

An analysis of modern pollen rain on an elevational gradient in southern Peru

Chengyu Weng^{*1}, Mark B. Bush^{*} and Miles R. Silman[†]

^{*} Department of Biological Sciences, Florida Institute of Technology, Melbourne, Florida 32901, USA

[†] Department of Biology, Wake Forest University, Winston Salem, NC 27109, USA

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Abstract: The sensitivity of pollen as an indicator of elevation in neotropical lowland and Andean forests was measured using modern pollen samples collected from moss-polsters along a transect between 340 m and 3530 m elevation and from surface sediments in lowland swamps (240 m) of Madre de Dios, Peru. A blind study, using samples collected from the same transect in the following year, provided a test of reproducibility. The results show (1) clear elevational distribution patterns and (2) the ability of calibration data to predict the altitude of the blind samples. Characteristic associations of pollen taxa are found under differing hydrologies and elevations. The floodplain pollen assemblages are characterized by abundant *Mauritia*, *Sloanea*, *Ficus*, *Iriartea* and *Arecaceae* pollen types. At higher elevations, these lowland types decrease or are absent. *Alchornea*, *Urticaceae/Moraceae*, *Bignoniaceae* and *Cecropia* are dominant components of the pollen rain of the low-elevation zone (< 1000 m). *Acalypha*, *Alchornea*, *Cecropia*, *Rubiaceae* and *Urticaceae/Moraceae* are important between 1000 m and 1600 m elevation. Pollen of *Hedyosmum*, *Alnus*, *Poaceae* and *Combretaceae/Melastomataceae* are abundant between 1600 m and 2000 m. *Cecropia* pollen dominates samples from low- to mid-elevation disturbed forests. *Alnus* pollen is most abundant, and *Poaceae* becomes rare, between 2000 and 2700 m. At high elevations above 2700 m, *Asteraceae*, *Poaceae*, *Polylepis*, *Muehlenbeckia*-type and *Myrsine* pollen are dominant. Statistical analysis of the data set using Detrended Correspondence Analysis (DCA) shows a precise correlation between community composition and elevation. The DCA axis 1 values are strongly correlated with sample elevation, exhibiting a linear relationship ($r^2 = 0.904$). The results provide an estimate of the sensitivity of pollen analysis in the Neotropics as a proxy for measuring elevation and, by inference, temperature.

Key Words: Andes, elevation, moss polster, palaeoecology, Peru, South America, transect

INTRODUCTION

It is well established that neotropical communities were strongly affected by Pleistocene climate change. Temperature and precipitation varied rapidly, with as much as 5 °C of cooling evident at all elevations for portions of the Pleistocene (Bush *et al.* 1990, 2001a; Colinvaux *et al.* 1996, Hooghiemstra 1984, Hooghiemstra *et al.* 1993, Ledru 1993, Liu & Colinvaux 1985, Salgado-Labouriau 1980, Salgado-Labouriau *et al.* 1997). The pacemaker of these changes was the precessional orbital cycles (19 000 and 23 000 y, Baker *et al.* 2001a, b; Bush *et al.* 2002, Hooghiemstra *et al.* 1993) and the advance of the Laurentide ice mass (Bush *et al.* 2002). Suggestions that the neotropics were an

important component of the feedback mechanisms that translated insolation variation into climatic change have heightened interest in palaeoecological records from the tropics. One such mechanism centres on the release of methane from the great tropical marshes in response to changed seasonality (Chappellaz *et al.* 1990, 1993; Street-Perrot 1992, 1993). The extent to which the tropics act as a magnifier or an instigator of global climate change is not known, and is likely to vary according to the phenomenon considered. However, the capacity for neotropical events such as the El Niño Southern Oscillation (Diaz & Markgraf 1992) to have global consequences is clearly evident.

Pollen analysis has been an important tool in revealing the importance of Pleistocene climate change, especially through tracking the vertical migration of tree species from which palaeotemperature estimates are inferred. This technique was pioneered in the tropics by van der Hammen & González (1960) and widely adopted

¹ Corresponding author. E-mail: cweng@fit.edu

by most other workers in the region. The quality of interpretations made by this technique is dependent upon a good understanding of the relationship between modern vegetation and modern pollen rain. The documentation of modern pollen rain contributed greatly to refining palaeoclimatic interpretations of similar ecosystems (Bradshaw 1981, Bradshaw & Webb 1985, Calcote 1995, Davis 1963, 1967; Davis *et al.* 1973, Flenley 1973, Jackson 1994, Sugita 1994). However, similar investigations in the neotropics are rare, and the reliability and precision of the inference remains largely untested.

In the neotropics, the most extensive study of montane floras and their pollen representation was conducted by Grabandt (1980, 1985) in Colombia. Grabandt's work provides a detailed image of montane pollen rain, however, the forest communities studied were dominated by *Quercus*, a genus that has its southern limit in Colombia. Consequently, the pollen rain of more southerly Andean forests is quite different. Similarly pollen-rain studies conducted in Costa Rica (Islebe & Hooghiemstra 1997, Rodgers & Horn 1996), and Panama and Costa Rica (Bush 2000, Bush & Rivera 1998) provide poor analogues for southern-hemisphere Andean forests as they are rich in *Quercus*. Additionally, all of the studies conducted to date have incorporated data collected from a relatively broad geographic region. Bush *et al.* (2001b) showed large turnover in species composition associated with geographic area, and concluded that the region from which modern calibration samples are drawn should be as small as possible. In this study, modern pollen data along an elevational gradient within a single small watershed were collected in order to minimize geographic variation. The result of modern pollen rain from the first elevational transect of modern pollen samples from Amazonia to the high Andes of Peru is presented.

STUDY AREA

The study was conducted in the headwaters of the Madre de Dios river in south-eastern Peru (approximately at 12°00'S and 71°00'W). The average annual rainfall in the lowlands is about 2300 mm with most precipitation falling between November and May. Rainfall between June and September is normally less than 100 mm (Terborgh 1990). Temperatures along the transect vary according to elevation with a moist-air adiabatic lapse rate of 5 °C per 1000 m change in elevation measured in the 2000 field season. In the lowlands mean annual temperature is 23 °C, but during the southern hemispheric winter southern air masses (*friajes*) can drop temperatures as low as 8.5 °C at 240 m elevation (*pers. obs.*).

The vegetation sampled forms a continuous gradient from tall forest and swamp in the meander belt of the

Manu–Madre de Dios river system at 250 m to open Puna at 3500 m elevation. Foster (1990) documented 2874 species in 1006 genera of 153 families for the entire transect. Collecting efforts in the region have been focused on the lowlands, so this species total is an underestimate. Overviews of the region can be found in Foster (1990), Gentry & Terborgh (1990), Terborgh *et al.* (1996), Pitman *et al.* (1999, 2001) and Ancaya (2002).

In the lowlands, habitat types range from rarely flooded high-ground forest to permanent swamps in the meander belt of the Manu–Madre de Dios drainage. Foster (1990) documented nearly 1400 species in 637 genera and 119 families in both the flooded and *terra firme* habitats in the study area. Tree-plot studies (Ancaya 2002, Pitman *et al.* 1999, 2001; Terborgh *et al.* 1996) document 676 species in 273 genera and 68 families. Families with the highest number of species overall are Fabaceae, Moraceae, Rubiaceae and Orchidaceae. For trees, Fabaceae, Moraceae, Sapotaceae, Lauraceae and Annonaceae are most speciose, while Arecaceae, Fabaceae, Malvaceae, Moraceae and Annonaceae have the most individuals (ranked in descending order of abundance). Diversity of lowland habitats ranges from 200 spp. ha⁻¹ in unflooded, high-ground forests to monodominant or codominant forests of the palm *Mauritia flexuosa* and an unidentified species of *Sloanea* (coll. EA401, Elaeocarpaceae) in permanent swamps.

Lowland habitats grade continuously into montane habitats along the transect with a monotonic loss of diversity starting above 1000 m (Gentry 1988). Familial composition also undergoes noticeable changes starting at 1000 m with the decline in importance of lowland families such as Arecaceae, Bignoniaceae, Fabaceae and Meliaceae, both in terms of species and number of individuals, and an increase in Clusiaceae, Rubiaceae, Melastomataceae and Lauraceae. By 1800 m, families such as Azalteaaceae, Chloranthaceae, Cunoniaceae and Podocarpaceae are conspicuous elements of the flora, and over 2500 m forests have increasing components of Araliaceae, Asteraceae, Cunoniaceae, Chloranthaceae, Myrsinaceae, Sabiaceae and Symplocaceae.

Several changes are noticeable at the species level along the transect as well. First, the dominant lowland palm *Iriarteia deltoidea* is replaced within a 100-m-elevation band at 1200 m by a similar iriarteoid palm *Dictyocaryum* sp. Other lowland palms are absent or greatly reduced above 1100 m except for the genus *Wettinia*, which is a dominant component of the understorey flora at mid-elevations throughout south-east Peru. A species in a monotypic family, *Azaltea verticillata*, becomes the dominant tree in mid-elevation forests along our particular transect. Its abundance varies throughout south-east Peru, but *Azaltea* is a dominant of many mid-elevation forests from Bolivia to Ecuador (R. Foster, *pers. comm.*). Finally, *Alnus* increases in abundance

conspicuously at 1750 m and continues up to 2800 m. *Alnus* and *Cecropia* dominate disturbed areas at the higher elevations along the transect.

MATERIALS AND METHODS

Samples were obtained during field trips in July 2000 and June 2001. An elevational transect from 3530 m down to 1000 m, comprising a transition from sub-Paramo to premontane forest, was sampled adjacent to the Paucartambo–Pilcopata road in the Kosñipata Valley. Additional samples were collected from mature forest at Pantiacolla between elevations of 340 and 880 m. Lowland samples came from around Cocha Cashu in Manu National Park (350 m) and from swamps along the Madre de Dios river upstream of the confluence with the Inambari river (240 m). Moss-polster samples were collected by taking multiple pinches of mosses from a 20-m² area every 50–100 m of descent. A 20-m² sample area was chosen because a high proportion of lowland forest pollen is only dispersed 5–20 m (Bush & Rivera 1998, Kershaw & Strickland 1990), and that this area

is large enough to receive input from numerous tree canopies, but small enough to be relatively homogeneous in habitat type. Wherever possible, the most mature forest was sampled, although the sheer cliffs above and below the road limited forest access in some locations. Trails were followed away from the road wherever possible. A parallel set of samples was also collected from disturbed settings as a contrast to the more mature locations. In the protected forests of the floodplain of the Rios Manu and Madre de Dios (240 m elevation) mud–water interface samples were collected from moist locations (Figure 1, Table 1).

Pollen was extracted from the moss-polsters or sediments following the method of Faegri & Iversen (1989). In the mud–water interface samples where volumetric analysis was possible, *Lycopodium clavatum* spores were added to allow calculation of pollen concentration (grains cm⁻³) (Stockmarr 1971). Pollen identifications were based on published atlases and keys (Absy 1979, Bartlett & Barghoorn 1973, Colinvaux *et al.* 1999, Heusser 1971, Hooghiemstra 1984, Markgraf 1978, Roubik & Moreno 1991) and the pollen reference collection at the Florida Institute of Technology (> 3000 species). At least

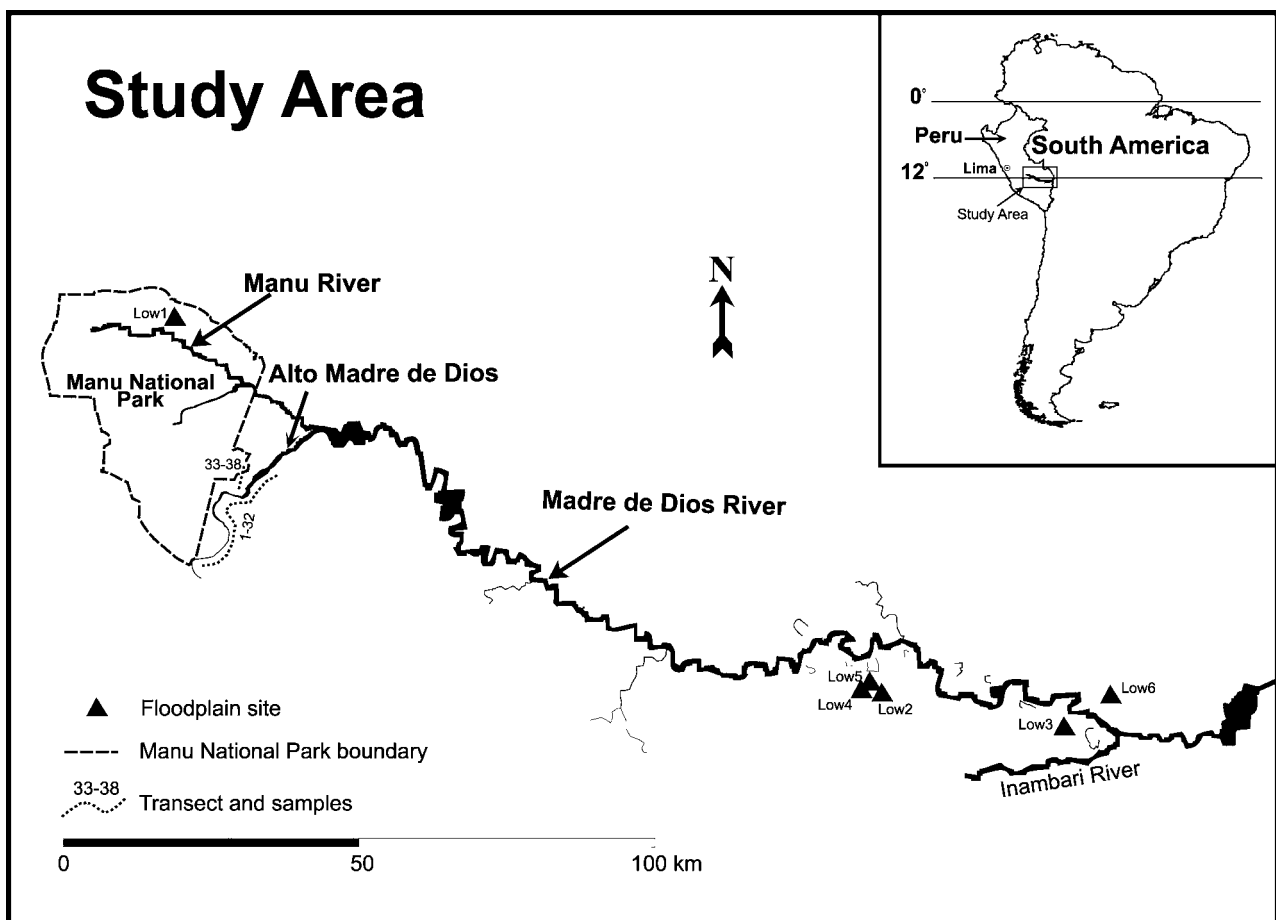


Figure 1. Map showing locations of the study area, investigation transect and lowland floodplain sample sites.

Table 1. Descriptions of samples and sampling site. Vegetation type and main plant genera and families are given in the site description.

| Samples | Lab No. | Elevation (m) | Vegetation | Major taxa | Sample type |
|---------|----------|---------------|---------------------------------------------|-------------------------------------------------------------------------|------------------|
| M1 | Manu#1 | 3530 | less-disturbed sub-puna | Poaceae, Cyperaceae, Asteraceae, Gentianaceae, <i>Polylepis</i> | moss polster |
| M2 | Manu#31 | 3430 | disturbed sub-puna | Poaceae, <i>Polylepis</i> , Asteraceae | moss polster |
| M3 | Manu#2 | 3330 | less-disturbed sub-puna | Poaceae, Cyperaceae, Asteraceae, <i>Polylepis</i> | moss polster |
| M4 | Manu#30 | 3230 | disturbed sub-puna, grazed by horses | Poaceae, Cyperaceae, Asteraceae | moss polster |
| M5 | Manu#3 | 3130 | less-disturbed sub-puna | <i>Podocarpus</i> , Melastomataceae, Ericaceae | moss polster |
| M6 | Manu#29 | 3030 | disturbed sub-puna | Poaceae, Cyperaceae, Asteraceae | moss polster |
| M7 | Manu#4 | 2930 | less-disturbed sub-puna | Bambusoideae, Melastomataceae, Ericaceae | moss polster |
| M8 | Manu#28 | 2850 | disturbed sub-puna | Bambusoideae, <i>Myrica</i> , Melastomataceae, Ericaceae | moss polster |
| M9 | Manu#5 | 2770 | cloud forest | <i>Alnus</i> , Bambusoideae, Melastomataceae, <i>Clusia</i> , Ericaceae | moss polster |
| M10 | Manu#27 | 2750 | cloud forest, a fire occurred previous year | <i>Alnus</i> , Bambusoideae, Melastomataceae | moss polster |
| M11 | Manu#6 | 2570 | cloud forest | <i>Alnus</i> , Melastomataceae, <i>Podocarpus</i> , <i>Hedyosmum</i> | moss polster |
| M12 | Manu#20 | 2400 | cloud forest | <i>Alnus</i> , <i>Clusia</i> , <i>Podocarpus</i> , <i>Hedyosmum</i> | moss polster |
| M13 | Manu#19 | 2330 | cloud forest | <i>Alnus</i> , <i>Gunnera</i> | moss polster |
| M14 | Manu#18 | 2240 | cloud forest | <i>Weinmannia</i> , <i>Alnus</i> , <i>Cecropia</i> | moss polster |
| M15 | Manu#17 | 2120 | cloud forest | Myrtaceae and <i>Clusia</i> | moss polster |
| M16 | Manu#16 | 2000 | cloud forest, streamside | <i>Cecropia</i> with more varied herbs | moss polster |
| M17 | Manu#26 | 2000 | cloud forest | <i>Clusia</i> , Myrtaceae and some <i>Podocarpus</i> | moss polster |
| M18 | Manu#25 | 1950 | cloud forest | <i>Clusia</i> , Myrtaceae and some <i>Podocarpus</i> | moss polster |
| M19 | Manu#15 | 1940 | cloud forest | <i>Cecropia</i> and Melastomataceae herbs | moss polster |
| M20 | Manu#21 | 1890 | cleared forest | <i>Cecropia</i> | moss polster |
| M21 | Manu#14 | 1800 | cloud forest | Bambusoideae, <i>Clusia</i> and Rubiaceae | moss polster |
| M22 | Manu#7 | 1700 | cloud forest | <i>Podocarpus</i> , Myrtaceae and bamboos | moss polster |
| M23 | Manu#8 | 1630 | cloud forest | <i>Podocarpus</i> , <i>Weinmannia</i> and <i>Dictyocaryum</i> | moss polster |
| M24 | Manu#13 | 1548 | cloud forest, streamside | dominated by <i>Cecropia</i> | moss polster |
| M25 | Manu#9 | 1450 | cloud forest, young secondary forest | <i>Cecropia</i> , Rubiaceae and Moraceae | moss polster |
| M26 | Manu#10 | 1400 | good secondary forest along river | <i>Cecropia</i> , Moraceae and bamboos | moss polster |
| M27 | Manu#32 | 1400 | secondary forest near a bridge | <i>Cecropia</i> , Tiliaceae and Annonaceae | moss polster |
| M28 | Manu#12 | 1340 | secondary forest | Moraceae | moss polster |
| M29 | Manu#24 | 1210 | young secondary forest along streamside | <i>Iriarte</i> , Euphorbiaceae | moss polster |
| M30 | Manu#11 | 1140 | secondary forest on streamside | <i>Cecropia</i> , <i>Iriarte</i> , Euphorbiaceae | moss polster |
| M31 | Manu#22 | 1080 | secondary forest | <i>Croton</i> , <i>Hevea</i> , Moraceae | moss polster |
| M32 | Manu#23 | 1070 | decent secondary forest | Moraceae, Bignoniaceae and <i>Iriarte</i> | moss polster |
| M33 | Manu880 | 880 | premontane secondary forest | Moraceae, Bignoniaceae, Rubiaceae and <i>Iriarte</i> | moss polster |
| M34 | Manu770 | 770 | premontane secondary forest | Moraceae, Bignoniaceae, Rubiaceae and <i>Iriarte</i> | moss polster |
| M35 | Manu670 | 670 | premontane secondary forest | Moraceae, Bignoniaceae, Annonaceae and Rubiaceae | moss polster |
| M36 | Mirad550 | 550 | premontane secondary forest | Moraceae, Annonaceae, Rubiaceae and <i>Cecropia</i> | moss polster |
| M37 | Mirad470 | 470 | premontane secondary forest | Moraceae, Rubiaceae, Annonaceae and <i>Cecropia</i> | moss polster |
| M38 | Ct1_7 | 340 | premontane secondary forest | Moraceae, Bignoniaceae and <i>Iriarte</i> | moss polster |
| LOW1 | Mod4 | 350 | Cochu Cashu landing | Rubiaceae, <i>Cecropia</i> | surface sediment |
| LOW2 | Mod3 | 240 | new oxbow | <i>Cecropia</i> | surface sediment |
| LOW3 | Mod5 | 240 | sedge swamp | Cyperaceae, <i>Mauritia</i> | surface sediment |
| LOW4 | Mod6 | 240 | vine swamp | <i>Hedyosmum</i> , <i>Mauritia</i> | surface sediment |
| LOW5 | Mod1 | 240 | swamp | <i>Mauritia</i> , <i>Sloanea</i> , <i>Ficus</i> | surface sediment |
| LOW6 | Mod2 | 240 | <i>Sloanea</i> swamp | <i>Sloanea</i> | surface sediment |

300 terrestrial pollen grains were counted for each sample. If one pollen taxon exceeded 33%, the count was continued until a total of at least 200 grains of other taxa was reached.

To reduce counting errors, pollen types were amalgamated into 75 taxonomically robust pollen types for statistical analysis. Percentage pollen data were log-transformed and analysed using the version of Detrended

Correspondence Analysis (DCA; Hill 1979, Hill & Gauch 1980) contained in PC-Ord 4.0 (McCune & Mefford 1999). Rare species were down-weighted.

Following the initial phase of this study six additional moss polsters were collected in the same valley by Bush and given to Weng in a blind experiment. The goal of this experiment was to see how accurately samples of unknown provenance could be located on the

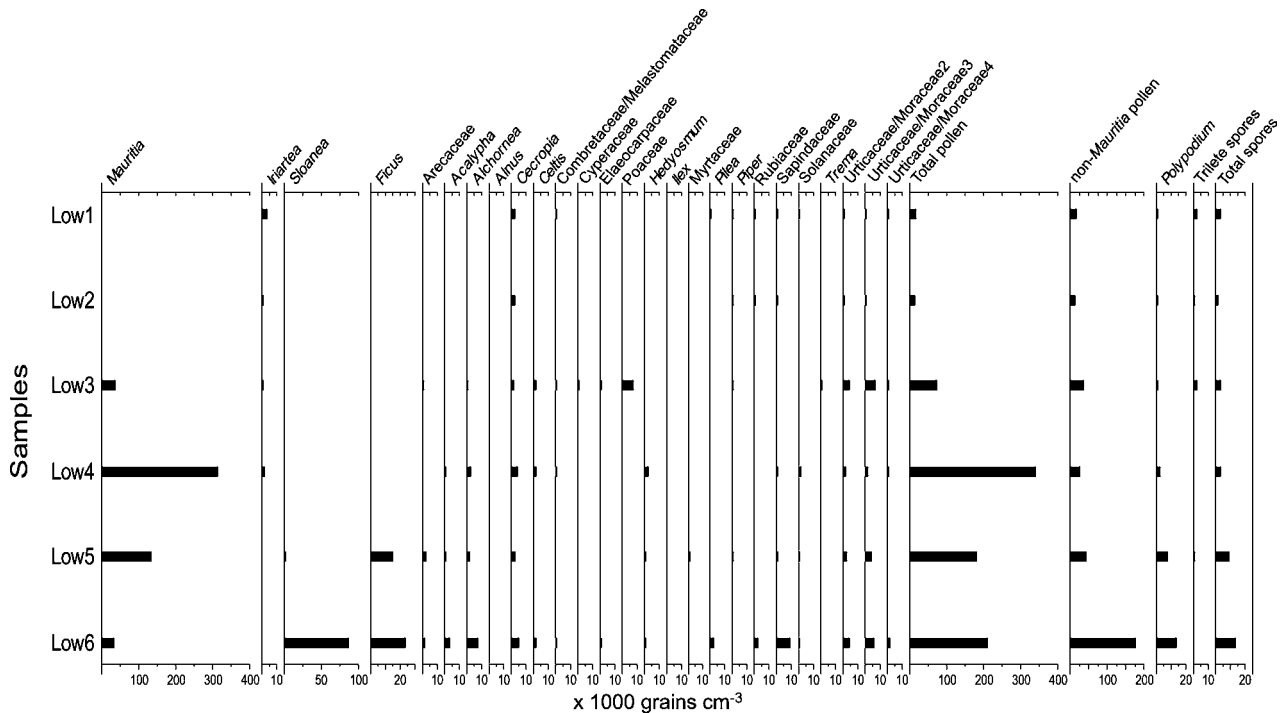


Figure 3. Concentration diagrams of selected pollen types for floodplain samples ($\times 1000$ grains cm^{-3}). Numbers attached with Urticaceae/Moraceae are pore numbers of the pollen type.

Zone 2, 1000–1600 m (medium elevations): This zone is characterized by relatively abundant *Acalypha* (5–20%), *Alchornea* (~10%) and Rubiaceae (5–20%). Urticaceae/Moraceae (~10%) and Combretaceae/Melastomataceae (around 10%) are moderately abundant. *Alnus* pollen is rare. *Cecropia* is moderate (10–20%) to dominant (~70%). *Iriartea* and Myrtaceae are also common. *Polypodium* is the dominant fern type.

Zone 3, 1600–2000 m (mid–high elevations). Abundant Poaceae (10–~35%), *Hedyosmum* (20–65%) and Combretaceae/Melastomataceae (~10%) are the characteristic taxa of this zone. *Alchornea* becomes important in the pollen assemblages. *Cecropia* pollen varies widely in abundance with a maximum representation of 80% in one disturbed site. *Alnus* begins to increase. *Polypodium* is the most important spore type.

Zone 4, 2000–2700 m (Upper Andean forest): This zone is dominated by *Alnus* (10–80%), and other types are generally scarce. Poaceae is very rare. *Polypodium* is also not as abundant as the nearby upper and lower zones, but still important.

Zone 5, > 2700 m (Sub-Puna-upper Montane): Pollen rain is dominated by Asteraceae (~20%) and Poaceae (~10–20%), and characterized by high percentages of high-mountain taxa: *Polylepis* (<10%), *Myrsine* (~5–20%), *Alnus* (~10%), and *Myrica* (~10%). The appearance of Ericaceae and *Muehlenbeckia*-type also distinguishes it from other zones. *Hedyosmum* is also abundant (5–10%), but already decreased from lower

elevations. This composition reflects grassland conditions with scattered shrubs. *Cecropia* is very rare or absent. Spores of *Polypodium* and *Lycopodium* are abundant.

DCA analysis

Results from the first two axes of DCA using percentage data show a clear separation of forest types along the first two axes (Figure 4). Axis 1 is generally consistent with a gradient of decreasing elevation. Lowland components *Mauritia*, *Sloanea*, *Ficus*, and *Arecaceae* all have highly positive scores on this axis, and high-elevation components *Muehlenbeckia*, *Polylepis*, *Myrica* and Ericaceae all have highly negative scores. All of the high-elevation samples are located on the negative extreme of Axis 1, whereas all samples from the low elevations below 1000 m are at the positive extreme of the axis, though relatively loosely distributed. Within the latter group, samples from the floodplain are separated into two subgroups by the low-elevation samples, which are located close to each other (Figure 4).

Three other groups are identified with elevation ranges of 1940–2400 m, 1600–2000 m, and 1000–1600 m, separately. The unconstrained grouping is similar to that of the zonation (a constrained classification) described in the previous section except for a few samples near the boundaries.

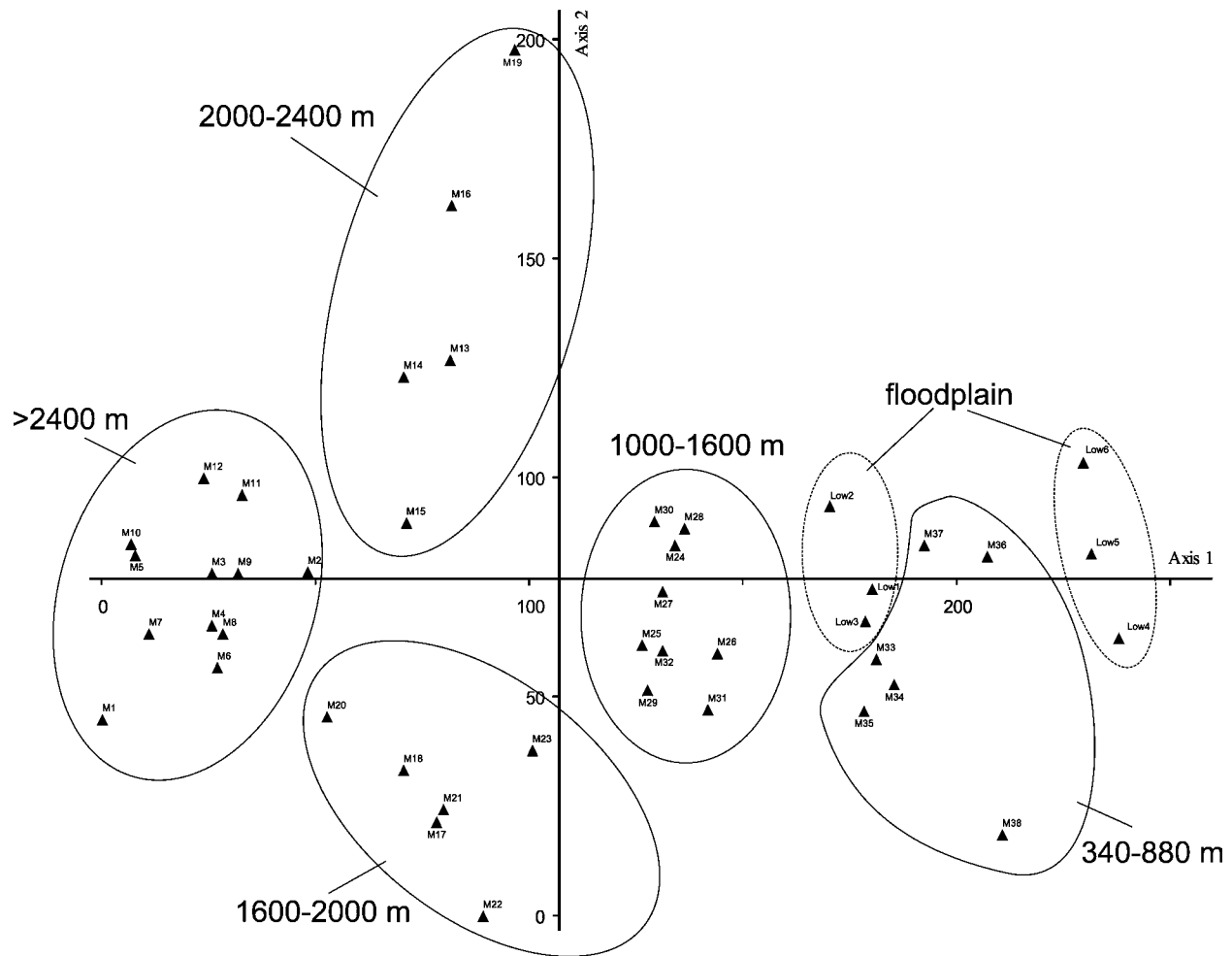


Figure 4. Scatter diagram of the first two DCA axes. Log-transformed percentage data of 75 pollen taxa were used for the analysis and rare species were down-weighted. The eigenvalues for the two axes are 0.319 and 0.116, respectively. Lines enclose samples from different elevation zones. These zones are roughly consistent with the pollen zones. Elevation values of the samples are shown in Table 1 (smaller sample number has higher elevation value).

Disturbed habitats in the lowlands that are rich in *Cecropia* pollen (M16, M19, M24, M28 and M27). These samples occur in the same sector of Axis 1 as other undisturbed samples. Similarly, *Alnus*-rich samples occur together with other upland samples on Axis 1, but have higher values on Axis 2 (M10, M11 and M12). As *Cecropia* and *Alnus* both have highly negative scores on this Axis 2, it may be because *Alnus*, which replaces *Cecropia* above 2000 m, is the invasive tree of disturbed habitats at higher elevations. Samples from mature forest at high elevation (M1, M3, M5 and M7) are distributed more towards the lower side of the axis 1 than the more disturbed samples (M2, M4, M6 and M8), but the values on Axis 2 do not show consistent difference between these two groups.

In order to test the relationship between elevation of the samples and their community composition, the elevation of each sample was regressed against its DCA axis 1 score (Figure 5). A negative linear relationship is evident

(slope = -13.9). Linear regression shows a very close relationship ($R^2 = 0.90$). The linear relationship between elevation and the DCA Axis 1 values is still strong even if only the presence/absence data of pollen taxa are used in the analysis ($R^2 = 0.85$). The six test samples (Figure 6) that were analysed in the blind experiment were found to ordinate close to samples from their true elevation. The estimated mean results are within 350 m of the true elevation values (Figure 5, Table 2).

DISCUSSION

Elevational characteristics of pollen rain in study area

Pollen rain of the lowland floodplain was characterized by a few lowland types: *Mauritia*, *Sloanea*, *Iriarte*, *Ficus* and other *Arecaceae*. Among them, *Mauritia* pollen is

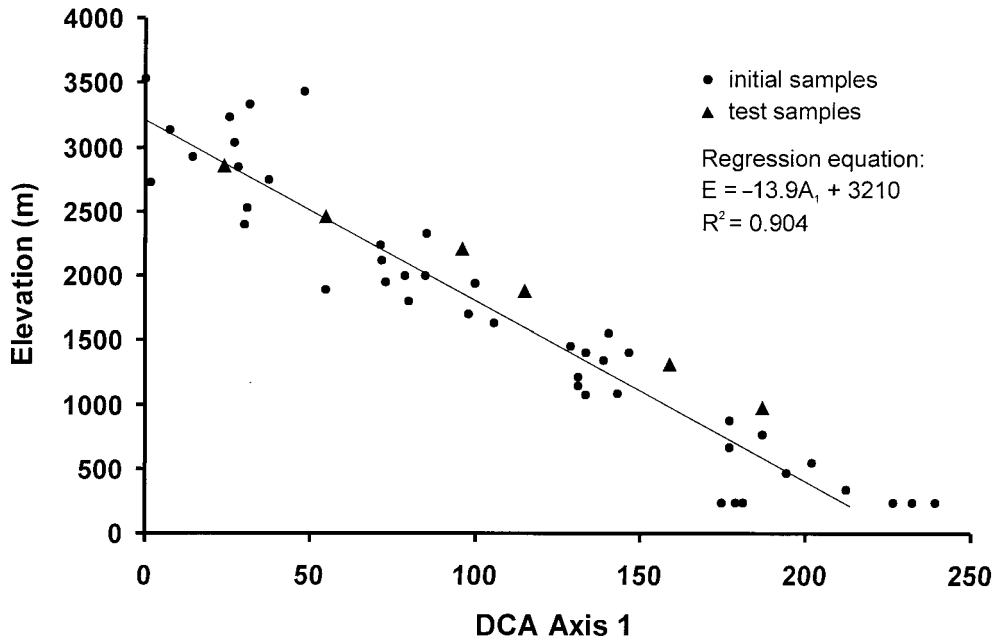


Figure 5. Regression of the elevation values and the DCA Axis 1 values using the percentage pollen data and mapping of the test samples. The regression line and the regression equation are also shown. In the regression equation: E, elevation value; A1, Axis 1 value of DCA.

probably the most dominant component in the lowland floodplain swamps and accounts for the high pollen concentrations of the swamp samples (Figure 3). If *Mauritia* was removed from the assemblages, the total pollen concentration of all lowland samples were similar. The only exception was Low 6, in which *Sloanea* was an

important pollen component (Figures 2, 3). At this site, *Sloanea* trees overhung the sampling site, and pollen of this genus formed as much as ~40% of the pollen sum (Figure 2). Apparently *Sloanea* produced copious amounts of pollen. At other locations, despite the local presence of *Sloanea*, this pollen type formed a small portion of the total

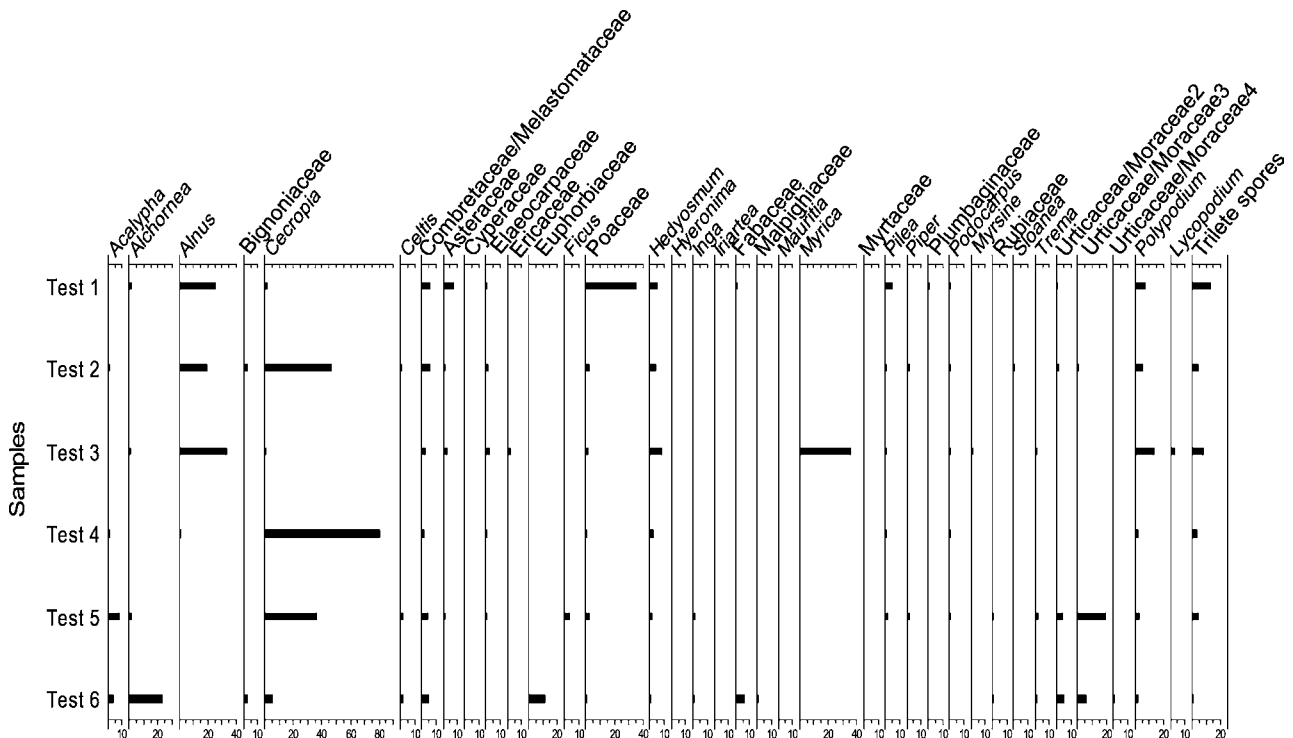


Figure 6. Percentage pollen diagram of the samples used to test the accuracy of the relationship between elevation and the DCA Axis 1.

Table 2. Estimated elevations of the test samples and their difference from the measured values. The measured elevation values were obtained from calibrated GPS readings, and the estimated elevation values were calculated from the regression equation in Figure 5. Difference is the difference of the elevation estimated from the elevation measured (minus means lower than the measured value).

| Samples | Elevation measured (m) | Elevation estimated (m) | Difference (m) |
|---------|------------------------|-------------------------|----------------|
| Test 1 | 2461 | 2456 | -5 |
| Test 2 | 2205 | 1883 | -322 |
| Test 3 | 2860 | 2885 | 25 |
| Test 4 | 1885 | 1623 | -262 |
| Test 5 | 1316 | 1011 | -305 |
| Test 6 | 975 | 624 | -351 |

terrestrial pollen (< 5%), suggesting poor dispersal. The pollen of *Mauritia*, *Sloanea* and *Ficus* were largely restricted to swamp settings, and their proportion of the pollen rain declined abruptly in open-water settings.

As would be expected, the distribution of pollen types showed strong elevational patterns. Some taxa exhibited very narrow elevational ranges in the pollen rain. *Polylepis* was seen only in high-elevation samples (> 2700 m), and was more abundant in the samples from the highest elevations (> 3400 m, up to 10%). *Muehlenbeckia*-type was also only seen at elevations > 2700 m, and was commonest between 2700 m and 3200 m. Similarly, *Myrica* pollen was very rare below 2700 m, but was a common component of the pollen sum at higher elevations. Lowland pollen taxa tend to have more general distributions in which they were found from the lowest elevations up to 2000 m with a sporadic occurrence at higher elevations. This spread across such a wide elevational range may be due to our inability to subdivide some important and speciose groups such as Urticaceae/Moraceae, *Cecropia* and *Alchornea*. Contrastingly, when dealing with monospecific genera with identifiable pollen types, the palynological record provided a closer match to the actual vegetation changes. *Iriarte* is replaced by *Dictyocaryum* at about 1300 m elevation. In the pollen record *Iriarte* was more common than *Dictyocaryum* up to < 1400 m. Above 1600 m only *Dictyocaryum* pollen occurred, but disappeared at about 1700 m where the palm also disappeared from the vegetation.

Some pollen taxa appeared at most elevations, but were only abundant within limited elevation ranges. Examples of pollen types with rather narrow representation maxima can be found for most elevational ranges. Asteraceae pollen increased in importance in the sub-paramo where they generally formed c. 20% of the pollen rain above 2900 m. Below this elevation Asteraceae seldom exceeded 5% of the pollen rain. *Myrsine* was a common component of pollen assemblages between 2700 m and 3300 m. However, an exception was a sample at 1890 m elevation, in which *Myrsine* pollen abundance was

much higher than in other samples, reaching ~55%. *Acalypha*-type pollen was most common between 1000 m and 1600 m. *Hedyosmum* pollen had a more complex distribution as it was most abundant at elevations of 1600–2000 m (15–65%) and common in most high-elevation samples. *Hedyosmum* pollen also appeared as a rare component of floodplain samples. Poaceae pollen was abundant in two elevational zones: between 1600 m and 2000 m, and above 3000 m. These two zones had different pollen sources, with most Poaceae pollen being derived from bamboo in the lower zone, and more from turf-forming grasses in the higher zone (Figure 2).

Alnus demonstrated a classically skewed distribution which was found in other Andean forest taxa, e.g. *Hedyosmum*, Urticaceae/Moraceae and *Podocarpus*. *Alnus* pollen was so widely dispersed that values of < 2% were almost certainly attributable to long-distance dispersal. When *Alnus* pollen was present at > 5% it probably reflected the local occurrence of the plant. *Alnus* accounts for > 5% at all elevations > 1700 m, but was by far the commonest pollen type (30–80%) in samples between 2300 m and 2800 m. The lowest *Alnus* tree seen growing on this transect was at 1735 m elevation, which closely corresponded with the lower limit of a substantial *Alnus* pollen representation. *Alnus* individuals were only occasional between 1735 m and 2300 m elevation, but between 2300 m and 2800 m *Alnus* was one of the dominants of the forest. Thus, through the lower and middle portion of its range *Alnus* pollen reflects the actual abundance of the tree. Above 2800 m *Alnus* became rarer in the landscape, but its pollen was still abundant (10–20%), probably due to low pollen production of local taxa.

Comparison with previous similar studies

Few investigations of modern pollen rain have been made in the humid Neotropics. The most comprehensive study was conducted in the Colombian Cordillera Oriental by Grabandt (1980, 1985). In that study, vegetation releves and pollen rain from 15 transects between elevations of 200 and 3800 m were compared. However, due to differences in forest composition and latitude, direct comparison of the Colombian data set with ours from Peru is of limited value. Grabandt's study area was 4–7°N latitude, 16–19° north of our site, and is dominated by oak (*Quercus*) trees, which are absent in Peru. *Quercus* is anemophilous and produces copious quantities of pollen, consequently, the abundance of *Quercus* pollen suppresses percentage representation of other taxa in the Colombian assemblages (Grabandt 1980). However, some general characteristics common to both areas are seen, especially from the transects with few *Quercus* and comparably greater elevation spans

(Grabandt's transects 10, 14 and 15, Grabandt 1980). Asteraceae and Poaceae, *Myrica* and *Myrsine* were most abundant at high elevations, and *Hedyosmum* was most abundant at mid-high elevations. *Alchornea*, *Acalypha* and Rubiaceae showed maximum abundances in premontane elevations (but not lowland). *Cecropia* was commonest at lower elevations below 2100 m.

Other investigations on modern pollen rain in lowland Amazonian forests have tended either to be somewhat cursory or to have described a narrow habitat range (Absy 1979, Bush 1991, Bush *et al.* 2001b). In her pioneering description of lowland Amazonian palynology, Absy (1979) described six samples from the mud–water interface of varzea (nutrient-rich) lakes near Manaus, Brazil. She found *Cecropia* to be the most abundant taxon in the pollen assemblages, ~30% in five of the six samples, and 11.5% in the other. *Symmeria* was abundant in her samples with between 10% and 16% of the pollen rain. Surprisingly, Asteraceae was nearly 10% for all samples and this may reflect dry-season establishment of a herbaceous marsh. Caryophyllaceae was high (3–6.5%). *Alchornea* was between 4% and 20% and other common taxa were *Miconia* (3–7%), Poaceae (1.5–4%), *Acalypha* (1–3.5%), and Myrtaceae (2–4.5%). *Mauritia*, *Ficus* and other Arecaceae taxa were rare members of these pollen spectra. These varzea samples are broadly similar to other varzea and some igapo (nutrient-poor) systems in western Amazonia (Bush 1991).

The previously described modern pollen rain that most closely matches our lowland Peruvian data are from Cuyabeno, Ecuador (Bush *et al.* 2001b). In the Ecuadorean samples, three types of forest were compared, *Mauritia*-rich, seasonally flooded, and terra firme. In the *Mauritia*-rich forests of Cuyabeno, *Mauritia* pollen was not as dominant as in the Manu area. Indeed, at Cuyabeno even in *Mauritia*-rich forests *Mauritia* pollen only accounted for 20–30% of the pollen reflecting a high diversity of other taxa mingled in the forests. At Cuyabeno, *Ficus*, *Iriartea* and other Arecaceae pollen although present in *Mauritia*-rich forest, were most abundant in seasonally flooded forests.

Use of modern pollen rain in palaeoecological reconstruction

The vertical migration of stenothermic species in response to climate change has become an important gauge of palaeotemperature. van der Hammen & Gonzalez (1960) demonstrated the use of adiabatic lapse rates to convert vertical plant species migration into change in temperature. Since then, such analyses have become a standard way to infer palaeotemperature from terrestrial pollen records. Thus, an accurate assessment of changes in modern pollen representation along an

elevational gradient is an important component of palaeo-environmental reconstruction.

Variation within and between our statistically derived zones is large. Because community boundaries are weak to non-existent, there is no clear delimitation of life zones. Here, multivariate statistics applied to the pollen data are a valuable tool to identify where the maximum turnover of species occurs.

The significant regression of elevations and DCA scores affirms the potential for accurate reconstructions of palaeotemperature. Two of our six test samples fall precisely on the regression line, and four others are consistently above the line. While the four overestimates of elevation may be due to chance ($P = 0.063$), they are probably influenced by a systematic factor. Misidentification of a pollen type cannot be ruled out, but as counts were made by one analyst and as individual counts were interspersed among other known samples that possibility is seen as small. As the known and unknown samples were collected in two different years (the same month each time), inter-annual differences in the phenology of flowering could account for the apparent error. If the accuracy (within 350 m elevation) obtained in this paper persists in other regions or in fossil samples, the accuracy for palaeotemperature reconstruction could be within 1.8 °C (lapse rate 5 °C per 1000 m; Vuille & Bradley 2000).

Even when only the presence–absence data were used in the analysis, the linear relationship between elevation values and the DCA Axis 1 values was still very good ($R^2 = 0.848$). Two important realizations follow. For some time there has been debate over the optimal size of a pollen count. Most pollen data sets are percentages based on total count of 300–500 pollen grains. A minimum of 300 grains is often used as this provides a basic reproducibility of percentages for taxa present at > 5% (Birks & Birks 1980, Moore *et al.* 1991). Extending counts beyond 300 grains further reduces variance in the data, but often is not considered to be cost-effective. In this area of extremely high biodiversity, presence–absence data at count sizes of 300 grains appear to convey almost as much information as percentile data. Consequently, it is evident that extended pollen counts are not necessary for palaeo-ecological reconstruction.

The second outcome of the presence–absence study is that it provides a data set that is more likely to be comparable with a fossil lake record than the percentile data. Moss polsters, even when collected from a 20-m² area of forest are still strongly biased by overhanging trees (Bush 2000, Grabandt 1985). Percentage data from polsters contain much higher proportions of entomophilous taxa than are normally found in lake sediments. However, the presence–absence data reflect ranges of pollen types rather than local abundances. Comparing presence–absence data from polsters with

data from lake sediment may provide a powerful tool to help calibrate palaeotemperature.

CONCLUSIONS

Modern pollen assemblages between 240 m and 3500 m elevation reflect local floras and provide a characteristic pollen spectrum for each elevation. As expected forest turnover along an elevational gradient provided a strong correlation with changing pollen spectra. Within the forested zone long-distance pollen dispersal is of rather small importance, and the downslope limit of forest taxa was reflected accurately in pollen spectra. However transport of pollen to elevations above the tree line does lead to significant over-representation of arboreal taxa in shrub and grassland settings.

An experimental approach using a blind study revealed that the sensitivity of pollen as a proxy for temperature appears to be $c. \pm 1.8^\circ\text{C}$. A similar relationship of pollen occurrence to elevation is also evident in presence-absence data. The strength of the presence-absence data is in reducing uncertainty over appropriate count sizes and in facilitating a direct comparison of moss-pollen data with fossil-pollen data from lake sediment.

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