A PALYNOCOLOGICAL HISTORY OF THE AMAZON RAINFOREST THROUGH GLACIAL CYCLES

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Abstract. Pollen data show that the lowlands of the Amazon basin were continuously forested throughout the last glacial cycle. There were no forest refugia and there was no arid land surface. Forest associations were subtly altered in response to lowered temperature and CO2 but the broad extent of diverse tropical forest remained intact. We have codified Amazonian pollen taxonomy into 400 taxa known to be preserved in lake sediments and have published these as a manual and atlas. Pollen from Lake Pata in a lowland rain forest site in the western Amazon of Brazil shows that lowland forest has occupied the site for >40,000 yrs. A pollen section from the Amazon fan, dated by radiocarbon and 2/30 magneto, was spanned the last 50,000 yrs, demonstrates that no more grass pollen came down the river system in glacial times than in the Holocene: the forest signal is maintained throughout. That are these forest histories with no possibility of savanna is shown by comparing the pollen with a record from the savanna of central Brazil where grass pollen is 50%-80% of the pollen sum unlike the 3%-15% of the Lake Pata and fan deposits. Claims that a pollen record from the 700 m-800 m plateau of Carajas shows a savanna phase in glacial times are based on the mistaken interpretation of modest increases in herb/tree ratios when in fact the changed ratios are due to local overrepresentation of herbaceous grasses and herbs. Only at the forest-savanna ecotones of the extreme southwest of the Amazon basin is there evidence of alteration precipitation as savanna encroached in glacial times on what is now forest. If this movement of ecotones should represent a general drying throughout the basin, this was clearly insufficient to break the forest canopy. Hypotheses to explain high Amazon species diversity should take account of the fact that forest has occupied the Amazon lowlands continuously at least since the late Tertiary.

Keywords: Amazon, Paleoclimate, Forest, Pollen, Palynology, Glacial, Pleistocene, Diversity.

INTRODUCTION

The ecological question, "Why has Amazonia so many species?" is linked to the paleogeographical question, "What has been the history of Amazonian climate?" One school of thought has argued that the high species diversity of equatorial lands is the result of low extinction because the environment was always benign. The co-founder of the theory of evolution, Wallace (1876), argued this way, saying that equatorial regions escaped the successive glaciations that eliminated so many species from the North, thus letting tropical species accumulate. We call this the 'museum' model of tropical species diversity. It explains why one hectare of Amazonian rain forest can hold more species of trees than the whole of Romania. This view has been modified by contemporary ecology to suggest that short-tern violence of the tropical climates cause local instabilities that prevent extinction by competitive exclusion. This 'intermediate disturbance hypothesis' adds to the safety of species in the tropical museum as they suffer neither geographical catastrophe nor competitive elimination (Connell 1978).

But an alternative view of tropical, specifically Amazonian, diversity has held sway for the last three decades with the 'forest refuge hypothesis' of Haffer (1969). This postulates that the lowland Amazon forest was not immune to glacial events but was in fact decimated by drought in glacial times so that the forest was reduced to small patches called 'refugia'. Vicariant speciation within these forest patches with each glaciation then led to the accumulation of species (France 1982). This might be called an 'engine' model of tropical diversity, since enhanced speciation is the declared cause of species richness rather than reduced extinction. There has never been much actual evidence that the required fragmentation of the forest by glacial climates actually occurred. We have recently reviewed the reported geomorphological evidence for former and land surfaces in the Amazon region and find them almost totally lacking in credibility (Colinvaux, De Oliveira & Bush, 2000). But the hypothesis should be susceptible to the direct test of pollen analysis of Amazonian sediments of glacial age. Accordingly we have devoted the last fifteen years to discovering ancient lakes in the Amazon lowlands and to reconstructing the history of lowland Amazon vegetation by pollen analysis. We find that the forest was not disrupted by aridity in glacial times as required by the refuge hypothesis. In this paper we summarize the results of these palynological investigations.

AMAZON POLLEN ANALYSIS

Two particular difficulties faced the project at the beginning. These were finding ancient Amazonian lakes with sediments undisturbed for more than 20,000 years and mastering the pollen signals from a flora with 80,000 species of vascular plants. The lake search was a long one because the many lakes of the Amazon floodplain are all relatively young, being subject to recapture by the meandering rivers. The best lacustrine records of glacial times all come from lakes in pseudokarst basins perched above the rivers on low inselbergs, typically so remote that they were difficult of access (Fig. 1). But these are supplemented by splendid pollen records from marine deposits off the mouth of the Amazon river.

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The difficulties with pollen analysis were of a different order. Not only does an Amazonian palynologist have to cope with the possibility of finding pollen from thousands of species of trees, but most of this pollen is distributed by animals: by insects, birds or bats, rather than the wind. Obviously the pollen signals of vegetation will be of a different class to the pollen signals of north temperate forests, where the trees are wind-pollinated and for which pollen analysis was invented.

Our first encouraging observation was that pollen was abundant in Amazon lake sediments where pollen concentrations are as high as in temperate lakes, though much more diverse. A significant part of this pollen accumulation comes from the few Amazon taxa that are wind pollinated, taxa like Moraceae, Cecropia, Ulmaceae, Urticaceae, Myrtaceae and Alchornea. But a large residue was made up of pollen types that appeared individually at less than two percent, typically as single grains in a pollen count. These were hard to identify so that in our first pollen diagram of glacial age Amazon deposits we declared >30% unknown pollen, believed to be forest trees, (Liu and Colínvaux 1985). Our solution to this problem was to set out pollen traps in forest plots of known species composition, afterwards comparing the pollen catch with reference pollen of the local species list. A significant proportion of the local zoophilous trees contributed pollen to the traps, and these pollen types were subsequently found in Amazon lake sediments. It appears that these pollen types are washed into lakes, yielding an highly diverse record of tree species actually growing in the watershed or catchment of the lake. From these studies we have been able to reduce the proportion of unknown Amazon pollen types to <5%.

There are thus two pollen signals in Amazon palynology: first a regional signal given by a few anemophilous taxa and second an highly local taxon list of trees in the lake-side community. Multivariate statistics of even the few anemophilous pollen types alone yield strong signals for forest types (Bush, 1991), then this conclusion can be checked against the species list of zoophilous pollen taxa. In all we now recognize 400 Amazon pollen taxa that are described in a pollen manual and atlas (Colínvaux, De Oliveira & Moreno, 1999).

To test the hypothesis of fragmentation of Amazon forests in glacial times is now straightforward as the pollen signals for the various forms of semi-arid and open vegetation of the Neotropics are utterly different from the signals for closed tropical forest. The most typical of tropical Brazilian savannas outside the modern Amazon, the cerrado sensu stricto, for instance, has from 60% to 80% Gramineae (Poaceae) pollen, while the remaining pollen being from weeds of open land and an highly selected short list of arboreal taxa that persist in savannas as well as forests (Salgado-Labouriau et al. 1997). By comparison the modern lowland rainforest at Lake Pata (Fig. 1) has a trace to <3% Gramineae with arboreal pollen consistently close to 90% (Colínvaux et al. 1996a). More than 400 taxa of forest trees have been recognized in the sediments of Lake Pata and two other lakes close to it (Colínvaux, De Oliveira & Moreno, 1999). The pollen spectra of closed forest and savanna are thus highly distinct, even though all the savanna pollen taxa can be found in low numbers in the rain forest, usually represented by different species in the family or genus recognized by pollen taxonomy.

THE PLEISTOCENE POLLEN RECORD FROM AMAZON LAKES

The first dozen or so pollen diagrams available from the lowland Amazon forests were restricted to the Holocene, many only to the latter part of the Holocene. All had the the expected anemophilous signal for forest, typically with Moraceae/Urticaceae in the region of 10% to 20% and Euphorbiaceae (Alchornea), Melastomataceae and Myrtaceae each in the 5% to 10% range. Detrended Correspondence Analysis (DCA) of the taxa present at 2% or more let the surface spectra of these records be assigned to the correct local variant of forest such as terra firme or igapo but all are unmistakably forest records despite local variations consequent on hydrology (Bush, 1991).
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The first pioneering Amazon pollen diagrams to be produced from Brazil were given in a Ph.D. thesis by M.L. Absy in 1979, but were never published in the reviewed literature. These were from riveaine lakes and varzeas with consequently significant additions of river bank and disturbance taxa to the basic rain forest signals. Occasional peaks of 10% or so of Gramineae pollen superimposed on the forest signal probably represent the common floating mats of vegetation or flood communities rather than dry intervals (Colinvaux 1987).

Similar riveaine histories were published from Ecuadorian Amazonia in the western lowlands (Frost 1988; Colinvaux et al. 1988). Like Absy's (op. cit.) Brazilian records, the pollen spectra were consistently of rain forest but recorded local hydrologic events by fluctuations in herb pollen from floating mats or pollen from colonists of mud flats such as Cecropia. Two nonriveaine lakes in Ecuadorian Amazonia occupied volcanic explosion craters (maares). They yielded histories of rain forest with minimal hydrological disturbance but failed to penetrate past the Holocene despite cores up to 19 m long (Liu & Colinvaux, 1988; Bush & Colinvaux, 1988). All these records show the unmistakable pollen signals of tropical lowland forest, being dominated by taxa like Moraceae/Urticaceae, Melastomataceae and Euphorbiaceae, yet each with its assortment of disturbance or rain forest pollen types.

The Lake Pata record: tropical forest through glacial times.

Eventually, many years after the start of Amazonian palynology, a continuous pollen history spanning at least the last 40,000 years was obtained from the lowland rainforest of Brazil with the Lake Pata record (Colinvaux et al. 1996a). Lake Pata occupies a small closed basin at 300 m elevation, on a low inselberg, near the equator in the west central Amazon of Brazil (Fig. 1). The sediments are about 6 m thick but sixteen, internally consistent radiocarbon dates show that just the top 1.6 m spans the last 40,000 years. Dates on two parallel cores of 18,000 B.P. identify the last glacial maximum (LGM) and pollen concentration measures show that pollen deposition was continuous despite local physical changes in sediment type (Colinvaux, De Oliveira & Bush, 2000). The closed tropical forest signal is present throughout, with total arboreal pollen remaining >80% and grass pollen always <3%. The rich diversity of forest taxa characteristic of the Holocene part of the section is present in the glacial age sediments also. This is, therefore, direct evidence that, at this one site at least, closed tropical forest occupied the lowlands without interruption throughout a glacial cycle.

Yet there was a difference in the pollen spectra of the LGM at Lake Pata: they were more diverse than the Holocene spectra by the addition of small percentages of a few extra pollen taxa that are associated in modern Amazonia with cooler climates on the hillsides at the periphery of the basin. Podocarpus, Rapanea, Hedyosmus and Humidra became noticeable in the glacial section, and Ilex became more abundant. These trees are rare in the modern Amazon lowlands, though they can be found in parts of the basin. Podocarpus, for instance, is known from small stands or lone individuals right down to sea level in the modern forest, but significant populations of Podocarpus species are found only above elevations of about 1,500 m. The same is true for the other taxa in this group: centers of population are at higher elevations. But the pollen data from L. Pata suggest population expansion of these taxa in the lowland forests at the LGM.

A similar phenomenon was observed in the pollen of two sections of road and stream cuts, 160 km apart, at Mera and San Juan Bosco in the Amazonian foothills of the Ecuadorian Andes (Fig. 1). The two sections were of old lacustrine deposits spanning between radiocarbon dates of 26,000 B.P. and 33,000 B.P., and therefore of glacial age. Pollen spectra at both sites were clearly of lowland forest, with Moraceae/Urticaceae etc. and many taxa of zoophilous pollen, but with additions of Podocarpus and others, even of Alnus (now found above 3000 m) that could be associated with montane vegetation (Liu & Colinvaux, 1985; Bush et al., 1990). A Podocarpus peak has also been found in late glacial pollen spectra from the eastern Amazon lowlands of Brazil (Behling, 1996). The spread of these populations into the lowland Amazon forests is clearly associated with glacial cooling, now estimated to be in the order of 6°C (Gulderson et al. 1994; Stute et al., 1995; Colinvaux et al., 1996b; Webb et al., 1997). But it is worth emphasizing that what is recorded here are local population events, not replacements of communities or the movement of vegetation types. In every instance tropical lowland forest remained as tropical lowland forest with most of its great diversity intact. The data simply require that the temperature shift from cooler glacial conditions to warmer interglacial times altered the centers of dispersal of a few of the most heat sensitive species, both within the permanent forest and at higher elevations. But the 6°C temperature shift did not disrupt the distributions of the great majority of the rain forest trees.

Marine records from the fan and shelf

The Lake Pata record is the only continuous sequence from sediments within the lowland Amazon forest spanning from full glacial times to the present yet published. The partial records from Mera and San Juan Bosco in Ecuador are consistent with the Pata record, as is the late Glacial appearance of Podocarpus in Behling's (op. cit.) record from the eastern Amazon. Yet extrapolating from these few records to deduce the glacial vegetation of the entire Amazon basin, an area larger than Europe, is obviously hazardous. Fortunately the Lake Pata history is given generality by the pollen data from the Amazon fan.

Pollen studies of marine deposits of sediment from major river systems have been shown to describe the regional vegetation of continental interiors elsewhere (Heusser and Shackleton, 1994). In glacial times of low sea level the Amazon sediment load is dropped into deep Atlantic water, where sediment has accumulated to form the immense deposit of the Amazon fan. This was cored under 4,000 m of water during Leg 155 of the International Ocean Drilling Program (ODP). The glacial age fan deposits have been combined with samples of Holocene deposits from the continental shelf to yield a well-dated section of the last 50,000 years (Haberle and Maslin, 1999). The pollen spectra of glacial times are closely similar to the pollen spectra from the Holocene. In particular, there was no more Gramineae pollen in the
Figure 2 - Piston-coring the sediments of an Amazonian lake.
From left to right, P.E. De Oliveira, P.A. Colinvaux, M.C. Miller.

river sediment load of glacial times than there was in the Holocene, or, indeed, can be shown to be in suspension in the modern river. All the spectra are consistent with the pollen records of Holocene riverine lakes, presenting typical pollen assemblages for tropical forest with a superimposed component of river-bank and floating mat communities. Because there was at no time more Gramineae pollen in the river system than at present, and because the observed pollen were all consistent with the signal of modern forest, we conclude that it was not possible for there to have been extensive savanna-grasslands in the Amazon lowlands at any time in a glacial cycle.

But there was one signal for climatic change in the pollen of the Amazon fan. The expanded populations of the heat intolerant species in glacial times are recorded by the appearance of Podocarpus, Alnus and others in the fan pollen, just as at Lake Pata and the Ecuadorian sites. The pollen data from the Amazon fan and continental shelf, therefore, make it plausible to extrapolate from the Lake Pata forest history to conclude that the Amazon lowlands were forested in glacial times as well as in interglacials.

Carajas and Rondonia: the modified aridity hypothesis

Pollen data from Carajas and Rondonia have been used to dispute the ubiquity of the glacial age forests (Van der Hammen & Absy, 1994). The Rondonia pollen data come from five core samples of valley fill from a site within 100 km of the present southwestern forest/savanna ecotone. The pollen spectra are comparable to the cerrado spectra of Salgado-Labouriau et al. (1997) without any hint of tropical forest. It is therefore likely that the forest ecotone moved at least 100 km eastward at some time in the past.

The pollen record at Carajas is more interesting because from a central Amazon site and coming from a continuous lake record comparable to that at Lake Pata, except that it was not from lowland forest (Absy et al., 1991). The present vegetation of the Carajas site is an edaphically constrained altitudinal savanna (campo rupestre) at 700 m elevation. Only a partial pollen diagram was published, but this showed abundant Gramineae, in both the Holocene and glacial sections with none of the taxon groupings we associate with tropical forest. There are very wide fluctuations in the percent Gramineae that we conclude can be parsimoniously and satisfactorily explained as due to fluctuations in the water level of the closed, pseudokarst lake, with consequent expansions and contractions of the surrounding marsh. But the original authors argued, instead, that the Gramineae pollen reflected long distance transport from a postulated glacial savanna in the lowlands. This interpretation is shown by detailed consideration of the few pollen data published from Carajas to be in error (Colinvaux, De Oliveira & Bush, 2000). The Carajas pollen data actually demonstrate remarkable stability of the peculiar peculiar vegetation through the climatic events of glacial cycles.

The movement of the southwestern ecotone, together with fluctuating lake levels at both Carajas and Lake Pata do suggest that precipitation or seasonality varied across this vast region through Pleistocene time. The pollen evidence, however, demonstrates that precipitation changes were within the tolerance of lowland forest communities throughout most of the Amazon basin.

AMAZON FOREST DIVERSITY ON A GEOLOGICAL TIME SCALE

The conclusion of our pollen study is that richly diverse forests occupied the Amazon lowlands at all
stages of a glacial cycle. The forest was never fragmented into refuges separated by broad savannas as required by the forest refuge hypothesis of Haffer (1969) and Prance (1982). Instead, the forest was always continuous and immense. This is the essence of the 'museum' model, a tropical region where environmental catastrophes were too few, or too local, to cause widespread extinction. But the pollen data also allow this model to be refined in that they suggest the importance of scale to the maintenance of diversity. The principal environmental shocks on Pleistocene time scales are given by changes in temperature, specifically the 6°C warming that comes with each interglacial to interrupt the far longer cool periods of glacial times. The pollen data show that the more temperature sensitive (i.e. heat intolerant) forest trees are reduced to residual numbers during interglacial times like the present, maintaining viable populations only at higher elevations at the periphery of the forest. When cooler times return with another glaciation, these trees once again flourish in the lowland forests. Doubtless other, less temperature sensitive trees make lesser population accomodations to interglacial warming that our present data are not able to resolve. But the extreme population changes of sensitive taxa like Podocarpus that we can monitor illustrate what is probably a general pattern. The Amazon basin is so large, and the total terrain so varied, that a vast and diverse array of different species can find opportunity to survive in every climate of the Pleistocene. Locally, the communities of Amazonian forests are in continual flux. In this way, high species diversity has been maintained since at least the start of the Pleistocene. The process will have begun with the Andean orogeny that created the modern Amazon drainage, perhaps in Miocene time.

REFERENCES


Behling, H. 1996. First report on new evidence for the occurrence of Podocarpus and possible human presence at the mouth of the Amazon during the Late-glacial. Vegetation history and Archaeology 5, 241-246.


Haberle, S.G. & Maslin, M.A. 1999. Late Quaternary vegetation and climate change in the Amazon basin based on a 50,000 year pollen record from the Amazon fan, ODPM site 992. Quaternary Research 51, 27-38.


