

Modern pollen-rain data from South and Central America: a test of the feasibility of fine-resolution lowland tropical palynology

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Abstract: Modern pollen rain data from a suite of sites in lowland South and Central America are analysed by means of detrended correspondence analysis (DCA) and two-way indicator species analysis (TWINSpan), and are shown to have discernible characteristics for major vegetation types: *varzea*, *igapo*, semi-deciduous, *cerrado* and *terra firme* forest. Data analysis demonstrates the potential for detailed palaeoclimatic reconstructions of lowland tropical environments, but also demonstrates the danger of making generalizations about palaeoecosystems based on few palaeoecological records.

Key words: lowland tropics, modern pollen, tropical forest, TWINSpan, DCA, South America.

Introduction

The reconstruction of past environments using fossil pollen as a proxy indicator of climatic change or human disturbance requires distinct plant communities to have characteristic pollen rain, for the pollen to be identifiable, and for a representative fraction of the pollen to be preserved. The large diversity of the lowland tropical forests (c. 80 000 higher plant species in Amazonia), the abundance of entomophilous taxa, and the stillness of the air within such forests, led Faegri (1966) to express severe misgivings regarding the feasibility of lowland tropical palynology. Faegri and van der Pijl (1979) noted that almost all the anemophilous taxa of the lowland forests were invasive, r-selected species that provided little information relating to the composition of the forests themselves, and were more-or-less ubiquitous. Concern was also expressed that the heat of tropical environments might degrade pollen, but Muller (1965) and others (Flenley, 1973; Liu and Colinvaux, 1985; Bush and Colinvaux, 1988), have since shown that pollen preservation is good in the anaerobic sediments of tropical lakes with anoxic bottom waters.

The climatic fluctuations of the Holocene are believed to have been subtle compared with the turmoil of the late Pleistocene in which temperatures in the lowland tropics wavered between those of the present and a 7.5°C cooling (Bush *et al.*, 1990; Piperno, Bush and Colinvaux, 1990). Holocene temperatures have probably fluctuated within $\pm 1^\circ\text{C}$ and precipitation may have varied by about 10% (Kutzbach

tracked in tropical sediments it is essential to determine the feasibility of the palynological separation of the various lowland forest types. Grabandt (1980) examined the modern pollen spectra of the Colombian Andes and found that the various habitats were identifiable from their pollen rain. However, there has been no comparable modern pollen study in the lowland neotropics. Given that many of the large, rare trees of the lowland rain forests are entomophilous, or have 'unknown' pollen types, we are faced with separating forest types on the pollen representation of understorey and wind-dispersed forest components that can often only be identified to family.

In this study, modern pollen rain data from a suite of lowland Central American and Amazonian habitats are presented to test the hypothesis that observed pollen rains from different lowland vegetation communities can be separated statistically. Given that as many as 50% of the lowland pollen taxa recovered in sediment core samples may be of unknown types (Liu and Colinvaux, 1985), and that many pollen taxa are identifiable only to family level, the null hypothesis is that no discernible pattern of pollen rain is evident between differing lowland vegetation communities.

Data sources and methods

The sites selected (Figure 1) lie within the *varzea* forests of central Brazil (Absy, 1979); *terra firme* Amazonian rain

tion of central Brazil (Salgado-Labouriau, 1973; 1978); the dry forests of northern Venezuela (Leyden, 1985); and the Pacific watershed semi-deciduous forests of Panama (new data). The sites are characterized by similar temperature and altitudinal limits (all are <950 m elevation), though they differ widely in flood inundation, precipitation and length of dry season (Table 1). The sites represent broadly-defined ecological groups [cf. Prance, 1980; Sioli, 1985]: *terra firme* (tall forest on raised dry ground, not subject to flooding, see Table 1), *igapo* (black-water forests rich in humic acids, subject to almost permanent flooding), semi-deciduous forests (forests that do not flood and where a significant proportion of trees shed their leaves, generally in response to a dry season water shortage) and *varzea* (white-water forests subject to periodic, irregular, flooding by waters rich in suspended inorganic sediments). These data include almost all of the published modern lowland pollen rain studies for the neotropics.

The new data presented are mud/water interface samples from core tops of lake sediments raised using a modified Livingstone piston sampler. Location details of the unpublished sites are given in Appendix 1. Standard palynological preparation techniques were employed (Faegri and Iversen, 1975; Stockmarr, 1971) pollen counts ranged from 200 to 500 pollen and spores. The pollen count size relative to the statistical usage is discussed below.

Taxa that attained values of greater than 2% in any sample were included in the statistical analyses (cf. Lamb, 1984). Over-representation by *Cecropia* was met by its exclusion from the calculation of pollen percentages, as per the exclusion of *Betula*, *Corylus*, *Pinus* and *Alnus* from many temperate percentage pollen diagrams (e.g., Girling and Greig, 1977). Thus percentages used relate to a non-*Cecropia* pollen total, and *Cecropia* is shown as a percentage of total pollen (Figure 2). The data were plotted as a percentage diagram using the program Macpollen (Eisner and Sprague unpublished); classified using two-way indicator species analysis (TWINSPAN) (Hill, 1979a; ter Braak, 1988), and then ordinated using detrended correspondence analysis (DCA) (Hill, 1979b), detrending the axes with second order polynomials (ter Braak, 1988). DCA and TWINSPAN have proven to be highly successful for hypothesis generation with palaeoecological data (Birks, 1985; Clark, 1986; Bush and Colinvaux, 1990; Bush *et al.*, 1990), for the display of modern analogue assemblages for pollen and molluscs (Clark, 1986; Bush, 1988), and were chosen for this study for their robustness and capacity to handle data sets with many 'zero' scores. DCA axes represent hypothetical environmental gradients that explain major variance in the data set (Hill, 1979b). Therefore, the taxa that drive the axes are those that are abundant in one, or a group of samples, and absent in other samples. Taxa that are abundant in all samples and those that are relatively scarce (unless their pattern mirrors

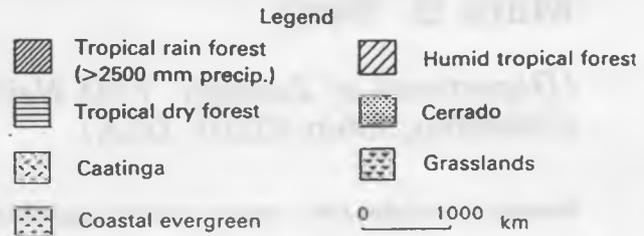
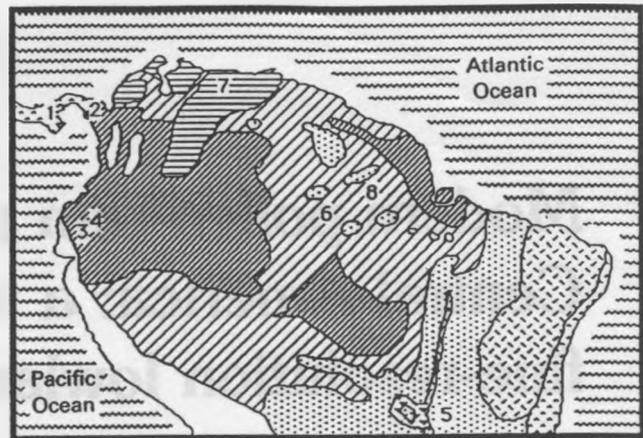


Figure 1 Sketchmap of the major lowland vegetation types of northern South America and Panama showing the approximate location of modern pollen sample sites: 1 La Yeguada and Laguna San Carlos; 2 Lake Wodehouse and Cana Swamp; 3 Kumpaka, Ayauchi, Anangucocha, Puyo Bog, Lago Sta Cecilia, Lago Agrio; 4 Mateococha, Macuracocha and Charapacocha (*igapo*); 5 *Cerrado*; 6 *Varzea*; 7 Lake Valencia; 8 Geral and Comprida.

the distribution of a more abundant taxa) have relatively little effect. The DCA will not be unduly influenced by slight variations in the percentage occurrence of the major taxa, and as the percentage occurrence of the most abundant taxa tend to be stabilized at a count of 200 pollen (Barber, 1976; Mosimann, 1965) this count size is adequate for present purposes.

The axial units of DCA ordinations are in standard deviations (SDs) of species turnover (Hill, 1979b). Separation of samples on the ordinate axes by 4.0 SDs of species turnover normally indicates no overlapping species (Hill, 1979b; Gauch, 1982). Separations greater than 1.39 SDs of species turnover suggest a c. 50% overlap of species (Hill, 1979b; Gauch, 1982). However, pollen assemblages do not conform to the underlying constraints of the DCA program to provide such statistical probabilities of separation (Birks, 1985). Nevertheless, separations in excess of 4 SDs of species turnover probably do indicate a strong difference between pollen rains.

Table 1 Some climatic factors for the vegetation types in the areas analysed.

Vegetation/Locality	mean annual temp (°C)	annual precipitation (mm)	dry season length (days)	Flooding (days)	Source
Dry forest, north Venezuela	25	1000	250	0	Leyden 1985
<i>Cerrado</i> , Brazil	24	1700	120	0	Salgado-Labouriau 1978
<i>Varzea</i> , Brazil	26	2200	90	irregular	Absy 1979
Dry forest, Brazil	26	2200	90	0	nd.
<i>Terra firme</i> , Ecuador	25	2500	60	0	Liu and Colinvaux 1985. nd.
<i>Igapo</i> , Ecuador	25	2500	60	300	Liu and Colinvaux 1985. nd.

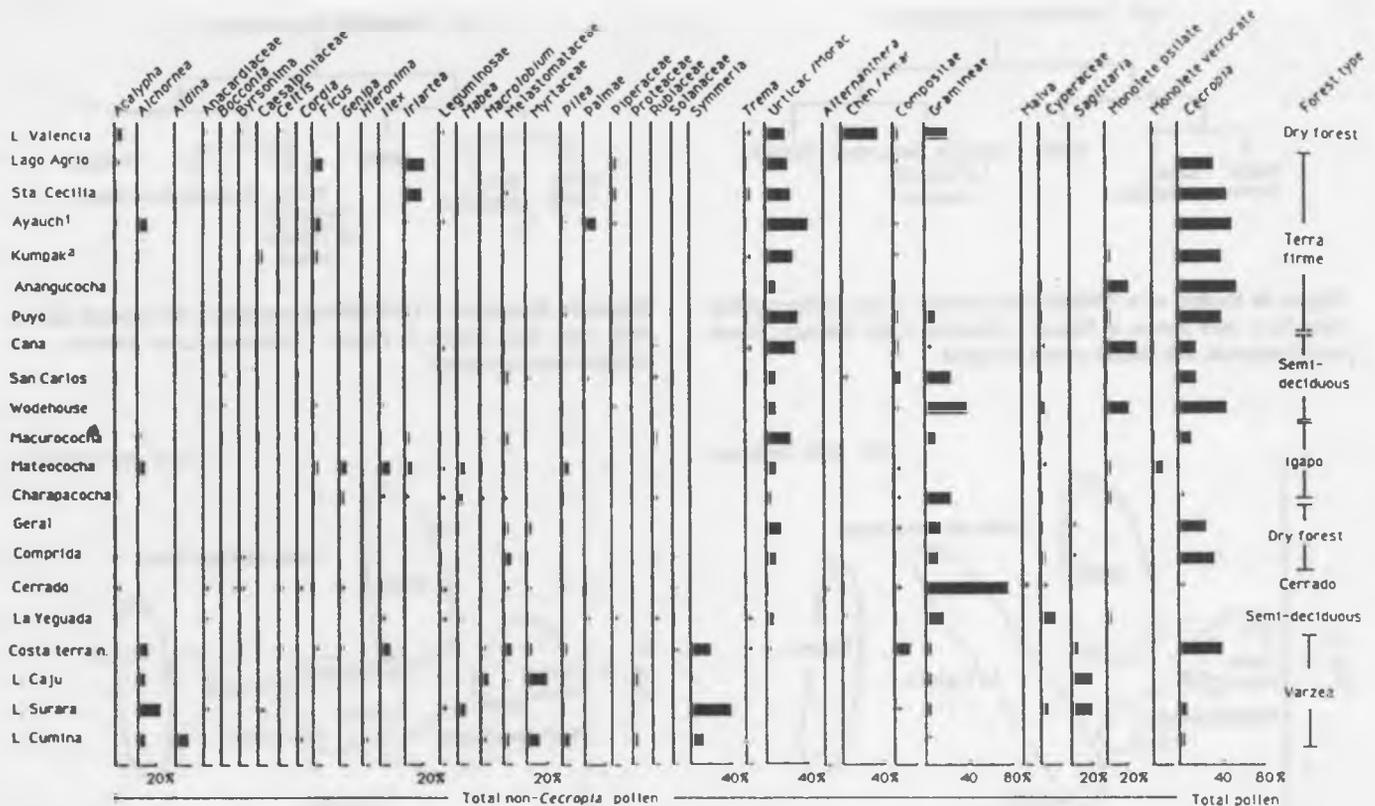


Figure 2 Modern pollen rain present as >2% of total pollen. Data are drawn from modern pollen traps (Salgado-Labouriau, 1973) and from mud/water interface and core-top samples (all other samples; Absy, 1979; Liu and Colinvaux, 1985; Bush and Colinvaux, 1988).

Results

One somewhat unusual and surprising feature of the collected pollen spectra is that no taxon is recorded in the pollen rain at every location (Figure 2). Although this may be a function of the relatively small counts used, it suggests a qualitative difference in the pollen spectra. The *Cecropia*, *Urticaceae/Moraceae* and *Melastomataceae*, are abundant in many of the samples, but they are by no means ubiquitous. The pollen of the prominent trees of the forest are rare, demonstrating that large entomophilous trees are under-represented as expected. However, some of these taxa not included in the analysis due to their scarcity, were found as single grains in some samples. They include strong indicators of forest type, e.g., *Pseudobombax*, *Didymopanax*, *Pithecellobium* and *Bocconia* (Bush and Colinvaux, 1988; Salgado-Labouriau, 1973).

Some distinctive patterns of pollen abundance are evident by simple inspection of Figure 2. The pollen rains from *terra firme* sites are richest in *Urticaceae/Moraceae* and *Piperaceae* pollen; *Symmeria* pollen is strongly associated with *varzeas*; and the halophytes, *Chenopodiaceae/Amaranthaceae* are strikingly abundant at Lake Valencia. The pollen of *Cecropia*, though over-represented in some samples is absent from over 20% of the sites. Where *Cecropia* is present it is often so abundant that to exclude it from the pollen sum seems a wise precaution.

The results of two TWINSpan classifications and three DCA ordinations are shown in Figures 3–5. The first axis of the first DCA (Figure 3) produces a separation of c. 7.5 SDs of species turnover, with the Lake Valencia site at the negative extreme of Axis 1, and all the other samples at the positive extreme. Lake Valencia is an outlier within the data

(Leyden, 1985). That Lake Valencia is so strongly separated from the other sites is a first indication that a strong statistical variation can be discerned between the modern pollen rains of lowland tropical sites. The second axis of this ordination clusters the *terra firme* sites at one extreme and the *cerrado* site at the other. This axis may represent an environmental gradient of increasing seasonality or dry season water stress. As Lake Valencia appears to be a statistical outlier, and in order to explain the maximum amount of variation between the other samples, Lake Valencia was excluded from subsequent analyses.

A hierarchical classification of the sites (excluding Lake Valencia) using TWINSpan is given as Figure 4a. This unconstrained classification in which all default parameters

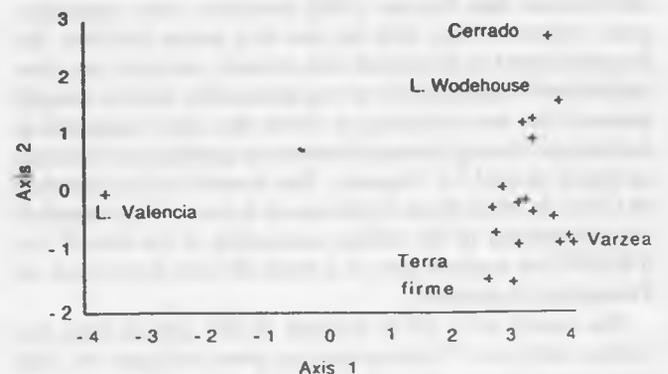


Figure 3 Results of DCA ordination of modern pollen data from sites shown in Figure 1, excluding Geral and Comprida. Eigenvalue of

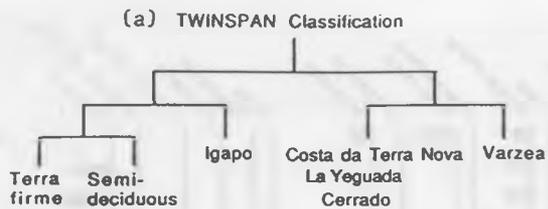


Figure 4a Results of a TWINSpan analysis of the modern pollen data from sites shown in Figure 1 excluding Lake Valencia, Geral and Comprida. All default values accepted.

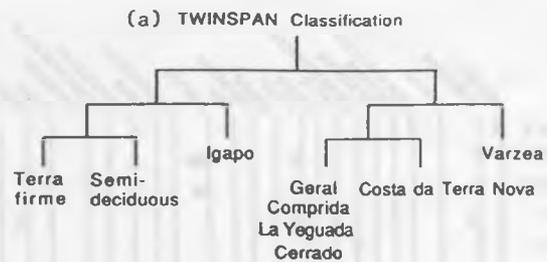


Figure 5a Results of a TWINSpan analysis of the modern pollen data from sites shown in Figure 1 excluding Lake Valencia. All default values accepted.

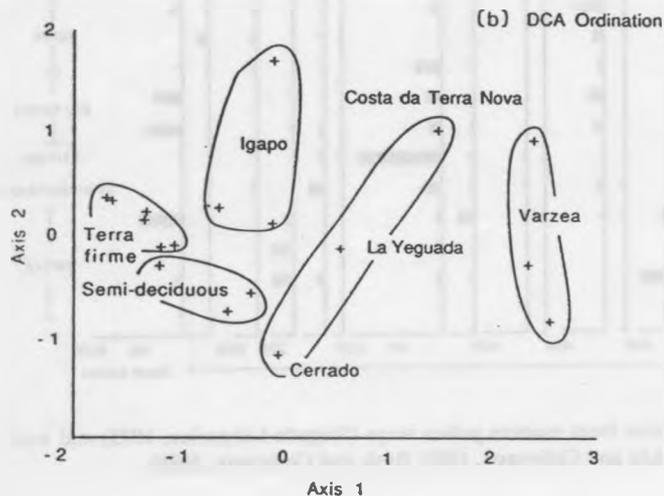


Figure 4b Results of DCA ordination of modern pollen data from sites shown in Figure 1, excluding lake Valencia, Geral and Comprida. Default settings are accepted throughout. Eigenvalue of DCA Axis 1-0.65; Axis 2-0.33. Samples are grouped according to the TWINSpan results (Figure 4a).

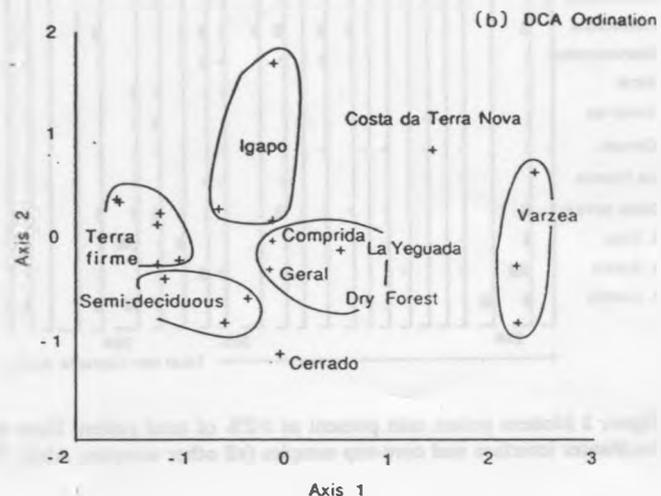


Figure 5b Results of TWINSpan and DCA ordination of modern pollen data from sites shown in Figure 1 excluding Lake Valencia. Default settings accepted throughout. Eigenvalue of DCA Axis 1-0.63; Axis 2-0.31. Samples are grouped according to the TWINSpan results (Figure 5a).

were accepted, divided the sites into ecologically interpretable groups, isolating the *terra firme*, *igapo*, semi-deciduous and *varzea* forests. The only complex of sites representing different habitats to be left grouped was the cluster of Panamanian Lake La Yeguada, cerrado vegetation and the river flood deposits of the Central Amazon at Costa da Terra Nova. The apparent similarity between La Yeguada and the cerrado site may be a result of intense landscape disturbance around La Yeguada. This disturbance has produced an environment that Piperno (1988) described as an 'anthropogenic cerrado'. Thus, with the few data points available, the program failed to distinguish true *cerrado*, an open, dry, fire-maintained landscape with strong seasonality, from a strongly seasonal but wet landscape in which the open vegetation is maintained through human disturbance (grazing and burning) as found around La Yeguada. The reason for the inclusion of Costa da Terra Nova in this group is not evident though it may be related to the strong seasonality of the site. If the TWINSpan analysis goes to a third divisive level Costa da Terra Nova is isolated.

The results of a DCA analysis of this second data set, without the Lake Valencia site are given in Figure 4b. The first axis separates the *varzea* samples from the *terra firme* samples and the *igapo* and *cerrado* samples are separated on the second axis. Moreover, the first axis is over 4.5 SDs of

from that of the other forest types. The length of the axis, and the inferred statistical separation is in part attributable to all taxa being relatively rare, i.e., none is found in every sample (Eilertsen *et al.*, 1990). On the second axis the statistical separation is less secure, with c. 3 SDs of species turnover and an eigenvalue of 0.33, but using the two dimensional separation of the sites no overlap exists between any of the main vegetation types (Figure 4b).

The best test of the robustness of an analysis is to enter extra data points. The sites added to the data set were Lagoas Geral and Comprida, located in strongly seasonal forests and lying close to an ecotone of *cerrado*/seasonal forest (Figure 1).

The resultant classification and ordination (Figure 5), from which Lake Valencia was again excluded, are strikingly similar to the results shown in Figure 4. The two primary axes are 4.3 (Axis 1) and 2.7 (Axis 2) SDs of species turnover in length and have eigenvalues of 0.61 and 0.31 respectively. The placement of the individual sites has scarcely changed while the new sites, Geral and Comprida, are shown to be related to the areas with the strongest dry-season. If the next cut of the TWINSpan analysis is plotted, the *cerrado* separates from La Yeguada and the two Brazilian sites. The similarity of the ordination results (Figures 4b and 5b) demonstrates the strength of the ordination: as does the

interpretability of the results also justify the earlier statement that it is unnecessary to have high pollen counts for a viable statistical analysis.

Discussion and conclusions

The results of the TWINSPAN and DCA analyses demonstrate that lowland pollen rain does vary significantly between habitat types and therefore the initial hypothesis is upheld and the null hypothesis is rejected. Different types of lowland tropical vegetation do produce characteristic and identifiable pollen rains. Even with this small data set it is apparent that *igapo*, *varzea*, *terra firme*, semi-deciduous and *cerrado* sites can be separated on their pollen rains.

Many more data points need to be plotted to establish the environmental factors that are driving the differences in observed pollen composition from lowland forests. However, these initial results clearly demonstrate the feasibility of obtaining accurate palaeoecological records from the lowland tropics. If the observed pattern of no taxon being present in every sample in the data set is maintained when, in the future, more samples are added, it should be possible to detect changes in lowland forest vegetation resulting from the magnitudes of climatic change that could be expected on a millennial time-scale (1 or 2°C, or a 10–20% change in precipitation). The next step is to improve the scale of study spatially, taxonomically and statistically through the study of modern pollen rain and associated vegetation types from a greater variety of habitats.

One of the unforeseen outcomes of this analysis was the realization of the danger of extrapolating climatic change from few empirical palaeoecological records. The statistical isolation of Lake Valencia from other lowland South and Central American pollen spectra is evident (Figure 3), and it is clear that the present vegetation surrounding this lake is

not characteristic of the other localities. For some years Lake Valencia was the only datum for climatic change at the Pleistocene/Holocene boundary in lowland tropical America (Salgado-Labouriau, 1980; Bradbury *et al.*, 1982; Leyden, 1985), was cited as providing evidence relating to climatic change in Amazonia (e.g., Haffer, 1987) and has been extensively quoted to support the concept of glacial refugia (Prance, 1982; Brown, 1987). It is clear that environmental conclusions regarding the climatic history of the Amazon basin should not be based on this unusual site. It is equally clear that vegetation changes documented in western Amazonia during glacial times (Bush *et al.*, 1990) cannot be assumed to be accurate predictors of change in the central Brazilian Amazon.

When fossil pollen assemblages from suites of lowland cores have been analyzed and many more modern analogue studies have been conducted, it does not seem unduly optimistic to believe that we can produce palaeoecological reconstructions from the lowland tropics as sophisticated as those from temperate latitudes (e.g., Davis, 1986; Webb, 1987; Huntley and Webb, 1989).

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Appendix 1 Location and character of unpublished surface sample sites

Lake Wodehouse, Darien, Panama. 600 m elevation.

Swamp area (c. 4km²) which floods in the wet season but retains an open body of water in the dry season; surrounding vegetation is mature semi-deciduous sub-montane forest.

Cana Swamp, Darien, Panama. 600 m elevation.

A swamp similar to lake Wodehouse but without standing water in the dry season; surrounded by semi-deciduous sub-montane forest.

La Yeguada, Veraguas, Panama. 650 m elevation.

Present vegetation around this 3 km² lake is disturbed semi-deciduous forest. Modern pollen samples were taken from immediately beneath a rise in *Pinus* pollen (planted around

the lake in the 1960s) at 20 cm depth in an 18 m sediment core.

San Carlos, Central Panama. 500 m elevation.

A small <1 km² lake surrounded by degraded semi-deciduous lowland forest.

Igapo lakes, Cuyabeno, Ecuador. 230 m elevation.

Macuracocha, Mateococha and Charapacocha are three lakes within the Cuyabeno forest reserve, Ecuador. All three lakes contract to small bodies of water during the brief dry season and then fill and flood the surrounding forest which is rich in *Macrobium acaciifolium* and *Genipa americana*.