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Amazonia during the last glacial

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Abstract

New data on the vegetational history and Quaternary geology of Amazonia permit an improved reconstruction of past environments in Amazonia during the last glacial period. Although limited, data from Rondonia, Carajas and Guyana show that, in certain areas, savanna-type vegetation and savanna forest had replaced the rain forest during the late Pleniglacial (ca. 22,000–13,000 yr B.P.). The Amazonian forest may have been split up into one major west Amazonian and several other medium-size forest areas. This suggests a decline in rainfall of 500 to 1000 mm (a reduction of 25 to 40%). Temperatures may also have been 2° to 6°C ($4 \pm 2^\circ\text{C}$) lower than today, possibly substantially influencing Amazonian vegetation. During the humid middle Pleniglacial (55,000–26,000 yr B.P.), rivers carried a lot of water and sediment, resulting in the deposition of lower terrace sediments with one dry interruption around 40,000 yr B.P. (Carajas and Katira). In Carajas, there is evidence of dry periods occurring at about 40,000 yr B.P., and during the early Pleniglacial (ca. 60,000 yr B.P.). Rivers carried little water and incised into the low terrace sediments during the dry late Pleniglacial. Water levels rose during the late glacial (13,000–10,000 yr B.P.) or at the beginning of the Holocene (10,000 yr B.P.). Sedimentation in (and of) the present inundation valleys commenced after that.

1. Introduction

Discussion on the possible replacement of (rain) forest by savanna vegetation in Amazonia, that may have resulted in forest “refugia” during glacial times, as originally proposed by biogeographers and geomorphologists (Haffer, 1969; Vanzolini and Williams, 1970; Vanzolini, 1973; Prance, 1973, etc.; see also Prance, 1982) is still going on. The answer to what really happened will depend very much on concrete historical vegetational data (especially palynological data).

There is extensive evidence on Late Pleistocene climatic changes to the west, north and south of Amazonia.

In the Andes (see overviews in e.g. Van der

Hammen, 1974, 1981, 1982, 1986a,b, 1988, 1991; Schubert, 1988; Markgraf, 1989), lake levels are generally high during the middle Pleniglacial interval (ca. 60,000 to ca. 26,000 yr B.P.), while glacier extension was maximal. The climate was moderately cold and relatively wet, although there are a few short colder and drier intervals during this period. Considerable amounts of fluvio-glacial and fluvial gravel were deposited: e.g. in the high plains of the Eastern Cordillera of Colombia and in the Venezuelan Cordillera. During the late Pleniglacial (ca. 26,000–21,000 to 14,000–13,000 yr B.P.), lake levels became very low, indicating precipitation values much lower than today; and glaciers started to retreat from their maximum extent. The climate was very cold; annual temper-

atures were 8°C lower than today. During the late glacial (14,000–10,000 yr B.P.), temperatures began to rise and lake levels started to increase, indicating an increase in rainfall. During the Holocene (ca. 10,000 yr B.P.–present), current conditions were established but with minor although marked fluctuations in rainfall. Middle Holocene annual temperatures were somewhat higher than today.

Evidence from the lower elevations of the Andes (1000–1500 m altitude; Monsalve, 1985; Bakker, 1990) suggests a lowering of vegetation zones, implying that (late) Pleniglacial temperatures possibly were 6°C lower during the (late) Pleniglacial than nowadays. As the lowering of temperature amounted to ca. 8°C at 2500 m, the temperature gradient may have been steeper than at present (probably related to generally drier air). Taking this into account, and an estimated 4°C drop in temperature during the late middle Pleniglacial at ca. 1100 m on the Amazonian Andean slopes of Ecuador (Liu and Colinvaux, 1985; Colinvaux and Liu, 1987), an late Pleniglacial lowering of temperature in the South American tropical lowlands between 2° and 6°C ($4 \pm 2^\circ\text{C}$) seems probable. While this may not have been a problem for Amazonian species, more montane elements could have invaded the area (as suggested by some west Amazonian pollen data now available; Espejo, unpublished data). It is interesting to note that CLIMAP (1976) had already predicted a lowering of temperature of at least that much for Amazonia, based on a computer model that used the glacial sea-surface temperatures as a major input (Caribbean glacial temperatures were only 1° or 2°C lower than today; CLIMAP, 1976; Gates, 1976).

During glacial-time low sea-level periods, northern Guyana (Georgetown) and Surinam were covered with dry grass savanna (Van der Hammen, 1963; Wijmstra, 1969, 1971) and Late Pleistocene low levels of Lake Valencia indicate a considerably drier climate in northern Venezuela (Salgado-Labouriau, 1986). On the present-day savannas of the Colombian and Venezuelan Llanos, large areas were covered with sanddunes during the Late Pleistocene, being more like a desert than savanna, and indicating a climate considerably drier than

at present (Roa Morales, 1979). On the other hand, lowland Panamá continued, at least partly, forested (Bush and Colinvaux, 1990), as did the lower eastern slopes of the Andes in Ecuador (Bush et al., 1990).

South of Amazonia, there is important new information from Salitre (19°S, Brazil; Ledru, 1992), showing wet climatic conditions during the middle Pleniglacial and late glacial, and dry condition during the late Pleniglacial. Southwest of Amazonia, there is information on a drier late Pleniglacial climate from Lake Titicaca (Ybert, 1988). All this shows clearly that tropical South America, at least north, west and south of the Amazon Basin, had a relatively dry (and colder or cooler) climate during the world maximum of the last glacial period (ca. 21,000–14,000 yr B.P.). Evidence of a former drier Amazonian climate has been presented by geomorphologists, but has been debated by others (see e.g. Prance, 1982). It is therefore most important to obtain information on the history of vegetation from Amazonia proper, and to consider and interpret it independent of the forest refugia theory that was initially based on biogeographical data.

Therefore, we will discuss next the palynological and Quaternary geological information that recently became available, and present some crucial new information. Finally, we will see to what conclusions all this may lead.

2. Recent data from Amazonia

2.1. Rondonia (Brazil)

In this section, palynological and sedimentological information (Van der Hammen, 1972; Absy and Van der Hammen, 1976) and additional recently obtained $\delta^{13}\text{C}$ data and AMS dates from Katira (Rondonia; approximately 9°S, 63°W) will be reviewed. The palynological data (Fig. 1) show replacement of Amazonian wet forest by grass savanna. At the time of publication no dates were available, as sample size and carbon content were insufficient for dating with conventional radiocarbon methods; only a young Cenozoic age (and supposedly a Late Pleistocene age could be established. However, using accelerator mass spectrometry, ^{14}C dating of very small samples is now

possible and has permitted to date two levels of the original Katira section and pollen diagram (samples C and E; Figs. 1 and 2). Dating was carried out at the Van der Graaff Laboratory of the University of Utrecht (The Netherlands), with the following results.

Sample Katira C, depth ca. 7 m. Black clayey material; pollen content indicating grass-savanna vegetation. Two fractions of the organic material were dated:

Carbon (wt%)	Analysed fraction	UtC-Nr.	$\delta^{13}\text{C}$ (‰)	Age (yr B.P.)
7	org. C. residue	1852	−16.2	44,000 ⁺³⁰⁰⁰ _{−2000}
50	alk. sol. fraction	1853	−15.6	18,500 ± 150

Sample Katira E, depth ca. 13 m. Dark grey clay; pollen content indicating humid forest. Two fractions of the organic material were dated:

Carbon (wt%)	Analysed fraction	UtC-Nr.	$\delta^{13}\text{C}$ (‰)	Age (yr B.P.)
38	org. C. residue	1854	−28.6	49,000 ⁺⁵⁰⁰⁰ _{−3000}
38	alk. sol. fraction	1855	−29.4	41,300 ⁺¹⁷⁰⁰ _{−1400}

The samples are from one of the boreholes made by Ferusa in Katira Creek (an affluent of the Rio Preto do Jamari), about 120 km southeast of Porto Velho (Figs. 1 and 2). Potential vegetation in this part of the Amazon Basin is a dense tropical rain forest. The nearest patches of more open natural vegetation are found 150–200 km to the south, on higher elevation tablelands with sandstone substrata. Several boreholes were made in a transect crossing the valley. Below the sedimentary valley fill, at a depth of approximately 25 m, a hard lateritic layer was found. The sediment from the base upward is represented by an older valley fill of brown coloured clay, passing at 15 m depth into dark grey clays with plant remains, at ca. 11 m to grey silty clays which are topped by a black silty clayey layer between ca. 5.5 and 8 m in our section. In the more central part of the original valley, this dark coloured layer is thicker and lies up to 8 m deeper in the section. At this place, the base should represent an erosion level (see Fig. 2).

On top of the black layer, there are yellow to red coloured silty clays locally containing older soil fragments. These sediments represent colluvial

deposits that filled the valley and covered the older deposits (Fig. 2). The uppermost 2 m are a yellow sandy clay. Thus, there seems to be an older sequence of brown clay topped by dark grey clays with plant remains and grey silty clays that was partly eroded at a later phase. Then, a younger sequence of sedimentation started with black silty clay, covered by yellowish to red colluvium. When the upper grey to dark grey part of the lower sequence was deposited, there was first a dense marshy (rain) forest vegetation in the valley (the dark grey part with plant remains), followed by grass savannah (the lighter grey upper part). The organic material of the dark grey layer, with abundant wet (rain) forest pollen, has $\delta^{13}\text{C}$ values of −28 to −29‰ in both the organic residue and the alkaline soluble fraction, indicating that it was produced by C3 plants in full agreement with the interpretation of the pollen spectrum, represented by arboreal taxa. The organic-rich layer probably formed as wet soil under forest. Stable organic remains that do not (or only slowly) decompose are known to accumulate in soils mixed with minerogenic materials; the more soluble part of the humus, however, easily disappears in time. When such a soil is “fossilized” (covered with sediment), the relatively old part of stable humus that accumulated over long periods of time is present together with the more soluble fraction from the later phase of soil development. In our case with sample Katira E, organic residue showed an finite age of 49,000 yr B.P. and, the alkaline soluble fraction about 41,000 yr B.P., both with a rather large standard deviation. This may be interpreted as a marshy forest soil that most likely formed between roughly >50,000 and 41,000 yr B.P. (with the end somewhere between 43,000 and 40,000 yr B.P.). The light grey clay that was deposited on top of the darker layer, apparently without a hiatus or erosional phase in between, according to the pollen spectrum, was deposited in a grass savanna, practically devoid of trees. Its age might be estimated as somewhere between 43,000 and 40,000 yr B.P., assuming that the organic residue of sample Katira C was formed in place, which seems quite probable.

The savanna phase is followed by an erosional phase in the central part of the valley (some 8 m

of incision). At this higher part in the valley, the basal part of the black silty sandy clay layer (sample C), a black soil, contains abundant organic residue dated between 47,000 and 42,000 yr B.P., while the alkaline soluble fraction showed 18,500 yr B.P. Both fractions have a $\delta^{13}\text{C}$ value of -15 to -16‰ indicating a substantial component of C4 plants such as tropical grasses. This is in agreement with the pollen spectrum, which indicates grass-savanna vegetation with very few trees. The black layer apparently represents a savanna soil that was formed in the entire valley. In view of the age range of organic residue, it should have been deposited during the same savanna period as the underlying light grey clay; that is, shortly after the end of the wet forest period. The dates of the alkali soluble fraction of Katira E and the organic residue of Katira C are almost the same, and have an overlap of only 1000 yr (43,000–42,000 yr B.P.). Perhaps part of the organic residue was redeposited via erosion of layer E higher up in the valley. In the light of the $\delta^{13}\text{C}$ values, this is unlikely because they indicate provenance from savanna vegetation. Whatever the case may be, data indicate the occurrence of a pronounced savanna phase at about 42,500(± 2500) yr B.P. The alkaline soluble fraction of Katira C showed an age of 18,500(± 150) yr B.P. According to the $\delta^{13}\text{C}$ value, savanna vegetation continued to prevail, and the top of the black layer must have been under savanna vegetation at that time. The black layer is covered by a yellow to red coloured colluvium with fragments of older eroded soils. It must have been deposited under extremely dry circumstances. This is also evidenced by the pollen content, which represents a grass savanna practically without trees. It seems probable that this colluvium and the savanna are from approximately this date or shortly thereafter. We have no pollen data on what may have happened between ca. 40,000 and 20,000 yr B.P. Perhaps the older soil was partly eroded before being covered again by savanna vegetation (see Fig. 2). In the deeper central part of the valley, where black savanna soil lies some 8 m deeper, a 3.5 m thick layer of grey clay with plant remains is intercalated between the black soil and the overlying 15 m thick yellow red colluvium that fills the valley at that site. This

intercalated layer is similar to the grey clay with plant remains from our section that corresponds to the earlier wet (rain) forest period. It therefore seems possible that it represents a wet (rain) forest interval after the 42,000(± 2500) yr B.P. and before the 18,500 yr B.P. savanna periods.

In summary, the savanna period(s) of Rondonia, according to pollen data, $\delta^{13}\text{C}$ data and colluvial sediments, are of the Late Pleistocene, of the last glacial age. The dates are from 42,500(± 2500) to 18,500 yr B.P. The savanna period(s) are preceded by a wet (rain) forest period. From the geological context, it seems probable that the dates correspond to two savanna periods, separated by a wetter forest period. The more recent savanna period, at and after 18,500 yr B.P., seems to have had the more extremely dry climate, judging from the thick colluvia deposited in the valley. We have no data from this site on when the rain forest invaded the area again but, on the basis of data from other sites in Rondonia (Absy and Van der Hammen, 1976) and from Carajas (Absy et al., 1991), this probably happened at the beginning of the late glacial or Holocene.

2.2. Carajas (Brazil)

Recently, paleoenvironmental vegetational data have become available from the Carajas area (southeastern Amazonia, Brazil). They include a well-dated pollen record covering most of the last ca. 60,000 yr, representing the first long Amazonian palynological record (Absy et al., 1991). The diagram is from one of a number of lakes on top of table mountains, at 700–800 m elevation, completely surrounded by Amazonian forest. On the plateau surfaces, patches of forest alternate with different types of more or less edaphic savanna vegetation. The area is located at the southeastern end of the drier corridor that crosses Amazonia from northwest to southeast, with annual rainfall values between 1500 and 2000 mm. The pollen diagram shows changes in the surrounding forest and in the vegetation on top of the hills. Wet intervals, when forest dominated (both on the hills and in the surrounding lowlands) and lake levels were high, alternated with intervals of extension of savanna vegetation

Fig. 1. Section, simplified pollen diagram, radiocarbon dates and $\delta^{13}\text{C}$ values from Katira Creek, Rondonia (Brazil). For the com pollen diagram, see Absy and Van der Hammen (1976).

ete

[illegible]

Fig. 2. Reconstruction of partial section through the Katira Creek valley. Based on three drilling logs by Feusa. Location of the study section is indicated.

(both on the hills and in the surrounding forest area) and low lake levels. Periods of drier climate and extension of savanna were dated approximately between 60,000 and 40,000 yr B.P., and between 22,000 and 11,000 yr B.P. During this later period of savanna extension, climatic conditions must have been extremely dry. The lake must have dried up almost completely. This interval corresponds to the late Pleniglacial and to the interval of very (cold and) dry climate west (the Andes), north and south of Amazonia. The other two intervals seem to correspond well with cold phases known from the late and middle Pleniglacial in the Andes (see above).

2.3. Mera (Ecuador)

Liu and Colinvaux (1985), Colinvaux and Liu (1987) and Bush et al. (1990) published some new

and interesting information from last glacial times, from the Andean eastern slopes towards Amazonia (Amazonian headwater areas), at an altitude of ca. 1100 m. River sediments and peaty intercalations were dated at 33,500 and 26,500 yr B.P. (late middle Pleniglacial, a cold and wet period in the northern Andes). Palynological data indicate a possible lowering of vegetation zones of montane forest by some 700 m, which might be interpreted as a lowering of average annual temperature by approximately 4°C.

2.4. The Middle Caquetá area (Colombia) and eastern Peru

Recently, a field and laboratory study of the Late Quaternary of the Middle Caquetá River area in Colombian Amazonia revealed interesting new

data on the history of the west Amazonian region (Van der Hammen et al., 1992a,b). Sediments on the present river plain were ^{14}C dated between ca. 13,000 yr B.P. and the present (30 dates). The low terrace, the lower part of which consists of sand and coarse gravel of Cordilleran origin, was dated by seven finite radiocarbon dates between 55,000 and 30,000 yr B.P. (and six infinite dates of >40,000 and >53,000 yr B.P.). There are still 5 m of sediment younger than 30,000 yr B.P. Taking into account the sedimentation rates calculated for the Holocene, this might very well represent about 4000 yr. This suggests that the lower terrace of the Caquetá River was deposited between (>) 55,000 and 30,000(–26,000) yr B.P., i.e. of the middle Pleniglacial age. In view of this age, the coarse sand and gravel deposits, the fact that the headwaters of the Caquetá River are in the high eastern Andes, and the fact that the extensive fluvioglacial-fluvial deposits and terraces in the eastern Andes are also of middle Pleniglacial age, it seems that formation of the lower terrace is related to a relatively colder and wetter climate in the Andes that probably was also cooler and wetter in western Amazonia. A few dates from Peruvian Amazonia, seem to indicate that a middle Pleniglacial low terrace is present over a wide area in western Amazonia (Rasanen et al., 1982; Campbell and Romero Pittman, 1989). The presence of sediment in the headwaters on the east Andean slopes of Ecuador, equally of middle Pleniglacial age, was already mentioned (Liu and Colinvaux, 1985, etc.).

Incision of the lower terrace should have taken place between 30,000(–26,000) and 13,000 yr B.P., during the late Pleniglacial which was a relatively cold and dry period. At around 13,000 yr B.P. sedimentation started in the newly formed valley. With the data now available it is impossible to conclude whether the incision took place at the beginning, during the entire time or at the end of the late Pleniglacial. In the Middle and Lower Valley of the Solimoes–Amazonas River, strong incision must have occurred during the same period, but was clearly related to the low “glacial” sea level (at least 80 m lower than at present; Irion, 1976).

From Colombian western Amazonia we obtained pollen data, partly published (Van der Hammen et al., 1992a,b) and partly unpublished,

showing predominantly Amazonian forest elements in river-valley deposits of the middle Pleniglacial low terrace near the junction of the Caquetá and Cahuinari rivers; however, there is an interval (possibly ca. 40,000 yr B.P.) of some local extension of savanna-type (Caatinga) vegetation (with grasses, *Byrsonima* and *Dydimopanax*), possibly on the edaphically drier sites. Apparently, Amazonian rain forest dominated in western Amazonia during much of the middle Pleniglacial, but during drier intervals of that period, locally savanna–caatinga-type vegetation could develop or extend somewhat locally. At the base of a sequence of marsh sediment on top of the lower terrace of the Caquetá River (northwest of Mariñame Island), a pollen diagram shows vegetation dominated by *Ilex* and accompanied by some pollen of more montane affinity. It might represent a late Upper Pleniglacial or early late glacial caatinga-type vegetation. In another section of the same area, a similar vegetation type dominated by *Ilex* was found, and radiocarbon dated to 30,000 yr B.P. (Espejo, unpublished data).

3. Discussion and conclusions

The data that have been presented and discussed point to the fact that most or all of warm and cold tropical South America had a cooler or colder climate and relatively high values for rainfall during the middle Pleniglacial (ca. 60,000–26,000 yr B.P.) and a considerably cooler or colder climate, becoming markedly drier between ca. 21,000 and ca. 14,000 yr B.P., during the late Pleniglacial (ca. 26,000 to 14,000–13,000 yr B.P.). For Lake Fuquene, in the northern Andes, the drop in rainfall during the dry late Pleniglacial, compared to the present, was estimated as at least 50%, and probably more (Van Geel and Van der Hammen, 1973). In the same area, the maximum drop in temperature at an altitude of ca. 2500 m, was estimated at ca. 8°C.

The available data on maximum temperature drops at different elevations in the (tropical) Andes, seem to indicate a somewhat steeper lapse rate during late Pleniglacial times (ca. 0.6°C/100 m today, ca. 0.7°C/100 m during the late

Pleniglacial; Bakker, 1990). This difference may be explained by the drier air of that time. If these data are right, the maximum lowering of temperature in the tropical lowland might have been 6°C. However, the sea surface temperatures in the Caribbean (today corresponding to the annual average temperature of the air), were only 1° or 2°C lower than today during the late Pleniglacial, according to the CLIMAP reconstruction (1976). As we do not have direct temperature data for late Pleniglacial Amazonia, it seems prudent to accept, for the time being, that the glacial-time lowering in that area may have been between 2° and 6°C ($4 \pm 2^\circ\text{C}$). Values on that order were already generated by the CLIMAP computer reconstruction of the Ice Age world (Gates, 1976).

During the relatively cold and dry part of the late Pleniglacial (eventually including part of the late glacial), savanna vegetation extended in the Carajas area (6°S, at the southeastern end of the dry Amazonian NE–SW corridor with present-day rainfall between 1500 and 2000 mm) and in Katira, Rondonia (9°S, with a present-day rainfall of approximately 2000–2500 mm), replacing the rain forest. Moreover, savanna replaced wet forest at Georgetown (and probably in the entire present coastal area of Guyana and Surinam) during (part of) the last glacial (Van der Hammen, 1963; Wijmstra, 1971).

A comparison of today's vegetation and rainfall in northern South America shows that, to reach climatic conditions permitting the natural extension of savanna woodland with open spaces of grass savanna, annual rainfall below 1500 mm (1000–1500 mm) seems necessary. To produce extensive natural grass savanna with very little forest (as seems to have been the case in Rondonia and Georgetown), a lowering to values between 500 and 1000 mm seems necessary.

Accordingly, late Pleniglacial data from Carajas and Rondonia indicate a decline in rainfall (compared with the present) between 500 and 1000 mm (a decline of 25–40%).

If we accept, as a first approximation, these ciphers of rainfall decline for Amazonia (respectively tropical South America as a whole) during the maximum of the last glacial (the dry late Pleniglacial) and apply them to the rainfall map

of the area (Fig. 3) we obtain an interesting picture (Fig. 4). With 500 mm (25%) decrease, the 2000 mm curve becomes a 1500 mm curve, as the approximate savanna–forest boundary, only explaining the fact that Carajas is in the savanna area (Fig. 4a). With the 1000 mm (40%) decrease, the 2500 mm curve becomes 1500 mm curve, which would be the approximate glacial-time boundary of savanna–savanna woodland and forest, explaining that not only Carajas, but also Katira and Georgetown are under savanna. In this way, extrapolation of the paleodata from Carajas, Katira and Georgetown leads to a picture of one major west Amazonian, and to several other medium-size forest “refugia”.

Data now available on lower and upper Amazonia also indicate that the river system suffered great changes during the last glacial (Van der Hammen et al., 1992a,b). The rivers must have carried a great deal of water and (partly very coarse) sediment during much of the middle Pleniglacial (related to relatively high rainfall in the Andes and Amazonia, and maximum glacier extension in the Andes) and deposited the low terrace sediments known at least from western Amazonia. During the late Pleniglacial, water carried by the rivers must have been seriously reduced, while the rivers incised into their earlier sediments. This incision was reduced on the middle course of the rivers (on the order of 10 m), but was very high on the lower course, especially on the Amazon River itself where incision may have been 100 m or more, directly related to glacial-time low sea level (Irion, 1976). This important erosion phase during a dry climatic interval is apparently even registered in the sedimentary record of Atlantic deep-sea sediments west and north of South America (Daimuth and Fairbridge, 1970).

During the late glacial (13,000–10,000 yr B.P.), the climate of northern South America became wetter, although apparently with marked local differences in degree and timing. The rivers carried an increasing quantity of water and a new cycle of sedimentary deposition began and continued in the Holocene. The increase in water level seems to have been considerable, locally leading to temporal permanent inundation of the (upper to) middle

Fig. 3. Rainfall map of Amazonia s.l. (northern South America, not including the andean and pacific areas). Based on the rainfall map of Reinke (1962), Nimer (1977), Simpson and Haffer (1978) and Figueroa and Nobre (1990).

river valleys (Urrego, 1991; Van der Hammen et al., 1992a,b). In the lower valley of the Amazon River, large-scale inundation of the glacial-time broad eroded valley took place because of the rapid post-glacial rise of the sea level, converting it well inland into an immense estuary or river lake. It seems to have taken thousands of years before this "lake" was filled with sediment and the present-day broad, seasonally inundated "varzeas" were formed (Absy, 1979).

During the Holocene, there were rather marked

rainfall changes resulting in periods of extensive and frequent river inundations, alternating with drier periods with reduced inundations (Absy, 1979; Van der Hammen et al., 1992b). These changes may have influenced considerably human riverine settlements and migrations. However, they are very small in comparison with the environmental changes that took place during the last glacial.

The conclusions on the vegetational history of Amazonia based on extrapolation of currently available paleodata, are independent of any theory

Fig. 4. (a) Area of > 1500 mm rainfall and approximate (rain) forest area, in case of a general 500 mm (25%) reduction of rainfall. (Carajas in savanna-savanna woodland area, as was the case during dry phases of the last glacial). Based on the rainfall map of Fig. 3. (b) Area of > 1000 mm rainfall and approximate (rain) forest area, in case of a general 1000 mm (40%) reduction of rainfall (Carajas, Katira and Georgetown in savanna-savanna woodland area, as was the case during dry phase(s) of the last glacial. Aracua and Mera are still the (rain) forest area. Based on the rainfall map of Fig. 3.

to explain existing centers of species diversity or endemism. For an explanation of these centers, like those presented by Haffer (1969) and Prance (1973, 1982), the existence or non-existence of forest “refugia” is of course of considerable importance, but other factors should also be taken into account, like changes in temperature, present-day climatic-ecological diversity, broad rivers, etc.

A glacial Amazonian type of situation may have repeated itself several times during the last glacial period (e.g. ca. 20,000, ca. 40,000 and ca. 65,000 yr ago), and one or several times during each of the many glacial periods of the Pleistocene [the last 2.5 million years; see Hooghiemstra (1984) and Hooghiemstra and Ran (1994) for the Andes and Wijmstra (1971) for the Guianas].

When discussing the high Amazonian alpha- and beta-diversity, however, we should also consider the 60 million year history of the Tertiary. In this respect it is interesting to note that the diversity of pollen types in Lower Miocene floodplain sediment in the Caquetá area (C. Hoorn, pers. commun., 1993) is about twice that in Holocene floodplain sediment of the same west Amazonian Caquetá River area (L.E. Urrego, pers. commun., 1993), 275 and 140, respectively. The cipher for Holocene sediment, is very near the average number of species found on 0.1 ha plots of present-day vegetation in the same area: 135 (Duivenvoorden, in prep; Urrego, unpublished data). These data suggest the possibility that diversity was considerably higher during the Miocene than during the Holocene and today, and hence, Plio-Pleistocene (glacial) extinction may have been a factor of importance in the explanation of present-day diversity. High Amazonian diversity may be inherited mainly from the Tertiary. While speciation may have occurred in the wet Plio-Pleistocene forest refugia, extinction due to the severe impact of dry (and cooler) climatic episodes may have dominated, and the now relatively high species diversity of western Amazonia may be the result of a relatively low extinction rate attributed to the comparatively low impact of dry climatic episodes in this large wet forest “refuge” area.

There is little doubt that the Pleistocene glacial–interglacial climatic history of Amazonia must have had a great impact on both flora and vegeta-

tion and it gives us a highly dynamic picture of Amazonia and its (rain) forests.

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