000	18 000
Valle Laguna Negra	-70.76	8.79	3450	CGSH	CGSH		
Valle Laguna Victoria	-70.79	8.80	3250	CGSH	CGSH	CGSH	
Horsefly Ridge	-82.24	8.83	1150	WTRF	WTRF		
Volcan Baru	-82.52	8.85	2600	CTRF	CTRF		
El Bosque	-75.45	8.85	3650	CGSH	CGSH		
Finca Lerida	-82.45	8.87	1630	WTRF	WAMF		
Volcan Irazu	-82.52	8.88	2300	CTRF	CTRF		
Paramo de Miranda	-70.85	8.91	3290	CGSH	CGSH	CGSH	
Panama	-80.87	9.00	100	TSFO	WTRF	TSFO	
Ocelot Pond	-79.59	9.12	20	TSFO	WTRF		
Soberania	-79.66	9.13	20	TSFO	WTRF		
Paramo Piedras Blancas	-70.83	9.16	4080	CGSH	CGSH	CGSH	
Pipeline Rd	-79.66	9.33	40	TSFO	WTRF		
Barro Colorado Island	-79.75	9.35	50	TSFO	WTRF		
Lago Chirripó	-83.48	9.48	3520	CTRF	WAMF		
Talamancas	-83.72	9.5	2500	CTRF	WAMF		
Lago de las Morrenas	-83.49	9.50	3480	CTRF	WAMF	CTRF	
Bog 70	-83.85	9.61	2670	CTRF	WTRF		
Tres de Junio	-83.87	9.62	2670	CTRF	CTRF		
Bog 68	-83.85	9.64	2670	CTRF	WTRF		
Asuncion	-83.75	9.64	3340	CTRF	CTRF		
Carara Biological Reserve	-84.62	9.73	0	TSFO	TSFO		
Quebrador	-83.84	9.74	3040	CTRF	CTRF		
Cataracta, Carara 1	-84.63	9.83	270	TSFO	WTRF		
Cataracta, Carara 2	-84.63	9.85	270	TSFO	WTRF		
Carara	-84.60	9.88	35	WTRF	WTRF		
Laguna Bonilla	-83.61	9.99	380	TSFO	WTRF		
Laguna Barva	-84.11	10.14	2840	CTRF	WTRF		
Laguna Botos	-84.18	10.18	2600	CTRF	WTRF		
Laguna Palmita	-84.95	10.18	60	TSFO	WTRF		
Bosque Alegre	-84.21	10.21	740	WTRF	WTRF		
Laguna González	-84.45	10.25	710	WTRF	WTRF		
Laguna Congo	-84.29	10.27	740	WTRF	WTRF		
Laguna Hule	-84.19	10.27	740	WTRF	WTRF		
Laguna María Aguilar	-84.18	10.27	770	WTRF	WTRF		
Monteverde, Heredia	-84.8	10.3	1500	WTRF	WTRF		
Volcan Poas	-84.19	10.3	2580	CTRF	CTRF		
Braulillo Carillo, Heredia	-83.94	10.3	630	WTRF	WTRF		
Lake Valencia	-67.75	10.32	403	STEP	STEP	TDFO	
Laguna Río Cuarto	-84.18	10.34	380	WTRF	WTRF		
La Selva, Heredia	-84	10.43	80	TSFO	TSFO		
La Pacifica, Guanacaste	-85.11	10.45	110	TSFO	TSFO		
Cantarrana Swamp	-84.00	10.45	36	TSFO	WTRF		
Sendro Sedro Swamp	-84.00	10.46	40	TSFO	WTRF		
Laguna La Palma	-84.73	10.49	570	WTRF	WTRF		
Laguna Cedeño	-84.71	10.49	610	WTRF	WTRF		
Tortuguero	-83.53	10.53	0	TSFO	WTRF		
Santa Rosa2	-85.64	10.83	0	TSFO	TSFO		
Santa Rosa1	-85.66	10.84	0	TRFO	TRFO		
Boca de Lopez	-75.36	10.85	0	TRFO	TRFO		
Cafetal, Guanacaste	-85.65	10.85	300	TSFO	WTRF		
Santa Rosa3	-85.62	10.86	280	TSFO	TSFO		
Santa Rosa4	-85.62	10.86	280	TSFO	WTRF		
Escondido	-85.61	10.87	280	TSFO	WTRF		
Volcán Cacao	-85.47	10.92	1000	WTRF	WTRF		
Sierra de Cuchumatanes5	-91.00	15.75	2800	WAMF	WAMF		

Table 6. Continued.

Site	Long.	Latitude	Alt.	Present biome	Modern	6000	18 000
Sierra de Cuchumatanes4	-91.25	15.75	3000	CTRF	CTRF		
Sierra de Cuchumatanes3	-91.5	15.75	3400	CTRF	CTRF		
Sierra de Cuchumatanes2	-91.75	15.75	3600	WAMF	WAMF		
Sierra de Cuchumatanes1	-92.00	15.75	4200	CGSH	CTRF		
Lago Quexil	-89.88	16.92	110	TSFO	WAMF	WEFO	WAMF
Lake Peten-Itza	-90.00	17.25	200	TDFO	TDFO	WEFO	
Lago Catemaco	-95.00	18.66	340	TRFO	WAMF		
Zempoala	-99.30	19.20	3100	WAMF	WAMF		
Quila	-99.20	19.30	2800	WAMF	WAMF	WAMF	
Lake Texcoco	-99.12	19.44	2330	WAMF	WAMF	WAMF	WAMF
Chalco Lake	-99.00	19.50	2240	WAMF	WAMF	WAMF	WAMF
Lake Pátzcuaro	-101.58	19.58	2044	WAMF	WAMF	WAMF	WAMF
San Jose Chulchaca	-90.13	20.86	1	TDFO	TDFO	WEFO	
Lake Coba	-87.55	20.86	100	WAMF	WAMF	WEFO	

appears important. For other sites where the reconstructed biome does not match the potential vegetation map a series of different explanations, particularly local site-specific factors such as human impact, can be invoked, these will be discussed fully. Taking our modern pollen to potential vegetation calibration, and the design of the matrices that drive it, we reconstruct vegetation at past time intervals with “cautious confidence”.

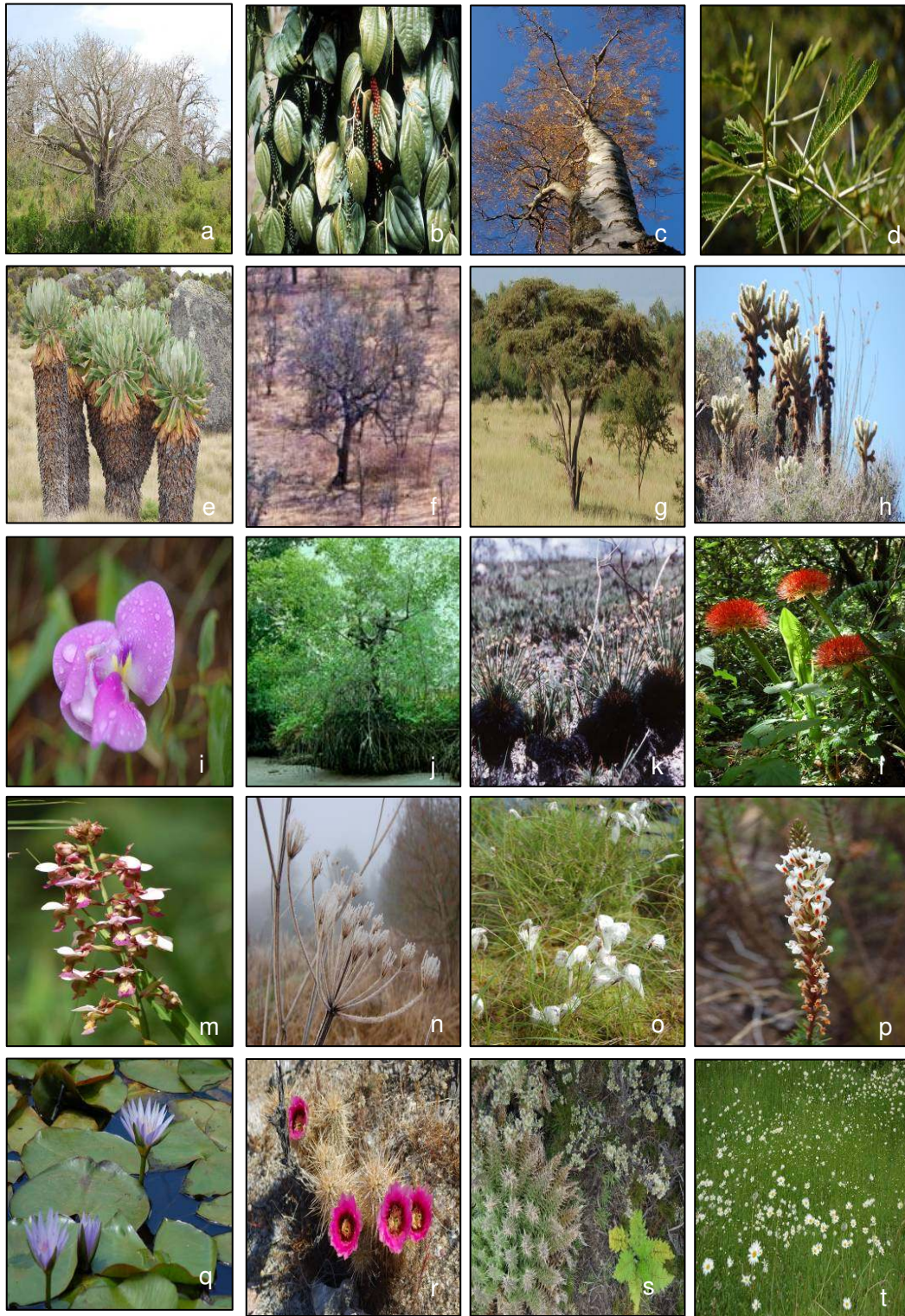
### 3.2 6000 $^{14}\text{C}$ yr BP biome reconstruction

The biomes reconstructed at  $6000\pm 500$   $^{14}\text{C}$  yr BP (Fig. 8) show relatively small patterns of change compared to the present. 49% of the sites retain the same biome assignment as present (Table 6). In southeastern Brazil, the majority of the sites that were previously assigned to the warm temperate forest biome remain unchanged. A number of sites (e.g. Serra Campos Gerais, Rio São Francisco, Aguads Emendadas) record tropical dry forest at  $6000\pm 500$   $^{14}\text{C}$  yr BP replacing tropical seasonal forest (Lagiuna Angel, Laguna Chaplin) record at the present. Sites assigned to tropical rain forest and tropical seasonal forest today mainly remain unchanged at  $6000\pm 500$   $^{14}\text{C}$  yr BP. Steppe continues to be reconstructed in southeastern Argentina, as today. However, a number of sites had substantially more arboreal components at  $6000\pm 500$   $^{14}\text{C}$  yr BP than today, for example Empalme Querandfes and Lake Valencia show a transition from steppe to tropical dry forest. An expansion of steppe is recorded at sites previously assigned to cold mixed forest on the Cordillera de los Andes. Unlike sites in southernmost South America that similarly record steppe, these sites also contain significant amounts of *Alnus* and *Podocarpus* indicative of “parkland” at this time. On closer inspection of the affinity scores, sites record an increased affinity to cool temperate rain forest, primarily due to increased amounts

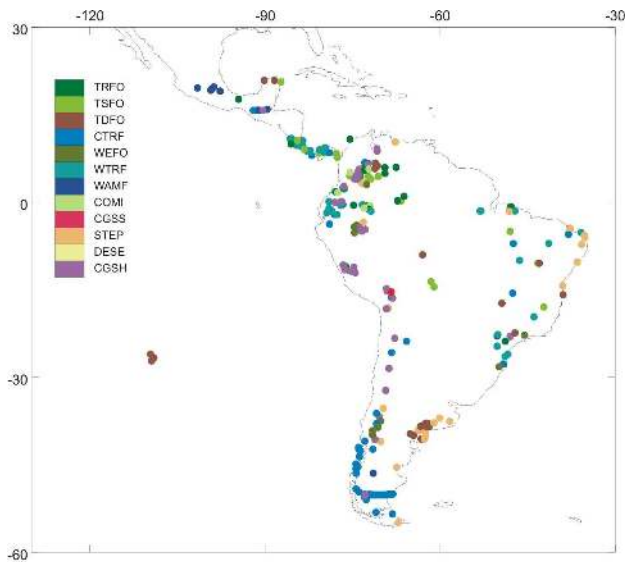
of *Nothofagus* pollen, although this was not sufficiently numerous to produce a cool temperate rain forest assignment. Southernmost South America continues to have a mixture of cool mixed forest, cool grass/shrubland, steppe and cool temperate rain forest biomes, the latter being dominant. Along the southern Andean spine, the assignments do not differ greatly from the modern assignment. There are broadly similar assignments to the present at Colombian sites although there is a slight increase in the number of cool mixed forest and cool temperate rain forest biome assignments relative to cool grass/shrubland of the present day. The sites where this occurs (e.g. Primevera, and Páramo de Peña Negra) are located at high altitude and may reflect either an extension of the forest line or increased distribution of Andean forest that predates early human impact. Sites in coastal northern South America show a transition to tropical dry forest and tropical seasonal forest from steppe and tropical dry forest respectively, both indicative of a relatively mesic environment. A number of sites on the Yucatán peninsula show a clear distribution of warm evergreen forest at  $6000\pm 500$   $^{14}\text{C}$  yr BP changing from the warm mixed forest and tropical dry forest reconstruction for the present day. These transitions are not recorded everywhere, for example sites located in the Mexican highlands retain the same biome assignment at the present – warm mixed forest.

### 3.3 18 000 $^{14}\text{C}$ yr BP biome reconstruction

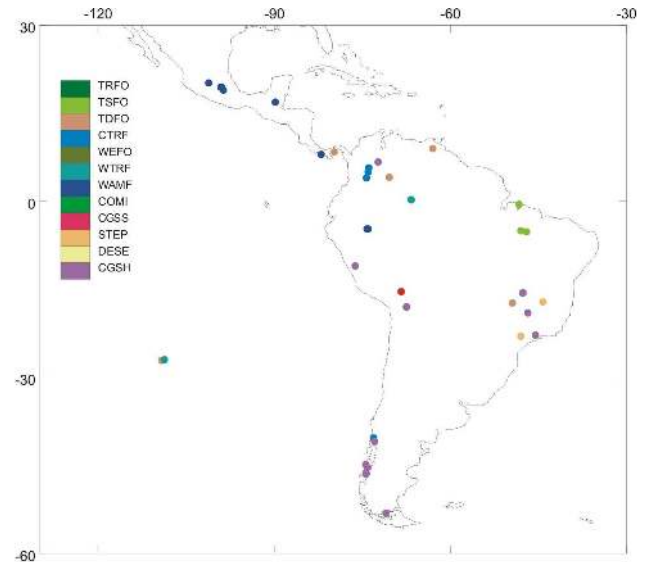
Vegetation at  $18\,000\pm 1000$   $^{14}\text{C}$  yr BP was substantially different from the present-day, or that reconstructed at  $6000\pm 500$   $^{14}\text{C}$  yr BP (Fig. 9). The intensity of this vegetation transformation is demonstrated by 74% of the sites change the biome assignment relative to the two previous periods. In Amazonia, tropical seasonal forest and tropical dry forest is recorded instead of tropical rain forest



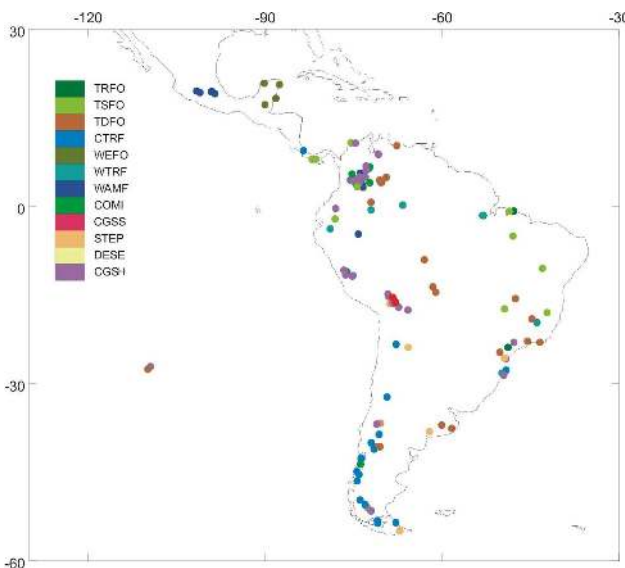
**Fig. 6.** Latin America plant functional types: (tropical rain green tree (a), tropical evergreen tree (b), temperate summer-green tree (c), tropical xerophytic tree/shrub (d), arctic shrub (e), desert shrub (f), dry tropical rain green tree (h), desert shrub (i), tropical forb (i), mangrove (j), xerophytic forb (k), tropical forb (l), temperate forb (m, n), grass (o), alpine forb (p), aquatic (q), desert forb (r, s) grass (t).



**Fig. 7.** Modern biomes reconstructed from surface pollen data (core top, trap, surface sediment) used to compare against the potential vegetation (Fig. 2).



**Fig. 9.** Biome reconstruction at  $18\,000 \pm 1\,000$   $^{14}\text{C}$  yr BP from radiocarbon dated fossil pollen.



**Fig. 8.** Biome reconstruction at  $6\,000 \pm 500$   $^{14}\text{C}$  yr BP from radiocarbon dated fossil pollen.

or tropical seasonal forest reconstructed for the present. A site on the present southern Amazonian boundary (Laguna Chaplin) records tropical seasonal forest. Sites in southern South America nearly all show a transition from cool mixed forest biomes and cool mixed forest to cool grass/shrubland and cool grassland. However, within this homogenous reconstruction a number of sites have a relatively high affinity to the cool temperate rain forest biome, due to a mix of *Donartia* and *Nothofagus* pollen: this ex-

plains why the northernmost site in this cluster records cool temperate rain forest. Sites in southeastern Brazil record a transition from tropical dry forest to tropical seasonal forest and cool grass/shrubland. Sites in Amazonia record mainly tropical seasonal forest, warm temperate rain forest or steppe; this combination indicating relatively mesic forest. In the Colombian lowlands, tropical dry forest continues to be assigned whereas Colombian highland locations reflect a marked change from cool temperate rain forest and cool mixed forest to the cool grass/shrubland biome. Sites in Central America show a change from tropical seasonal forest to tropical dry forest, e.g. El Valle. The Mexican highland sites remain unchanged, continuing to support warm mixed forest with the pollen records being dominated by *Pinus* and *Quercus*.

## 4 Discussion and conclusions

### 4.1 Modern reconstruction

Previous applications of the biomisation method in Africa (Jolly et al., 1998a; Elenga et al., 2000), China (Yu et al., 1998, 2001), Australia (Pickett et al., 2004), Eastern North America (Williams et al., 2000), Eurasia (Tarasov et al., 1998a), Europe (Prentice et al., 1996a, b; Tarasov et al., 1998a, b; Elenga et al., 2000), Japan (Takahara et al., 2001) and Western North America (Thompson and Anderson, 2000) demonstrate that technique is able to translate multi-site pollen data to coarse resolution vegetation reconstructions that works well over a range of vegetation types. The Latin American results presented here provide a further test of this ability. The ability of the biomisation method to

reconstruct biomes derives in part from the relatively coarse vegetation classification (Fig. 2); which conceals significant intra-biome variation; for example, we do not distinguish subtypes of the warm evergreen forest biome which contains *Araucaria* in southern and southeastern Brazil and *Podocarpus* in the northern Andes. The success of the biomisation technique is in part due to reconstructions being carried out at a regional scale, allowing the methodology to be adapted to the local flora, bioclimatic gradients and pollen spectra. For example, the treatment of *Quercus* pollen in Latin America is quite different from that in a European context. Similarly, in Africa *Podocarpus* is assigned to the warm temperate broad-leaved evergreen PFT (Jolly et al., 2001), although this taxon is a coniferous needle-leaved tree, in Latin America it is assigned to cool and intermediate temperate conifers. This regional focus also allows the pollen to plant functional type allocations to be based on good ecological information concerned with environmental tolerances to growth limits and an understanding of how representative the pollen is of the surrounding vegetation. This is particularly important as the pollen taxa identified to the generic level (the taxonomic level usually identified to) exhibit considerable plasticity in their growth form and environmental tolerance. For example, within the genus *Cordia*, commonly a woody shrub of open thorn woodland, of the northern Andes (Cleef and Hooghiemstra, 1984) two species of *Cordia* are herbs in cerrado (Pereira et al., 1990; Sarmiento, 1975), the genus is also present (*C. lomato-loba* and *C. sagotii*) in Amazonian *terra firme* forest and Guyanese lowland rain forest (Steege, 1998). Furthermore the specific nature of pollen production, dispersal and incorporation into a sedimentary environment exhibits considerable variability that is part dependent on site characteristic. All these factors have a bearing on the results and need to be considered in the designing of the input matrices into the biomisation process and interpretation of results.

Biomes are mainly accurately reconstructed for the present-day even though large areas of Latin America are covered with vegetation that has been altered by a long history of human land use (Behling, 1996; Binford et al., 1987; Fjelds , 1992; Gn cco and Mohammed, 1994; Gn cco and Mora, 1997; Marchant et al., 2004; Northrop and Horn, 1996). One possible reason for this may relate to the nature of the “modern” samples. Within our analysis the modern samples are largely derived from sedimentary columns rather than surface trap pollen data, and hence they may stem from the last 500 years and be reflective of a period prior to intensive human-induced change. However, the signal of vegetation clearance does impact on the modern reconstruction as shown by the large number of sites recording cool grass/shrubland, particularly at lower and mid-altitudes that should support cool mixed forest or cool temperate rain forest. These assignments are thought to result from human impact with the pollen spectra being dominated by Poaceae and hence recording more open vegetation. To quantify the

nature of this impact, it is possible to tailor the biomisation methodology to include elements of the pollen spectra, such as agricultural and ruderal taxa, that may indicate human impact (Marchant et al., 2002). The ability to reconstruct potential, rather than actual vegetation, may also relate to the type of impact; although spatially relatively widespread, forest clearance is often only partial with many localised patches of forest and secondary vegetation remaining. This results in the floristic composition of the remaining vegetation, in palynological terms at least, closely reflecting the original vegetation composition. For example, the forest surrounding the F quene-II site is a successional type of forest whereas the natural vegetation would be a Andean forest type dominated by *Quercus* and *Weimannia* mixed with *Croton*, *Oreopanax* and *Phyllanthus* (Van Geel and Van der Hammen, 1973). In addition to the relatively coarse potential vegetation and biome classification, mapping the highest biome affinity score to each site as a single dot also allows the method to be relatively robust. Although this is suitable for the relatively coarse reconstructions necessitated by the continental/sub-continental scale, when investigating a small area, more information can be preserved from the analysis. Indeed at a regional scale information on sub-dominant biomes can be kept (Marchant et al., 2001a), new more defined biomes (Bigelow et al., 2003) or at a site-specific scale where the affinity scores to all the biomes can be retained (Marchant et al., 2001b, 2002b).

Despite the overall agreement between potential and reconstructed biomes a number of locations show anomalies. Due to the floristic and structural similarities between warm and cool grasslands (Tarasov et al., 1998a), grass-dominated biomes can be particularly difficult to distinguish from one another. Differentiation is possible by the other plants within steppe and cool grass/shrubland, although there remains a high affinity score to the cool grass/shrubland at low altitudes with the reverse for the steppe biome at high altitudes. Another facet is that some lowland sites show reconstructions of highland biomes, e.g. sites in central Panama and Amazonia recording warm temperate rain forest. This result is driven by the presence of genera that are typical of montane vegetation, e.g. *Hedyosmum*, *Podocarpus* and *Quercus*. A possible explanation for the presence of these highland elements is that they are relictual; relatively isolated today they were previously much more widespread under the glacial climate norm of the Quaternary. This suggestion is supported by the similarity, at a generic level, of the flora in highland Brazil and the northeastern Andes, and the isolated patches of savanna within Amazonian forest and the Brazilian cerrado. Furthermore, it is interesting that the presence of highland elements appears to be greater when the moisture levels are high. For example, within the Choc  Pacific region, where rainfall exceeds 15 000 mm yr<sup>-1</sup>, montane elements appear more common than within Amazonia (Cleef, personal communication).

Notwithstanding some of the anomalies mentioned, the biomisation method applied to Latin American pollen data can reconstruct large-scale vegetation patterns despite many pollen taxa having different ecological interpretations under different environmental settings (Grabandt, 1980), representation of parent vegetation by pollen likely to be subject to inter-annual variability (Behling et al., 1997b), and tropical vegetation is difficult to reconstruct through pollen assemblages (Bush, 1991; Mancini, 1993; Bush and Rivera, 1998; Behling et al., 1997). These factors demonstrate the importance of basing the input matrices for the biomisation process on all the available ecological information that allowing for the multiple assignment of the pollen taxa to the PFTs.

## 4.2 Late Quaternary biome change and palaeoenvironmental interpretations

### 4.2.1 6000±500 <sup>14</sup>C yr BP

Compared to the present, the sites at 6000±500 <sup>14</sup>C yr BP record either the same biome or one indicating more xeric vegetation. Dry environmental conditions in southern Brazil extend from the early Holocene until approximately 4500 <sup>14</sup>C yr BP when there was an increase in arboreal taxa (Alexandre et al., 1999). Maximum aridity in southeast Brazil was reached between approximately 6000 and 5000 <sup>14</sup>C yr BP, prior to the transition to a modern climate (Behling, 1997a). The driest phase in central Brazil is at approximately 5000 <sup>14</sup>C yr BP; relatively moist climate conditions similar to today setting in after 4000 <sup>14</sup>C yr BP (Ledru, 1993; Marchant and Hooghiemstra, 2004). Although fire has been proposed as being responsible for late Holocene variation in the forest/savanna boundary in Brazil (Vernet et al., 1994; Desjardins et al., 1996; Horn, 1993), this relative aridity is thought to reflect an extended dry season during this period (Behling, 1997b). An extended dry season may explain why *Araucaria*-dominated forest were still restricted in their distribution relative to the modern day, not significantly increasing in range until approximately 3000 <sup>14</sup>C yr BP (Behling, 1997a). From our analysis the temporal perspective is missing, hence, we are unable to indicate if the vegetation reflects a stable dry period, or a period where there are alternating periods of dry and humid climates linked for example to El Niño activity (Martin et al., 1993; Sifeddine et al., 2001). A relatively dry phase is also recorded in northwestern Argentina between 7500 and 5800 <sup>14</sup>C yr BP (Schäbitz, 1991). Although pollen assemblages do not lend themselves well to distinguishing moisture from temperature changes, stable hydrogen isotope analysis on mosses show the vegetation of southern South America is highly sensitive to changes in moisture regime (Pendall et al., 2001). The predominance of steppe in southeastern Argentina agrees with the reconstruction by Prieto (1996): steppe characterising the area between 7000 and 5000 <sup>14</sup>C yr BP. Locally high moisture levels at sites closer to the Atlantic Ocean (Prieto,

1996) may explain why sites under strongest maritime influence (Aguads Emendadas, Cerro La China) changes from steppe to tropical dry forest as the local environment is able to support more arboreal taxa. In southwestern Patagonia a sustained increase in *Nothofagus* pollen has been detected from around 6800 yr BP thought to result from locally increased moisture levels (Villa-Martinez and Moreno, 2007). Locally increased moisture levels in this part of Latin America during the mid Holocene are thought to stem from intensification of the southern Westerlies (Gilli et al., 2005).

Farther west, cool temperate rain forest assignments indicate a similar climatic regime and the maintenance of Valdivian rain forest (Villigran, 1988). 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 <sup>14</sup>C yr BP (Baied and Wheeler, 1993; Villigran, 1988). In lowland Chile, the period of maximum aridity occurred between 9400 and 7600 <sup>14</sup>C yr BP with drier than present conditions continuing until 5000 <sup>14</sup>C yr BP (Heusser, 1982), this could explain the increased presence of steppe at sites along the southern Andes. On the central Peruvian Andes, a dry warm climate was encountered between 7000 and 4000 <sup>14</sup>C yr BP (Hansen et al., 1994).  $\delta^{18}\text{O}$  measurements from an ice core record taken from highland Peru show that mid-Holocene climatic warming and drying was recorded from 8200 to 5200 <sup>14</sup>C yr BP with maximum aridity between 6500 to 5200 <sup>14</sup>C yr BP (Thompson et al., 1995). Farther north on the Bolivian Andes, a dry phase is recorded from approximately 5500 <sup>14</sup>C yr BP (Abbot et al., 1997). The slight increase in the number of arboreal biome assignments at northern Andean sites can be interpreted as an up-slope shift of forest line. This conforms to the suggestion based on pollen data by van Geel and van der Hammen (1973) that the vegetation zones in the northern Andes were several hundred of meters higher than the present at approximately 6000 <sup>14</sup>C yr BP. Relatively dry conditions have also been indicated for lowland Colombia for the mid-Holocene although the onset of dry conditions varied considerably between sites – occurring between 6500 and 4500 <sup>14</sup>C yr BP (Behling et al., 1999). Added complexity is caused by steep environmental gradients associated with non-climatic factors. 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).

Farther north, the assignment of Lake Valencia to the tropical dry forest is in agreement with the site-specific interpretation that more arboreal taxa (*Bursera*, *Piper* and *Trema*) were present after approximately 10000 <sup>14</sup>C yr BP due to the onset of a more humid climate (Bradbury et al., 1981); these tropical rainforest taxa are indicative of a seasonal climate with relatively dry conditions. This appears to be a regional signal as early Holocene evergreen forests of northern Venezuela were replaced by semi-deciduous elements during the mid-Holocene (Leyden, 1984). Enhanced precipitation

over Central America would have been accompanied by a northward shift of the ITCZ, enhanced southerlies and cooler equatorial sea surface temperatures (Harrison et al., 2003). Low lake levels in central Panama also indicate that environmental conditions at this period were more xeric (Piperno et al., 1991b; Bush et al., 1992) whereas sites on the Yucatán peninsula show a shift to warm evergreen forest where the warmer conditions that characterise the early Holocene persisted until approximately 6500  $^{14}\text{C}$  yr BP (Brown, 1985). This result may stem from locally high moisture levels as a result of maritime influence, a similar mechanism having been proposed to explain a comparable shift in coastal Brazil and Argentina. Despite the majority of the 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  $^{14}\text{C}$  yr BP although there is considerable variation in the timing of the onset of more humid conditions so it may be that such a mesic period falls outside our temporal window.

One of the main mechanisms used to explain moisture shifts is fluctuations in the Southern Oscillation and the migration of the ITCZ (Martin et al., 1997). Martin et al. (1997) suggests that during the mid-Holocene, the ITCZ was located farther north than its present-day position (Fig. 1) – this would produce a summer rainfall deficit and increased winter precipitation; in short greater seasonality. 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). 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 (Fig. 1). Therefore, moisture changes over northeastern South America are likely to result from the importance of convective moisture sources; reduced precipitation, particularly in mid latitude western South America, following reduced intensity of 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 (ENSO) were more frequent in the mid-Holocene (Markgraf, 1998). This later suggestion may also have led to the increased fire frequency indicated in southeast Brazil (Alexandre et al., 1999).

The spatial relationship between Latin American and Africa (Servant et al., 1993; Jolly et al., 1998a) warrants further investigation (Marchant and Hooghiemstra, 2004). A particular target for the investigation could be the impact and feedbacks of vegetation changes on climate. For example, large changes in African vegetation about the Sahel are suggested to have been important in influencing Indian monsoon dynamic (Doherty et al., 2000). Such a phenomena of vegetation feedbacks on the climate system appears weaker in

South America than in Africa although it is likely to have had an impact as yet unqualified. Certainly Latin America would benefit from targeted model applications in the same way that has been applied to Africa (Kubatzki and Claussen, 1998; Doherty et al., 2000). This modelling of climate dynamics Latin American represents a special challenge for climate models and modellers (Valdes, 2000) primarily due to the steep environmental gradients and rapid transition from one biome to another (Fig. 2).

#### 4.2.2 18 000±1000 $^{14}\text{C}$ yr BP

The dating of the LGM in Latin America can be problematic (Bush et al., 1990; Hooghiemstra et al., 1992; Ledru et al., 1996, 1998; Sifeddine et al., 2001); late Pleistocene sediments often containing sedimentary gaps at, or about, the LGM (Ledru et al., 1998), that are compounded by slow sedimentation rates. These sedimentary constraints make characterisation of the LGM vegetation highly contentious and have fuelled debates on LGM climates spanning two decades (Hooghiemstra and van der Hammen, 1998; Colinvaux et al., 2000; Thomas, 2000). Indeed, it has been suggested that some of the sites used in our analysis do not contain a sedimentary record of the LGM (Ledru et al., 1998) although due to application of a 2000 year-wide time window, we are able to include some of these sites with contentious sediments.

The LGM in Latin America, like most of the tropics, was characterised by a cold dry climate (González et al., 2008) with temperature reduced by about 4°C and precipitation by about 30% (Farrera et al., 1999). Ice caps were present on the southern tip of South America which spread onto the plains and the coastal area (Heine, 1995). Evidence from glacial moraines also indicates considerable expansion of Andean glaciers (Hollis and Schilling, 1981; Villagran, 1988; Birkland et al., 1989; Seltzer, 1990; Thouret et al., 1997). Most of southern South America was characterised by an erosional environment; locations that would later accumulate sediments were glaciated, or subject to fluvial activity (Heine, 2000). This situation is recorded by ice cores from the high Andes that contain large amounts of dust about the LGM, this being derived from surrounding deflating desert areas (Thompson et al., 1995). This cold, arid environment is clearly reproduced by the vegetation which shows a transformation from the cool temperate rain forest to the cool grass/shrubland biome. Although *Nothofagus*-dominated forest is thought to have been extrapolated from coastal Chile at the LGM (Hollis and Schilling, 1981), fossil beetle assemblages in basal peat from Puerto Eden (49° S, 74° W) indicate that *Nothofagus*-dominated forest survived glaciation within the Chilean channels (Ashworth et al., 1991). An earlier date of deglaciation of the Taitao Peninsula indicates there was relatively local migration from Chiloé Island that may explain the rapid re-growth of *Nothofagus*-dominated forest (Lumley and Switsur, 1993). Along the Chilean Pacific coast the present cool evergreen



forest was shifted approximately 5° northwards relative to the present day; not as a discrete forest type but as a parkland type vegetation mosaic (Villagran, 1988), not forming closed forests until the early Holocene (Schäbitz, 1994; Heusser, 1995). This vegetation is evidenced with the analysis presented here by the northernmost site (Laguna Six Minutes) recording cool temperate rain forest. However, it is unlikely this represents closed forest persisting in the area, trees being present within a woodland/steppe vegetation mosaic (Villagran, 1988). The rate of spreading of this forest into the Holocene would probably have been strongly dependent on the density of the parent plants from the initial seeding fraction (Huntingford et al., 2000). The maintenance of cool temperate rain forest taxa, albeit at relatively low levels, may result from high moisture levels as recorded by high lake stands at this time (Markgraf et al., 2000). These may reflect outbreaks of polar air and subsequent generation of low-pressure systems in the western Atlantic; combined with lower temperatures this situation would lead to a positive water balance. Indeed, the presence of relatively local moisture sources would have been important at the LGM and allow us to explain regional patterns of biome change outside the influence of the ITCZ migrations (Markgraf et al., 2000).

Considering the sites along the northern Andes, it is clear from the vegetation that climate was colder during the LGM, reductions up to 12°C may have been reached at very high altitudes (Thompson et al., 1995). A substantial temperature depression during the last glacial period is mirrored by a significant impact on the vegetation composition and distribution. From our analysis it is apparent that the tree line was significantly lower at the LGM, concordant with a suggested lowering of vegetation zones by approximately 1000 to 1500 m relative to the present-day position (Monslave, 1985; Wille et al., 2001). At lower elevations in western Colombia, a more conservative depression of the vegetation has been suggested from Timbio (Wille et al., 2000). Indeed, the spatial character of the cooling and drying in the Neotropics is still under debate (Markgraf, 1993; Colinvaux, 1996; Hooghiemstra and Van der Hammen, 1998; Farrera et al., 1999; Boom et al., 2002). Greater temperature change at high altitudes compared with those at low altitudes and at the sea surface (CLIMAP, 1976) can be explained in terms of changes in lapse rate (Bush et al., 1990; Peyron et al., 2000; Wille et al., 2001) or compression of vegetation belts (Van der Hammen and Absy, 1994). The lapse-rate gradient is partly influenced by atmospheric moisture levels (Barry and Chorley, 1990). As precipitation was reduced at the LGM, an overall steeper lapse rate, particularly at higher altitudes where moisture reductions would have been highest, seems likely (Wille et al., 2001). The extent to which lapse-rate changes can be used to explain spatially different signals from the data must be used with caution, particularly as most palaeoclimatic reconstructions have been carried out with some kind of modern analogue approach (Farrera et al., 1999). These reconstructions commonly do not take into ac-

count non-climatic parameters which would impact on vegetation composition and distribution such as volcanic activity (Kuhry, 1988), fire (Cavelier et al., 1998; Rull, 1999), UV-B insolation (Flenley, 1998) or atmospheric composition, in particular changing CO<sub>2</sub> levels (Woodward and Bond, 2004). For example, concentrations of CO<sub>2</sub> reduced to glacial levels (200 ppmV) have been shown to have a very significant impact on tropical vegetation (Jolly and Haxeltine, 1997; Boom et al., 2002; Marchant et al., 2002b; Wu et al., 2007a, b).

In south-east Brazil vegetation at the LGM was characterised by tropical dry forest and tropical seasonal forest; this latter vegetation type may have been restricted within deep valleys and along waterways; site-specific records from southeast Brazil indicate open grasslands (campo limpo) with forest elements being retained as gallery forest (Behling, 1997a). Some model reconstructions of global vegetation patterns have indicated that there was an increase in warm evergreen forest in Brazil at the LGM at the expense of tropical seasonal forest (Prentice et al., 1993). This pattern of change is supported by the data presented here where plants generally found at high altitudes today were more common in Amazonia at the LGM. Clapperton (1993) used geomorphic data to infer a very sparsely vegetated landscape on the Brazilian Highlands, possibly relating to our reconstruction of steppe for a site in eastern Brazil. However, the cool grass/shrubland biome appears to be a common type of vegetation at this time. Cold climates in eastern South America could have resulted from the incursion of polar cold fronts that would occasionally reach northwards of the equator (Ledru, 1993; Behling and Hooghiemstra, 2001). This phenomenon could combine with equatorward shift of polar high-pressure areas and mid-latitude cyclones resulting in displacement and compression of the subtropical anticyclone between mid latitudes westerlies (Dawson, 1992). This climatic regime would result in more restricted migration of the ITCZ and pronounced aridity that would have been compounded by lower sea surface temperatures and associated reduction in atmospheric moisture.

At altitudes of approximately 3000 m in northern Peru vegetation about the LGM comprised a mixture of wet and moist montane forest elements with open woodland (Hansen and Rodbell, 1995); this vegetation association having no modern analogue. Although the Andes remained relatively moist at the LGM, particularly in the northern part where the concave shape of the mountain chain entrap moisture from the rising air (Fjeldså et al., 1997), it is not certain what occurred in the lowland areas to the east of the Andes (Colinvaux, 1989; Colinvaux et al., 1997; Bush et al., 1990; Thouret et al., 1997). In the Colombian lowlands two sites are characterised by the tropical dry forest biome, this agrees with the suggestion from a pollen study at Rondonia that very open savanna characterised the catchment at the LGM (van der Hammen and Absy, 1994). Similarly, sparse vegetation cover would have been present on the Plateau of Mato Grosso (Servant et al., 1993) and is likely to have extended along the

coastal areas of Guyana and Surinam (Wijmstra, 1971) – this scenario is supported by our analysis, i.e. a site in lowland Panama recording tropical seasonal forest. Although the majority of the area presently covered by drier types of tropical forest would probably have been replaced by more open woodland at the LGM, environmental changes in savannas at the LGM appear to have been spatially complex. Whether the drier, cooler, conditions resulted in restricted range forest refugia cannot be answered from the available evidence although the vegetation appears heterogeneous as a mosaic of Andean, savanna and tropical rain forest taxa combined. Indeed, this reiterates the suggestion by Colinvaux et al. (2001) and now widely accepted within the palaeoecological community, that plants responded to Quaternary climate changes as individuals not as biomes. Therefore, to fully investigate vegetation response to climate change is necessary to retain information contained within the affinity scores to the subdominant biomes (Marchant et al., 2002), or to carry out the analysis at the PFT level. Indeed this approach would allow investigations into which elements of the vegetation were particularly sensitive to environmental change. Expansion of savanna could have been aided by reduced CO<sub>2</sub> concentrations and the resultant competitive advantage attained by C<sub>4</sub> grasses over C<sub>3</sub> plants (Haberle and Maslin, 1999; Marchant et al., 2002).

Within highland México, warm mixed forest continues to be reconstructed due to the presence of *Pinus* and *Quercus*-dominated forests. Although the same biome is recorded at all time periods, it unlikely to be analogous to present day mixed forest; this was characterised by sparsely forested temperate scrub (Binford et al., 1987). This continued reconstruction also could be demonstrating that certain locations are unlikely to register a change due to their position in bioclimatic space: those sites located far away from the boundaries of adjacent biomes would need a massive climatic change to result in an ecosystem shift. Such a situation has clearly been shown for the Holocene where the sites to undergo biomisation show little change relative to the modern (Ortega-Rosas et al., 2008a, b). Indeed, a site located in northwestern México records a transition from cool conifer forest to warm mixed forest about 6000 yr BP (Ortega-Rosas et al., 2008b). Similarly, a strong aridity signal is directly recorded by low lake levels in central México due to reduced northern excursion of the ITCZ, trade wind circulation, and ensuing reduced oceanic-land moisture transfer (Markgraf et al., 2000) that would have been reflected in ecosystem response. For example, forest on the Pacific side of the Central America contained a mosaic of high and low altitude forest species; a similarly novel type of forest has also been shown for Mera, Ecuador (Liu and Colinvaux, 1985) and Peten, Guatemala (Leyden, 1984). Of the two sites that record the warm evergreen forest biome at this period a site in Guatemala was dominated by Chenopodiaceae, *Juniperus*, *Pinus* and *Quercus*.

We have presented vegetation reconstructions throughout Latin America at 6000±500 <sup>14</sup>C yr BP and 18 000±1000 <sup>14</sup>C yr BP using an objective method based on biomes, constituent PFTs that are described by a set of unique pollen spectra. As a unified methodology has been applied to the pollen data, this reconstruction of biomes provides an objective basis for interpreting large-scale vegetation dynamics, and the environmental controls on these over the late Quaternary and can be used as a dataset for model-data comparisons at 6000 and 18 000 yr BP. Changes at 6000±500 <sup>14</sup>C yr BP, although relatively small, indicate a transition to more xeric vegetation. The changes at 18 000±1000 <sup>14</sup>C yr BP are more homogenous and indicative of a cooler, drier climate. These reconstructions are consistent with numerous site-specific interpretations of the pollen data. The success of the reconstruction has in part been determined by the coarse resolution of biome definitions, and using the most dominant biome for description and interpretation of the results. To develop understanding of vegetation response to environmental change, and possible feedbacks, information that is presently redundant should be retained and the results combined with climate/vegetation modelling initiatives. It is apparent from the relatively sparse coverage, in comparison to Europe and North America, that the late Quaternary vegetation history of the Neotropical phytogeographical realm remains still relatively poorly resolved despite its importance in model testing, developing biogeographical theory (Tuomisto and Ruokolainen, 1997), and understanding issues concerned with biodiversity and human-environment interactions. It has been shown that environmental change is rarely spatially uniform and as such necessitates an even greater number of sites to determine more precisely this complexity and the driving mechanisms behind this. New sites, located in key areas, combined with the application of a range of proxies of environmental change, are required to refine our understanding of Neotropical ecosystem responses to late Quaternary climatic variations.

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