

Quaternary Ice-Age dynamics in the Colombian Andes: developing an understanding of our legacy

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Pollen records from lacustrine sediments of deep basins in the Colombian Andes provide records of vegetation history, the development of the floristic composition of biomes, and climate variation with increasing temporal resolution. Local differences in the altitudinal distribution of present-day vegetation belts in four Colombian Cordilleras are presented. Operating mechanisms during Quaternary Ice-Age cycles that stimulated speciation are discussed by considering endemism in the asteraceous genera *Espeletia*, *Espeletiopsis* and *Coespeletia*. The floristically diverse lower montane forest belt (1000–2300 m) was compressed by *ca.* 55% during the last glacial maximum (LGM) (20 ka), and occupied the slopes between 800 m and 1400 m during that period. Under low LGM atmospheric p_{CO_2} values, C_4 -dominated vegetation, now occurring below 2200 m, expanded up to *ca.* 3500 m. Present-day C_3 -dominated paramo vegetation is therefore not an analogue for past C_4 -dominated vegetation (with abundant *Sporobolus lasiophyllus*).

Quercus immigrated into Colombia 478 ka and formed an extensive zonal forest from 330 ka when former *Podocarpus*-dominated forest was replaced by zonal forest with *Quercus* and *Weinmannia*. During the last glacial cycle the ecological tolerance of *Quercus* may have increased. In the ecotone forests *Quercus* was rapidly and massively replaced by *Polylepis* between 45 and 30 ka illustrating complex forest dynamics in the tropical Andes.

Keywords: non-analogue vegetation; plant migration; Quaternary speciation; paramo; pollen analysis; *Quercus*

1. INTRODUCTION

The Quaternary Ice Ages had a profound impact of the geographical distribution of vegetation belts. Between the LGM (*ca.* 20 ka) and the Mid-Holocene the forest line in Europe migrated more than 2000 km: from areas close to the Alps (e.g. Hungary (Willis *et al.* 2000, 2001)) during the LGM to northern Scandinavia at the present day (e.g. Van der Hammen *et al.* 1971). In the tropical mountains migration of vegetation belts was mainly altitudinal. In the Colombian Andes the uppermost forest limit migrated during the same interval from *ca.* 2000 m elevation during the LGM to 3200–3400 m under modern conditions (e.g. Van der Hammen 1974). As a consequence, a single pollen record from a strategic elevation in the northern Andes may detect the full sequence of migrations of vegetation belts. A similar reconstruction in Europe needs a series of pollen records along a north–south transect through the continent. This significant difference in the registering mechanism demonstrates why pollen records from the tropical mountains may be superior as records of climate change.

The present paper focuses on vegetational and climatic change in the northern Andes. The numerous palynolog-

ical studies of the past four decades now demonstrate, indisputably, the complexity of vegetation responses to environmental change. The main factors that forced these changes were temperature, precipitation and atmospheric carbon dioxide concentrations (p_{CO_2}). The intra-Andean sedimentary basins in the Eastern Cordillera of Colombia contain uninterrupted sequences of lacustrine sediments that vary in length from the last two glacial cycles (Fúquene basin) to the complete sequence of Quaternary Ice Ages (Bogotá basin). Palynological studies with high temporal resolution from both basins will soon be published.

The purpose of the present paper is to give an integrated sketch of factors that have roles in the complex vegetation dynamics of the northern Andes. Individual plant taxa have responded to climate change but most of the component taxa in a vegetation belt reacted in similar ways. In addition, some belts were more compressed than others during past altitudinal migrations (Wille *et al.* 2001). Van der Hammen *et al.* (2002) showed how the three Cordilleras of Colombia differ in altitudinal vegetation distribution. Although differences are small, they are sufficient to be relevant in palaeoecological reconstructions. The montane ecosystem was much more dynamic in the past than was previously realized and, at the end of this paper, we discuss the degree to which present-day ecosystems are an adequate analogue for reconstructions of the past.

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One contribution of 14 to a Discussion Meeting Issue 'The evolutionary legacy of the Ice Ages'.

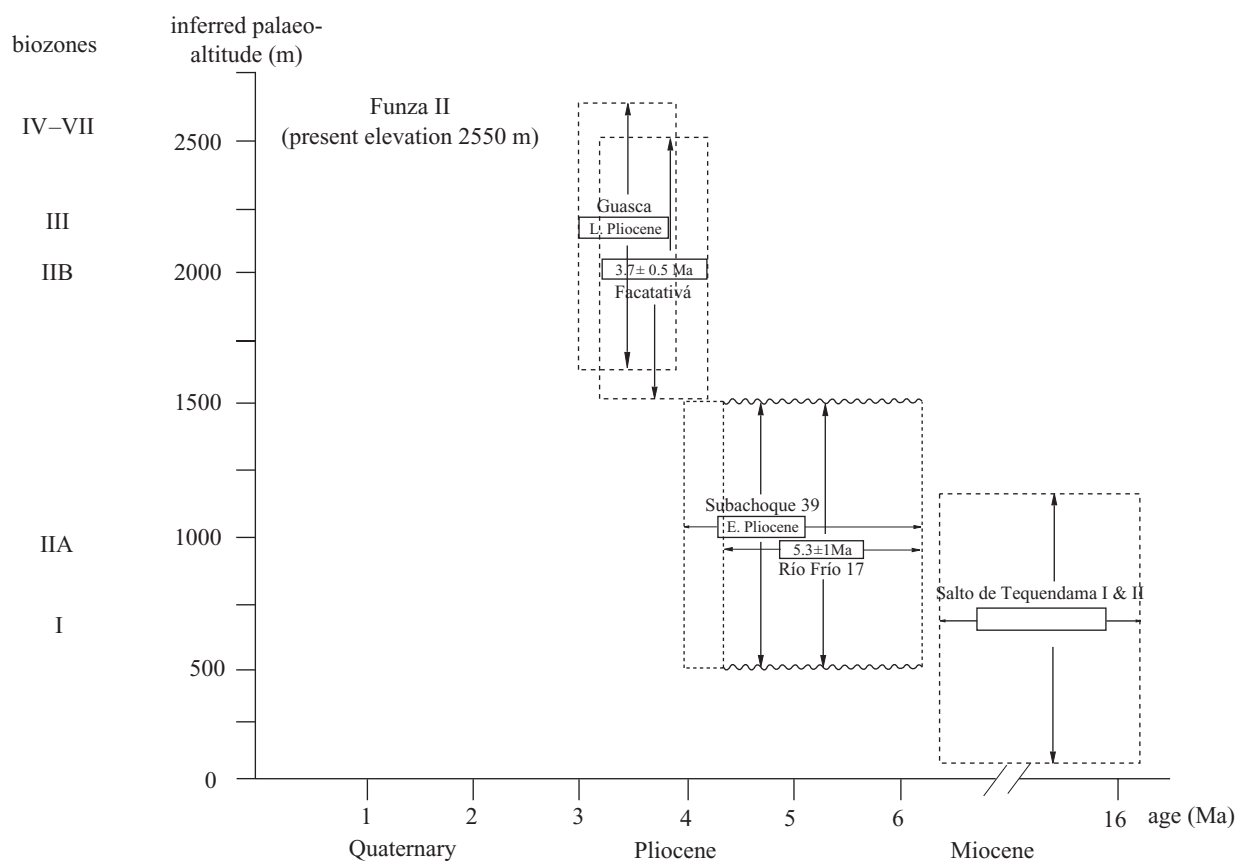


Figure 1. Five sediment sections collected in the outer parts of the basin of Bogotá were analysed for pollen and macrofossils. Time control was based on absolute dating of intercalated volcanic ashes. By comparing these fossil floras with modern ones at various elevations, the altitude of deposition at the site was estimated. The boxes and arrows show the uncertainty in measured age and inferred altitude. The series of sections, arranged from old to young, show the main upheaval of the Eastern Cordillera of Colombia between 6 and 4 Ma. Since the Late Pliocene, sediments accumulated at the same elevation as the present high plain. As a consequence, the signal in sections Tequendama up to Guasca show a mixed signal of tectonic uplift and climate change. The pollen records from the deep boreholes of Funza reflect climate change. In addition, the Funza records also show clear evidence of floral change by evolutionary adaptation (e.g. *Borreria*) and immigration of Northern Hemisphere trees *Alnus* and *Quercus*. (Adapted from Wijninga (1996).)

2. NEOTROPICAL ARCHIVES OF QUATERNARY ICE AGES

(a) *The sedimentary basins of Bogotá and Fúquene*

The region containing the basin of Bogotá consists of folded and faulted Cretaceous and Palaeogene to Oligocene sandstones, shales and clays, outcropping in the mountains around the high plain (Van der Hammen *et al.* 1973; Helmens 1990). Palynological and palaeobotanical studies of outcropping sediments on the high plain of Bogotá (Wijninga 1996), showed depositional environments of increasingly higher altitude (from *ca.* 800 m to *ca.* 2550 m elevation) from the Miocene to Late Pliocene time. The main uplift of the Eastern Cordillera must have taken place between 7 and 4 Ma (figure 1). During latest Pliocene time a lake came into existence; subsidence took place at more or less the same rate as sediment accumulation, resulting in a thick sequence of lacustrine sediments, the pollen from which records vegetation change, and climate change inferred from it through the past 3 Myr (e.g. Van der Hammen *et al.* 1973; Hooghiemstra 1984; Helmens 1990; Andriessen *et al.* 1993). Only a narrow ridge of hard rock retains the more than 500 m thick mass of lacustrine sediments in the basin of Bogotá. The

outer side of this ridge, falling to elevations of 200–500 m, forms the valley slopes of the Magdalena River. This ridge of hard rock rises *ca.* 200–300 m above the floor of the palaeolake and does not prevent pollen grains from the lower montane forest (at present 1000–2300 m) and the tropical lowland forest (less than 1000 m) from reaching the high plain. Therefore, pollen spectra from the lacustrine sediments of the Bogotá basin contain contributions from all main vegetation belts. Accordingly down-core changes in the amounts of pollen from the different altitudinal vegetation belts can be interpreted as altitudinal shifts in those belts.

(b) *Altitudinal vegetation distribution and Quaternary speciation*

The reconstructed position of the UFL is the main indicator of palaeotemperatures. The altitudinal position of the basins of Bogotá and Fúquene, *ca.* 2550 m, is well placed to provide a sensitive pollen signal of UFL changes. During the coldest part of the last glacial the minimum elevation of the UFL was *ca.* 2000 m and the palaeolake was surrounded by grass paramo. During interglacial conditions the UFL reached *ca.* 3200–3500 m and the

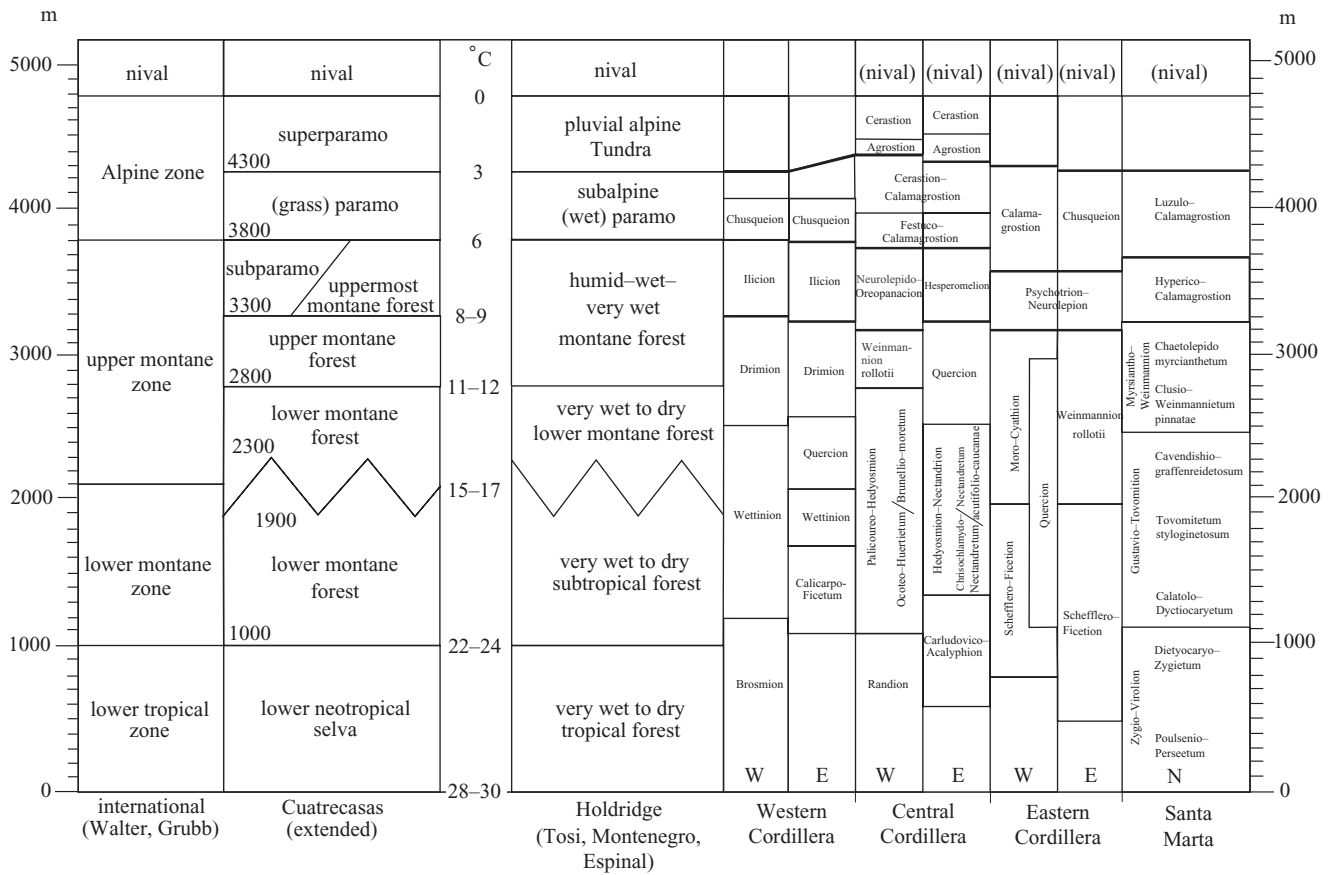


Figure 2. Synthetic scheme showing the altitudinal distribution of the main vegetation belts and major plant communities in Western, Central and Eastern Cordillera and along the slopes of the Sierra Nevada de Santa Marta. A comparison is shown with different systems of altitudinal vegetation zonation found in the international literature. (Adapted from Van der Hammen *et al.* (2002), p. 167.)

palaeolake of Bogotá was located in the lower levels of the upper montane forest belt (the Andean forest belt), sometimes close to the lower montane forest belt (the sub-Andean forest belt).

Extensive studies of the altitudinal distribution of the modern vegetation in the three Cordilleras of Colombia (ECOANDES 1983, 1984, 1989, 1995, 2003) have improved our understanding of regional differences substantially. Figure 2 shows that the main vegetation belts have different positions and altitudinal spans in the Western, Central and Eastern Cordilleras of Colombia and in the Sierra Nevada de Santa Marta. The overall results of altitudinal vegetation change during the Quaternary were similar in all Cordilleras. The treeless vegetation (paramo) above the UFL was most widespread during glacials, whereas it was limited to small areas on mountain tops during interglacial times (Van der Hammen 1974). As a consequence, glacials offered good opportunities for gene flow because paramo formed large continuous areas. During interglacials paramo areas were small and limited to the highest parts of the mountains, forming an archipelago of small isolated ‘paramo islands’ in the high Andes. The fossil pollen records show that such oscillations in patterns of plant distribution were repeated many times during the Quaternary Ice Ages and these may have stimulated significant speciation. Such a mechanism may explain why the currently restricted paramo biome has a high level of endemism (Van der Hammen & Cleef 1986; Luteijn 1999).

Much speciation occurred, for example, in the closely related asteraceous genera *Espeletia*, *Espeletiopsis* and *Coespeletia*. Distribution maps (Cuatrecasas 1979) and recent taxonomic revisions (Luteijn 1999) are available for these genera. *Espeletia* has 60 species extending from northernmost Ecuador to the Cordillera de Mérida in westernmost Venezuela. *Espeletiopsis* has 21 species and a more limited distribution in the northern part of the Eastern Cordillera and the adjacent Venezuelan Cordillera de Mérida. On the basis of plant distributions, the Colombian–Venezuelan border area near Cucutá and San Cristobál has been suggested as the centre of origin of the Espeletiinae (Cuatrecasas 1979). The genus *Coespeletia* contains six species, all limited to the Venezuelan Cordillera de Mérida. The three genera mentioned cannot be identified palynologically, nor can their pollen grains be distinguished from the other composite genera (although some authors claim that some asteraceous genera can be identified). The Asteraceae record of the long Quaternary pollen records from Colombia show continuous abundant representation; in the fossil record the evolution of so many asteraceous species is hidden. Quaternary Ice Ages caused immense and repeated changes in environmental conditions in the northern Andes and offer a plausible mechanism for speciation leading to the high floral diversity in the northern high Andes (Van der Hammen & Cleef 1986). In addition, immigration of taxa from elsewhere enriched the north Andean flora significantly (e.g. Cleef 1979) but is not further elaborated on in this paper.

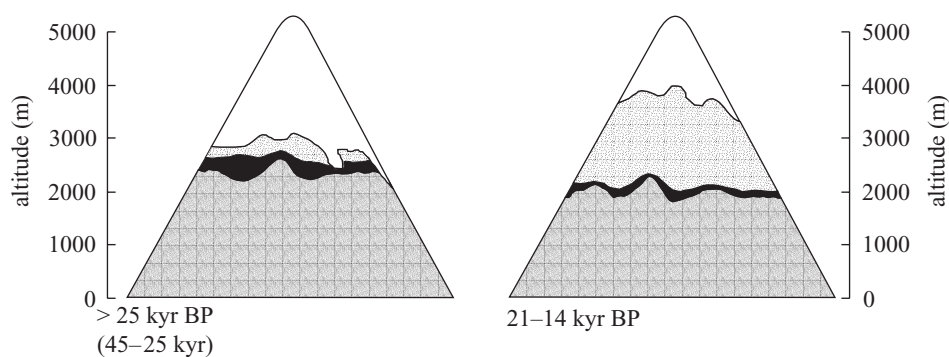


Figure 3. Main vegetation distribution in the Sierra Nevada del Cocuy. During climatologically humid conditions (45–25 kyr BP) glaciers reached their lowest altitudes and the belt with subparamo and *Polylepis* dwarf forest was wide. During climatologically dry conditions (21–14 kyr BP) the grass-paramo belt was wide. White, glaciers; light grey, paramo; black, *Polylepis* zone (subparamo); dark grey, montane forest. (Adapted from Van der Hammen (1981).)

Although long Quaternary pollen records do not offer examples of speciation at the specific level (the level of pollen identification does not allow for it), there is much evidence on the development of biomes or vegetation formations. We discuss here the long Quaternary pollen records Funza-1, which is 357 m long and represents the past 1.6 Myr (Hooghiemstra (1984); a corrected chronology was published by Andriessen *et al.* (1993)). The early Andean forest, with an age of *ca.* 1.5 Ma, showed a different altitudinal zonation from today. The upper limit of *Podocarpus* was at low elevation and marked the start of *Hedyosmum–Weinmannia* forest. At the upper limit of *Weinmannia* we inferred a transition to *Vallea–Miconia* forest. At the upper limit of *Vallea*, timberline forest with *Polylepis* became dominant. At higher elevation, but significantly lower than today, *Polylepis* forest became transitional to *Hypericum*-dominated shrub paramo. Up to 0.6 Ma *Borreria* was present in the Pleistocene lowermost paramo whereas from 0.48 Ma *Borreria* is no longer present in the paramo spectra. This is interpreted as evidence for a lower position of the uppermost forest line during the Early and Middle Pleistocene. We hypothesize that the immigration of *Quercus* at that time significantly changed the altitudinal zonation and composition of the main northern Andean forest types.

(c) *Repeated compression of forest belts during Quaternary Ice Ages*

In a cross-section through the Andes at Bogotá latitudes, Van der Hammen (1974) illustrated the altitudinal vegetation distribution at the present day and during the LGM. In that scheme, vegetation belts were shown to have moved upslope and downslope, all of them more or less equally compressed or expanded. A first refinement of this scheme (Van der Hammen 1981) found that the paramo zone was wide under the climatologically dry conditions of the Late Pleniglacial (21–14 ka) but narrow during the more humid conditions of the Middle Pleniglacial (45–25 ka; figure 3).

New pollen sites from lower altitudes between 780 m and 1750 m have been studied by Behling *et al.* (1998) and Wille *et al.* (2000, 2001). Wille *et al.* (2001) concluded that the lapse rate was apparently steeper during the LGM (0.76 °C per 100 m) than it is today (0.6 °C per 100 m) and described the degree to which vegetation belts were displaced and compressed during the LGM in the

southern Colombian Andes at Popayán latitudes (figure 4; table 1).

From table 1 it is clear that the lower montane forest (sub-Andean belt) experienced the greatest compression of all the vegetation belts during the Quaternary Ice Ages; its altitudinal span during the LGM was only 600 m, compared with 1300 m today. Although the lower limit of the lower montane forest belt is less clearly defined than its upper limit, the vertical interval can confidently be estimated at 55% that of the present day; the difference in surface area depends very much on the locality under consideration. The salient physical factor at the transition from the lower to the upper montane forest belt is the occurrence of night frost; a few frosty nights may have a decisive impact of the floral composition. As a consequence, the 'average temperature of the coldest month' is a more relevant variable with which to explain vertical vegetation distribution than is the 'average annual temperature', a recommendation for the use of the 'biome method' (elaborated for Colombia in Marchant *et al.* (2001)) rather than the widely used 'Holdridge system' (Holdridge *et al.* 1971).

From phytogeographical studies it became clear that the lower montane forest belt received many taxa from northern and southern latitudes by migration and from high and low elevations by adaptation (Van der Hammen & Cleef 1986) and is floristically richer than the upper montane belt. Environmental stress increases with altitude, which explains the generally decreasing floral diversity with altitude (A. M. Cleef, personal communication). Climatic humidity modulates the richness of the vascular flora, as exemplified by the difference in the overall richness patterns on the two sides of the Eastern Cordillera of Colombia (Keizer 2000). In summary, on Quaternary time-scales, the lower montane forest experienced most change and we hypothesize that this may have caused an extra loss of species compared with vegetation belts that experienced less dynamic histories.

(d) *Carbon dioxide concentration selecting between C₃ and C₄ plants in the paramo*

We know from Antarctic ice cores that the atmospheric p_{CO_2} was 180 ppmv during the LGM (Petit *et al.* 1999) compared with 280 ppmv in modern, pre-industrial, times and this has important implications for the interpretation of past vegetation patterns. Plants with a C₄ metabolism

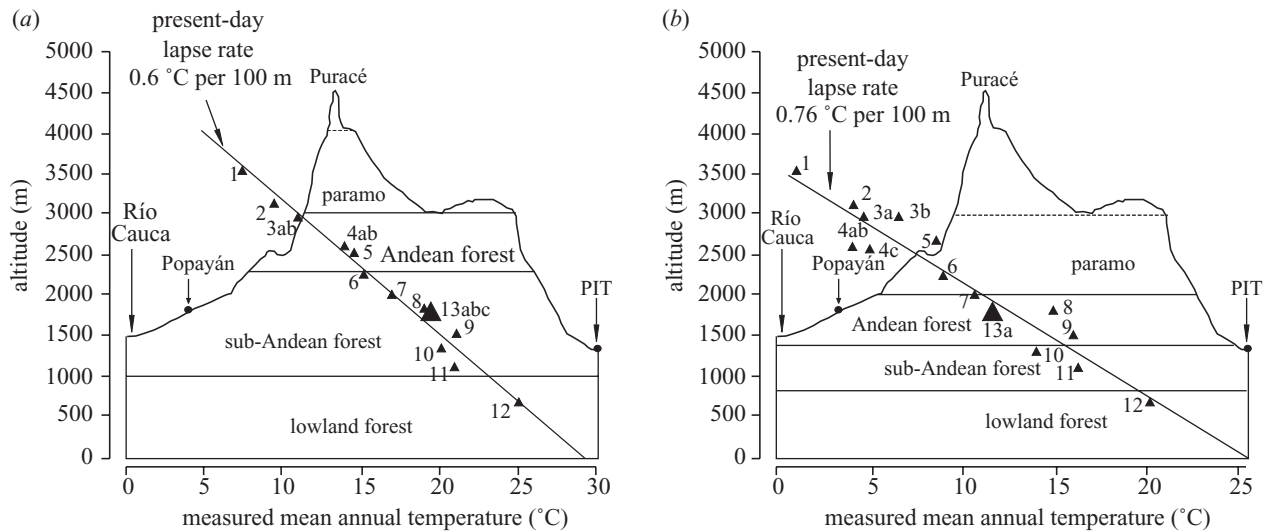


Figure 4. Altitudinal distribution of main vegetation belts along a cross-section in the south Colombian Andes at Popayán latitude. (a) Modern vegetation distribution and modern mean annual temperatures at 16 sites. Temperature decrease per 100 m (lapse rate) is *ca.* 0.6 °C. (b) Vegetation distribution during the LGM inferred from 18 pollen sites. Temperature decrease per 100 m was *ca.* 0.76 °C which reflects much drier atmospheric conditions. Note: in contrast to the widely used cross-section of Van der Hammen (1974), the lower montane forest belt was maximally compressed during glacial times, suggesting that the lower limit of night frost descended significantly under dry glacial conditions. For an explanation of the sites see Wille *et al.* (2001).

Table 1. Modern altitudinal ranges of main vegetation belts and estimates of ranges for the period of the LGM based on multi-site pollen data. The reduction in altitudinal range is given as a percentage.

vegetation belt	modern altitudinal range (m)	LGM altitudinal range (m)	compression
tropical lowland forest	0–1000	0–800	<i>ca.</i> 20%
lower montane forest	1000–2300	800–1400	<i>ca.</i> 55%
upper montane forest	2300–3200	1400–2000	<i>ca.</i> 33%
subparamo, grass paramo	3200–4200	2000–3000	<i>ca.</i> 0%

have a competitive advantage both under dry conditions and at low p_{CO_2} , although C_4 plants, on average, need higher temperatures for optimal metabolism than do C_3 plants. In the present-day paramo, C_4 plants are limited to some genera in the Cyperaceae (*Bulbostylus*, *Cyperus*) and Poaceae (*Muhlenbergia*, *Paspalum*, *Sporobolus*) (Cleef *et al.* 1993). Crassulacean acid metabolism plants may also resist dry conditions, but this photosynthetic pathway is found only in families that produce little biomass (Bromeliaceae (*Puya* may be an exception and produce significant biomass), Crassulaceae, Cactaceae, Isoetaceae and Orchidaceae). At present, C_4 plants grow at low elevations in the dry inter-Andean valleys. During the LGM, dryness and low atmospheric p_{CO_2} might have given C_4 plants an advantage in competition with C_3 plants up to *ca.* 3500 m elevation (figure 5). But mountain tops were too cold to bear C_4 plants so there, in small areas, C_3 grasses grew in a region generally dominated by C_4 plants. Screening the wealth of vegetation relevés from the Colombian paramos collected by A. M. Cleef (1981), substantiated the widespread dominance of C_3 vegetation in the paramo. But a few relevés showed a very high cover of C_4 plants (Boom *et al.* 2001), dominated by *Sporobolus lasiophyllus* (Poaceae). This species, with a savannah affinity, in the high Andes grows from the dry paramos of

Colombia to the dry puna of Peru (Cleef *et al.* 1993). Such small patches of C_4 -rich vegetation are probably relicts from the last ice age during which paramo vegetation was mainly composed of small tussocks and tufts of C_4 grasses. First evidence shows that fossil n -alkanes found in the sedimentary record and their $\delta^{13}\text{C}$ values offer possibilities to reconstruct the changing contribution of C_3 - and C_4 -derived biomass through time (Boom *et al.* 2002).

3. COMPLEX DYNAMICS OF NORTH ANDEAN ECOSYSTEMS

We are beginning to realize that vegetation change in the northern Andes during the past 40 kyr was complex. The contributions of present-day vegetation belts were significantly different in the past. Changes in the altitudinal extent of paramo belts mainly depends on precipitation; a wider grass-paramo belt under dry conditions and a wider shrub-paramo belt under humid conditions (Van der Hammen 1981). Changes in the altitudinal position of the montane forest belts seem to have depended mainly on the altitude at which night frosts began; the extension of north Andean forest belts mainly depended on temperature (Wille *et al.* 2001). We may anticipate that the altitudinal position of the UFL is influenced by temperature

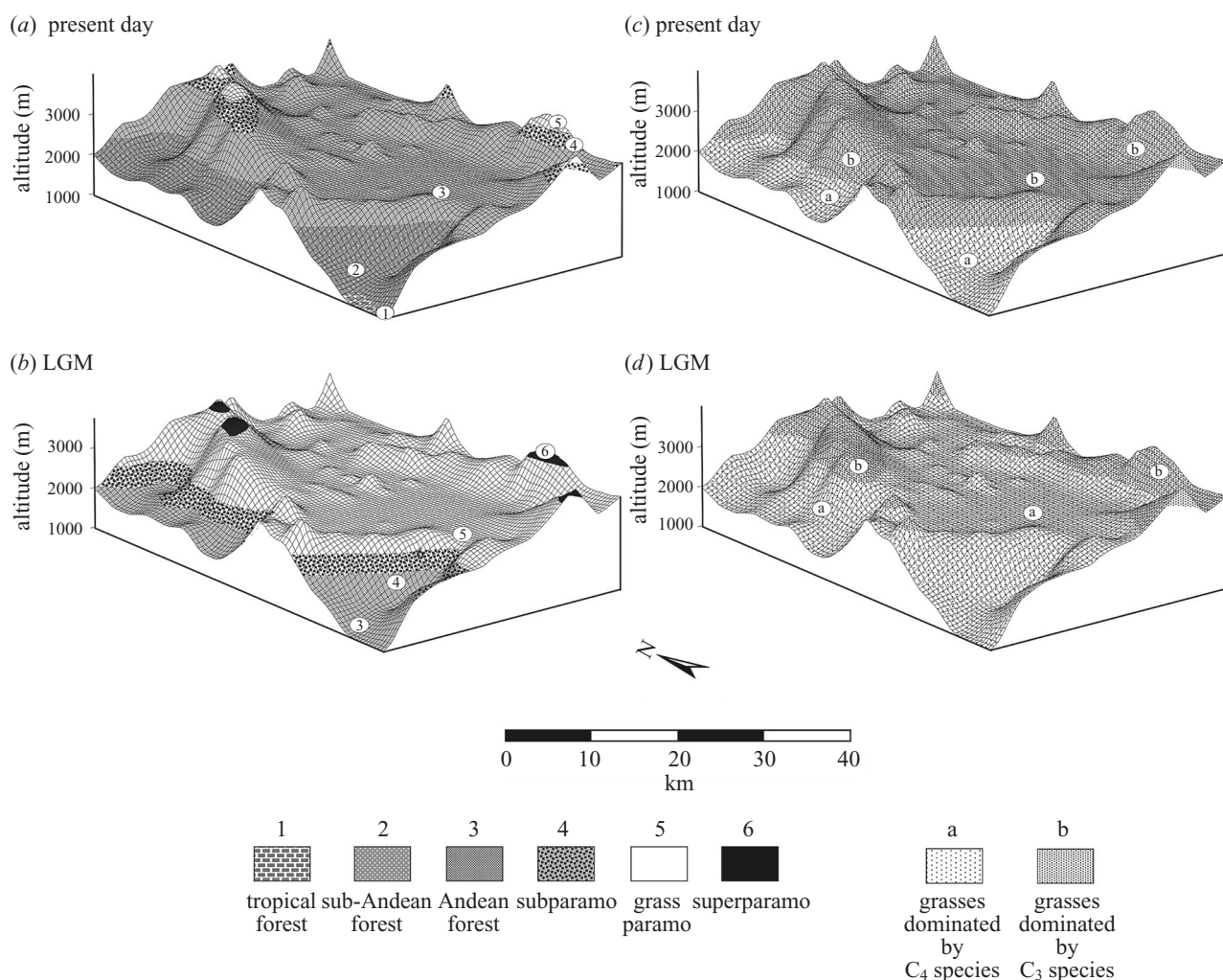


Figure 5. Cross-sections showing the altitudinal vegetation distribution in the area of the high plain of Bogotá at 2550 m. (a) Present-day vegetation belts (top) and LGM vegetation belts (bottom). (b) Altitudinal distribution of plants with a C₃ and C₄ photosynthetic metabolism. The present-day paramo vegetation consists mainly of cold-resistant C₃ grasses and herbs, while C₄ plants are limited to low-elevation dry inter-Andean valleys (top). During the LGM, when atmospheric p_{CO_2} was reduced by some 50%, C₄ plants (Poaceae and Cyperaceae) dominated the paramo vegetation, while only the highest mountain tops bore C₃ grasses because of the low temperatures. (Adapted from Boom *et al.* (2002).)

as well as precipitation, but our understanding of the impact of precipitation on the UFL is limited to a number of case studies from which no general conclusion has been drawn. Although a correct estimate of the altitudinal position of the UFL is essential in palaeotemperature reconstructions, we must conclude that factors forcing UFL change are still insufficiently known to fine-tune environmental reconstructions. Boom *et al.* (2001) showed that the atmospheric p_{CO_2} influences the competition between C₄ plants (mainly herbs) and C₃ plants (most trees but also some herbs). So, a UFL altitudinally lower than today during glacial conditions is attributed to lower temperatures as well as to lower p_{CO_2} values.

The closure of the Panamanian Isthmus was followed by an immense exchange of taxa between the two continents (Stehli & Webb 1985). The FAD of the oak tree (*Quercus*), a Northern Hemisphere element, was registered at 478 ka in the Funza-1 pollen record (Van 't Veer & Hooghiemstra 2000) and from 423 ka *Quercus* left a small but uninterrupted signal therein; the very first registrations of fossil oak pollen may relate to long-distance transport but the record of *Quercus* rapidly became significant and

a reliable indicator of its local presence. Because the Panamanian Isthmus is low-lying, we suppose that *Quercus humboldtii* entered Colombia as an element of the lower montane forest belt (at present *Quercus* forest occurs upslope from 1100 m (Cleef & Hooghiemstra 1984)). During the following 200 000 years it must have competed with components of the existing montane forest types and probably gradually reached higher elevations in the upper montane forest. Although only one species has been described for Colombia, it is plausible that more species will be established after a taxonomic revision of the genus *Quercus*. During the period of 330–135 ka, zonal forests with *Quercus* and *Weinmannia* developed, replacing partly *Podocarpus*-dominated forest in the uppermost Andean forest belt. Whereas oak forest was first dominant during interglacial conditions, it also gradually became abundant during cool to cold conditions. Thus, the ecological range of *Quercus* in Colombia may have doubled since its FAD. This apparent extension of ecological range may have resulted from adaptation to new niches, but may also partly reflect our ignorance on the full range of ecological tolerances of current taxa. Knowledge about ecological

ranges of tropical plants is limited (Marchant *et al.* 2002) and needs improvement to better serve palaeoecological reconstructions.

During the last interglacial, corresponding to MIS 5e, oak forest was abundant in the Fúquene basin (pollen record Fuquene-7 (Mommersteeg 1998)) and continued to be so during most of the last glacial (MIS 3), when it attained a significant extension of its ecological range. But oak forest was significantly less common in the Bogotá basin *ca.* 80 km from that of Fúquene. Interestingly enough, representation of oak forest was relatively high during MIS 5c, MIS 5b, during the transition from MIS 5a to MIS 4, and during much of MIS 3, compared with that in the last interglacial (MIS 5e) (H. Mommersteeg and H. Hooghiemstra, unpublished data). Thus, even during the last glacial cycle, pollen record Funza-2A shows that the importance of oak forest was not consistently related to climatic conditions. Several factors may have played a role, such as changes in the dominance of forest trees in response to environmental change (Tallis 1991), evolutionary adaptation (Cleef *et al.* 1993), or even stochastic variation.

Pollen records from the Fúquene basin also show other intriguing phenomena. About 40 ka the contribution of *Quercus* was largely replaced by that of the rosaceous tree *Polylepis*. *Quercus* has a broad ecological range and occurs in Colombia from 1100 m up to the UFL where, under modern conditions, it forms extensive zonal forests. *Polylepis* constitutes important forested areas near the upper forest limit, but also occurs as patches of forest in the grass paramo up to an altitude of *ca.* 4300 m (Cleef & Hooghiemstra 1984). This interesting change in the floral composition of the ecotone forest is the subject of further study.

4. DISCUSSION AND CONCLUSIONS

Pollen records are being produced with ever-increasing temporal resolution. Most striking in these pollen-based documents is the continuity of change. The different ecosystems of the northern Andes seem to have been continually in competition with each other and to respond sensitively to environmental change. Plant species respond individually to change as far as their ecological tolerances permit (Sauer 1988; USGS 2000). Although most taxa of a biome share many macro-ecological requirements, others are close to their tolerance limits for one or more factors and may disappear from the forest after slight environmental change. This process may explain quasi-stochastic changes in dominance of forest trees in pollen records (Tallis 1991).

Ecosystems are often considered to be in equilibrium with their physical environments. However, highest-resolution pollen records show that the composition of vegetation was apparently changing with such high frequency that stable equilibrium hardly ever existed; continuous change seems to have been the rule in these tropical montane ecosystems. The abundances of several taxa (e.g. *Quercus*, *Polylepis*) are not uniquely related to climate and seem to imply rapid evolutionary adaptation, particularly following immigration. The glacial atmosphere, with its low p_{CO_2} values, was so different from the present one that C_4 plants covered the Andean slopes

between 2000 and 3500 m elevation where C_3 plants dominate today.

We hypothesize that after more long pollen sequences with high temporal resolution and reliable chronologies become available, support for the concept that tropical ecosystems are almost continuously adapting to environmental change will increase. It is suggested that high-resolution palynological studies over a full glacial cycle will show us hitherto unrecognized dynamic aspects of tropical ecosystems. Present results give enough reason to be suspicious of the widely used paradigm that the present may be taken as the key to the past.

The present paper is mainly based on results from the PhD projects of Hermann Mommersteeg (NWO-VvA 753-718-214), Juan Carlos Berrio (WOTRO WB 84-461), Michael Wille (NWO 750.197.08) and Arnoud Boom (NWO 750.196.16). All are thanked for fine cooperation, and NWO and WOTRO are thanked for financial support of these projects. We thank the organizers of the scientific Discussion Meeting 'The evolutionary legacy of the Ice Ages' for inviting our participation. Antoine Cleef is thanked for constructive comments on an earlier version of this manuscript. Vladimir Torres, Arnoud Boom and Juan Carlos Berrio are thanked for assistance with preparing the figures.

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Discussion

D. K. Ferguson (*Department of Palaeontology, University of Vienna, Vienna, Austria*). If the Isthmus of Panama formed 3–4 Ma, why did it take *Quercus* and *Alnus* so long to reach Colombia?

H. Hooghiemstra. We assume this connection started as an archipelago of islands that gradually formed a more continuous migration route. It is plausible that taxa with pioneer qualities (*Alnus*) migrated with higher speed than taxa which do not have such qualities. Moreover, *Quercus* also has to bring the root fungi on which they seem dependent and also has relatively heavy nuts to transport. This explains why *Alnus* arrived half a million years before *Quercus* did.

E. Vrba (*Department of Geology and Geophysics, Yale University, New Haven, CT, USA*). Why did C₄ vegetation spread on several continents in the latest Miocene?

H. Hooghiemstra. A fascinating question indeed. Although we know that environmental conditions changed markedly during the Miocene as far as I know there is no good explanation.

E. Vrba. Is the effect of Andean uplift detectable in the pollen record of altitudinal shifting vegetation zones?

H. Hooghiemstra. Wijninga's (1996) pollen records

showed that the accumulated sediments on the high plain of Bogotá were deposited in increasingly colder environments. Although a cold episode could lead to an overestimation of tectonic uplift, the general trend shows a clear signal of tectonic uplift possibly, during Pliocene time, modulated to a low degree by altitudinally shifting vegetation belts as result of climatic change.

J. Carrión (*Department of Plant Biology, Murcia University, Murcia, Spain*). Is there any evidence of long-term impact of herbivorism in the region? For changes in the grassland-dominated ecosystems could be also related to plant–animal interactions (e.g. consumption, selection pressures for C₃/C₄ perennial grasses, etc.). We palynologists often have a rather phytocentric approach.

H. Hooghiemstra. The pollen record does not give us information on the impact of herbivores. It is relevant to mention that during the last decade the morphology of specific dung fungi has been published by van Geel *et al.* (2003). When element analysis is applied, the record of phosphorus may also be indicative of input of animal-derived organic matter in the palaeolake. New studies, therefore, have better chances to be able to address such interesting questions.

C. Janis (*Department of Ecology and Evolutionary Biology, Brown University, Providence, RI, USA*). I have pointed out that the earlier savannah-adapted large mammal fauna was probably extinct by that time: maybe there would have been a few llamas but no equivalent to African fauna today.

K. J. Willis (*School of Geography and the Environment, University of Oxford, Oxford, UK*). In your conclusions you suggested that the Quaternary was important for speci-

ation in *Espeletia*. How did you date the lineage split of this genus: is it possible to do this through pollen morphology?

H. Hooghiemstra. Indeed it would be fascinating to unravel the evolution of *Espeletia* and related taxa along the Quaternary time-axis. Pollen morphology does not offer us possibilities to key out all species and I do not expect this will ever be possible in the future. I think this question might be better tackled by DNA sequencing of modern species.

K. D. Bennett (*Department of Earth Sciences, Uppsala University, Uppsala, Sweden*). Does the pollen record show any evidence of arrivals or extinctions, apart from *Alnus* and *Quercus*?

H. Hooghiemstra. Some 30 taxa show their moment of arrival, including *Paepalanthus*, *Tristerix*, *Lysipomia*, *Cedrela*, *Dodonaea* and *Drimys*. Extinctions are more difficult to trace. We used a pollen sum of 300 grains, which is not very high when considering the high floral diversity. This easily explains that most rare taxa continued to be registered occasionally.

Additional reference

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GLOSSARY

FAD: first appearance date

LGM: last glacial maximum

MIS: marine isotope stage

UFL: upper forest line