# The influence of biogeographic and ecological heterogeneity on Amazonian pollen spectra

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ABSTRACT. The influence of gamma- ($\gamma$) and beta- ($\beta$) diversity on modern pollen rain is assessed using data from three Amazonian forests. Pollen rain of 79 forest locations was collected in modified Oldfield pollen traps between 1991 and 1993. Pollen diversity in the traps was high with > 280 palynomorph types recognized. Gamma diversity was assessed by comparing lowland terra firme forests in Cuyabeno, Ecuador, with two terra firme forests near Manaus, Brazil. The influence of $\beta$-diversity on local pollen rain was investigated using samples collected from neighbouring terra firme forests, seasonally flooded forests, and *Mauritia*-rich forests at Cuyabeno, Ecuador. Multivariate analyses revealed that $\gamma$-diversity produces a stronger signal in the pollen rain than $\beta$-diversity. However, $\beta$-diversity is accurately reflected in the pollen rain when the diversity is an expression of strong environmental gradients.

KEY WORDS: Amazonia, $\beta$-diversity, Brazil, Ecuador, $\gamma$-diversity, modern pollen, multivariate analysis, pollen rain, tropical forest

## INTRODUCTION

The Amazonian forests are renowned for their high species diversity. A single hectare of western Amazonian forest can contain > 340 tree species, providing the highest $\alpha$-diversity of any ecosystem yet documented (Pitman *et al.* 1999). Diversity between habitats ($\beta$-diversity) is also high resulting in a mosaic of different forest types. Successional stage, hydroperiod, slope and edaphic conditions are all important determinants of forest type. As these conditions can

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change within short distances the grain of lowland Amazonian forest can be very fine (Gentry 1989). Some boundaries between communities are subtle, while others appear to be clear. Even to the inexperienced eye, the frequently flooded *Mauritia* palm swamp (morichal) looks quite different from the drier (terra firme) forest. However, more commonly, an environmental gradient producing an ecotone supports an intergradation of communities that form a continuum of floristic change. Local endpoints of these continua are identified as a forest 'type' and are used in analyses of β-diversity (Balslev *et al*. 1987, Pitman *et al*. 1999), but the intermediate communities are less certainly ascribed to one forest type or another. Thus, although it is common to refer to a landscape as a mosaic of β-diversity, it should be recognized that each piece of the mosaic blends into those that surround it.

Although fine-scale heterogeneity is an important component of local diversity, there is also a large-scale component. It is a basic biogeographic observation that distance between communities and species turnover are positively correlated (Cox & Moore 2000). This regional species turnover is equivalent to Cody's (1975) γ-diversity (used henceforth), and Whittaker's (1960) β-diversity on a large scale. Thus, even in the absence of other factors, the species composition of eastern and western Amazonian forests is expected to differ considerably.

The ability to use pollen to characterize different lowland neotropical communities is critical if palynological reconstructions can become sufficiently detailed to identify Holocene climate change. Faegri (1966) raised doubts as to whether lowland tropical forests would produce unique pollen spectra. He noted that only about 2% of taxa were anemophilous and that these tended to be early successional or understorey taxa, e.g. *Cecropia, Celtis* and Urticaceae. Faegri suggested that these few anemophilous species would mask the subtle, but potentially more informative, signal from the 95% of species that are zoophilous (Faegri 1966). A further criticism is that many pollen types remain unidentified or can only be identified reliably at the family level.

Previous studies of tropical pollen spectra have revealed that various types of montane forest can be dissociated from lowland forests (Behling *et al*. 1997, Bush 1991, Bush *et al*. 2001, Grabandt 1980, Islebe & Hooghiemstra 1997, Rodgers & Horn 1996). However, the species that drove the statistical separations within these records were often taxa that were anemophilous (e.g. *Quercus, Alnus, Ulmus, Myrica*); the zoophilous lowland taxa were not major players in these analyses. Within the tropical lowlands where pollen spectra from specific community types have been identified, a few key indicator taxa have lain at the heart of the statistical separations. Mangroves have been isolated from other forests (Rodgers & Horn 1996), savannas have been separated from forest (Bush 1991, Salgado-Labouriau 1997), and morichal has been separated from terra firme forest (Behling & Hooghiemstra 1999, Salgado-Labouriau

1997). Each of these separations can be reduced to statistical dissimilarity based on a few key taxa: the presence of pollen of *Rhizophora* in mangroves, the abundance of Poaceae and herbs in savanna, and the presence of *Mauritia* in the morichal. However, within Amazonia each of these vegetation types is in a sense peripheral. Mangroves only exist in brackish regions, savannas exist as scattered islands within the forest, and morichal is confined to swamps, streamsides and lake shores.

Regional differences in the family composition of forests within the Amazon basin were recognized by Gentry (1990), but more detailed insights into the γ- and β-diversity of these systems have come from two recent studies. In the first of these, Terborgh & Andresen (1998) investigated the γ-diversity of tree taxa in terra firme forests in central Amazonia versus those in Ecuadorian Amazonia. They found that the forests of the two regions differed in the presence and abundance of tree families, resulting in a compositional difference that was statistically significant (Terborgh & Andresen 1998). Clearly, that forests differ at such a high taxonomic level is encouraging to palynologists. However, this survey of forest composition had complete inventories of families, and statistics based on the real abundance of individuals. Given that palynology has some resolution at the genus level in Amazonia, it might be expected to depict γ-diversity accurately. However, unlike the study of Terborgh & Andresen, palynologists must work with an incomplete representation of taxa because many floristically important families contribute little or no pollen to the pollen rain, e.g. Lauraceae and Lecythidaceae. Furthermore, pollen representation is biased by the relative production of different species. For example, *Cecropia*, a dioecious, anemophilous genus, may be over-represented in the local pollen rain by a factor of 17 compared with estimates made from its basal area (Bush & Rivera 1998). Contrastingly, hermaphroditic bird-pollinated species are commonly under-represented by a factor of $< 0.1$ compared with their basal area (Bush 1995, Bush & Rivera 1998). Thus, the real difference between spatially discrete terra firme floras may not translate into palynologically discrete pollen floras.

In the second study, Pitman *et al.* (1999) showed that there is considerable species overlap between adjacent habitats with as few as 15% of species differing between habitats. Many of the instances of turnover was a species-for-species replacement by congeners. If the principal signal of shifts in community composition is at the species level, or in the proportions of species in the flora, palynology may be a rather blunt tool for identifying β-diversity.

In this paper we test two simple hypotheses:
(1) that γ-diversity has a stronger influence than β- diversity on pollen spectra.
(2) that the pollen spectra of forests growing under different hydrological regimes within the same climatic regime can be reliably distinguished from one another.
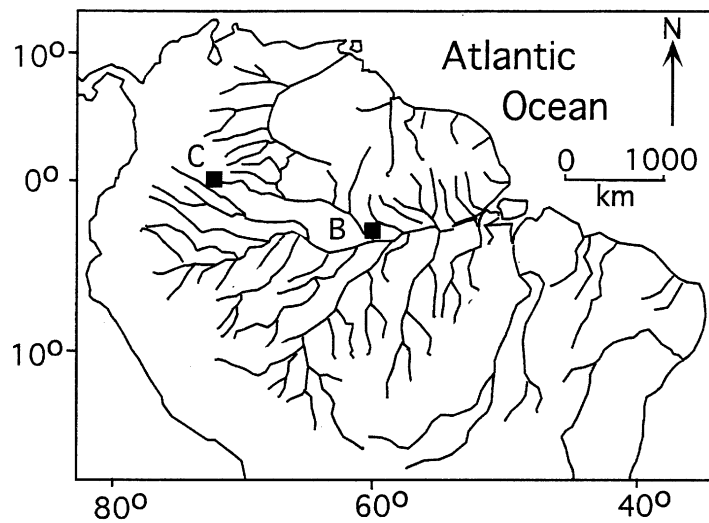
Figure 1. Sketch map showing the location of Cuyabeno (C), and the two BDFF forest sites Dimona and Campo 41 (B).

## STUDY AREAS

The forest sites selected for our study were the Cuyabeno Faunal Reserve, Ecuador (0°0′4″N; 76°10′11″W), and the Biological Diversity of Forest Fragments Project (BDFFP) sites, near Manaus, Brazil (3°S, 60°W; Figure 1). Cuyabeno is a region of wet tropical forests dissected by seasonal black-water creeks and rivers. For a detailed description of the Cuyabeno reserve see Asanza (1985, 1999) and Sosa-Asanza (1994). Mean annual temperature at Cuyabeno is ~ 27 °C with an annual precipitation of ~ 3300 mm. During the dry season the average precipitation is 160 mm and the temperature is 27.6 °C. This marked dry season at Cuyabeno lasts from late December until early March. In this time water levels in the *igapo* lake systems fall sufficiently to allow grasses to grow on the exposed lake beds. The wet season rains bring black-water flooding that inundates the lake basins and low-lying sections of the forest (Asanza 1985, 1999). At Cuyabeno, the forest is readily divided into three basic types according to local hydrology. *Mauritia* swamp forest grows on land that is flooded up to about 2 m depth for *c*. 180–200 d per annum, seasonally flooded forests grow on soils that are wet and irregularly flooded for *c*. 80 d per annum. The terra firme forests develop on uplands that have non-flooded soils throughout the year (Asanza 1985, 1999; Brandbyge & Asanza 1982; Sosa-Asanza 1994). We do not refer to the *Mauritia* forest as morichal in this paper because at our sample sites this is a more diverse forest than *Mauritia* swamps that we have encountered elsewhere in Amazonia. Indeed the *Mauritia*-rich forest contained many taxa that were found in the terra firme and seasonally flooded forests, such as: *Alchornea* (Euphorbiaceae), Araliaceae, *Arum* (Araceae), *Bactris* (Arecaceae), Caesalpinioideae, *Calathea* (Marantaceae), *Casearia*

(Flacourtiaceae), *Cecropia* (Cecropiaceae), Lecythidaceae, *Geonoma* (Arecaceae), *Heliconia* (Heliconiaceae), *Iriartea* (Arecaceae), *Mabea* (Euphorbiaceae), *Miconia* (Melastomataceae), *Nectandra* (Lauraceae), Papilionoideae, *Pourouma* (Moraceae), *Pouteria* (Sapotaceae), *Solanum* (Solanaceae).

The BDFFP sites of Dimona and Campo 41 lie in a zone of moist tropical forest. Both sites have a mean annual temperature of ~28.5 °C and receive ~ 2500 mm of precipitation per annum with a dry season from June to October. During the dry season monthly precipitation exceeds 100 mm in all months, but may be less than 150 mm in some (Laurance, *pers. comm*). Both sites support mature upland vegetation and judging from the lack of charcoal in forest soil profiles, the forest at Campo 41 has not been extensively burned in the last 4500 y (Piperno & Becker 1996).

The high species diversity of the BDFFP plots is manifested by the identification of *c*. 1300 tree species in 63 families, and α-diversities of 280–285 species ha$^{-1}$ with stems > 10 cm dbh (de Oliveira & Mori 1999). Gentry (1990) observed that these forests are unlike most neotropical forests in that a few relatively large genera account for an unusually high proportion of the species present. Four families account for more than half of all individuals in the BDFFP plots: Lecythidaceae, Leguminosae, Sapotaceae and Burseraceae. These forests also have high β-diversity that ranges from edaphic scrublands (not sampled in this study) to mesic forest (Laurance *et al*. 1999). Although lacking extensive wetlands, some low-lying portions of Campo 41 become small ponds (< 0.2 ha) during the wet season (Mori & Becker 1991), though no standing water was observed in our field visits in October and March 1991–1993.

Thus all sites supported terra firme forest, Campo 41 and Cuyabeno had seasonally inundated forest, and Cuyabeno had *Mauritia* swamp forest.

METHODS

Modern pollen was collected at each site between 1991 and 1993 using modified Oldfield pollen samplers (Bush 1992). Traps were placed on the ground so that the head of the trap was 10 cm above the soil surface. In *Mauritia* forest, where flooding was expected to be 2 m deep, the traps were fixed to tree trunks at 20 cm above the previous year's watermark on the trunks. The trap heads were replaced on an annual basis, the old head being bagged and returned to the laboratory for processing. At Cuyabeno, six different forest patches (two of each forest type) were selected. The patches were chosen for being representative of local forest types and were at least 200 m distant from each other. Within each patch 10 pollen traps were set. Over the course of a year, 26 of the traps were destroyed due to the activities of humans, animals, flooding and treefalls: 34 traps were recovered. Because of the high rate of loss (43%), the collected traps were not evenly spaced within the forest. Each trap used in this analysis was > 20 m from its nearest neighbour. At Dimona and Campo 41, the forest

had been gridded into quadrats and our traps were set so that each was 40 m from its nearest neighbour.

In the laboratory, the acetate fibres and Whatman filters were removed from the funnels and placed in a plastic bag. Four *Lycopodium* tablets were dissolved and poured into this bag. Water with some detergent was added to the bag and the contents were thoroughly massaged. The resulting slurry was filtered through a 350-μm sieve and the process repeated until the remaining fibre appeared clean. The filtrate was then centrifuged and a routine palynological preparation (acetolysis, and HF) followed. Samples were mounted in glycerol and counted at ×400 and ×1000 on a Leitz Ortholux II photomicroscope. Bush counted the Cuyabeno samples and Moreno counted the Campo 41 and Dimona samples. At least 300 pollen grains were counted in each sample, and where a single taxon was massively over-represented, 200 'other' grains were counted. Pollen was identified using published descriptions (Roubik & Moreno 1991), and our modern pollen reference collection of > 3000 types. A consistent problem encountered when working with such a diverse flora is that some pollen types, e.g. *Alchornea*, encompasses at least *Alchornea* and *Apparisthemum* (Colinvaux *et al*. 1999). The extreme forms are readily separable, but there is a continuum of forms blurring the distinction between the extremes. A false separation of forms is statistically more misleading than a lumping of types.
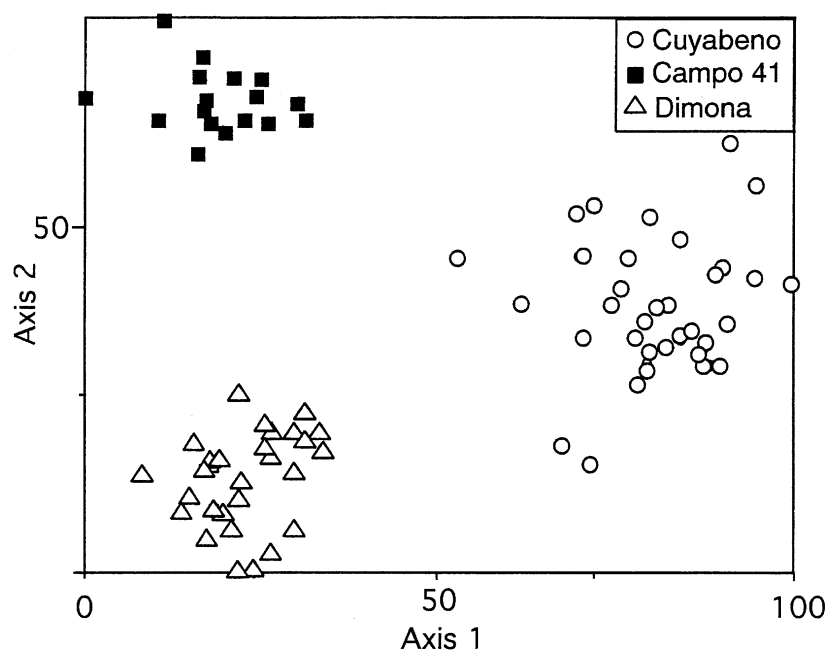


Figure 2.   DCA results of ordinating 183 pollen taxa in the modern pollen rain from Cuyabeno, Campo 41 and Dimona. Data for each taxon represent the mean percentage of the total pollen rain collected in 2 years of trapping (1991–1993). Data were normalized by log transformation and rare species were downweighted. Axis 1 eigenvalue 0.28, Axis 2 eigenvalue 0.17.

Therefore, we are conservative in assigning types to the 280 palynomorphs and reduce the data set to 183 named pollen taxa. To reduce the effect of inter-annual variability in flower production, the pollen counts of both years were summed before percentages were calculated. Pollen diagrams were plotted using TILIAGRAPH (Grimm 1992).

All statistics are based on the mean value of 2 y of pollen collection data for each location. Pollen counts were log transformed prior to multivariate analysis to reduce the effect of over-represented taxa (Birks 1986). Data were analysed using the modified version of DCA (Hill 1979a, b) in PC-ORD4 (McCune & Mefford 1999) that overcomes the sequence sensitivity problems identified by Oksanen & Minchin (1997). DCA was applied to the full data set of 183 identified taxa and rare taxa were downweighted. To ensure that patterns obtained from the first ordination were not the product of observer (pollen counter) bias, a second ordination was conducted in which the data set was reduced to 30 pollen taxa that would undoubtedly be common to both counters.

RESULTS

More than 280 different palynomorph taxa were encountered in this study. Unidentified taxa were 10–30% of grains counted in each sample; a fairly typical proportion for closed-canopy diverse Amazonian forests (Bush & Colinvaux 1988, Frost 1988, Liu & Colinvaux 1988). Pollen accumulation in the traps was highly variable, ranging from 2000 grains $cm^{-2}$ $y^{-1}$ to 25 000 grains $cm^{-2}$ $y^{-1}$, a
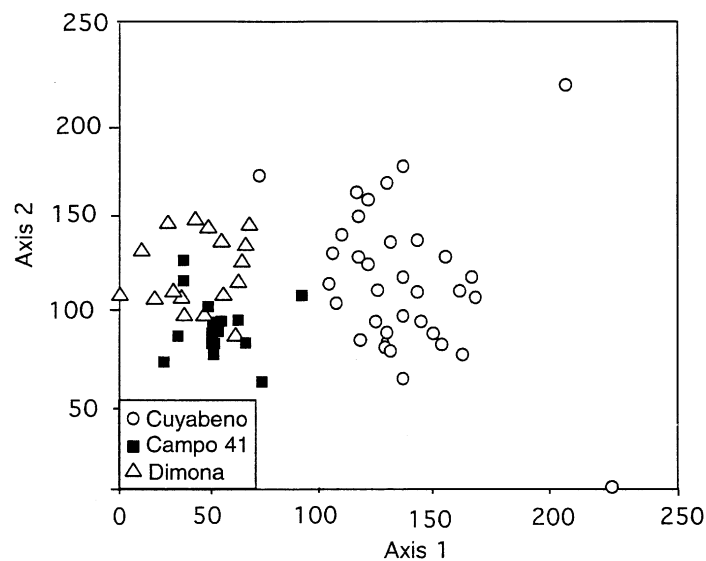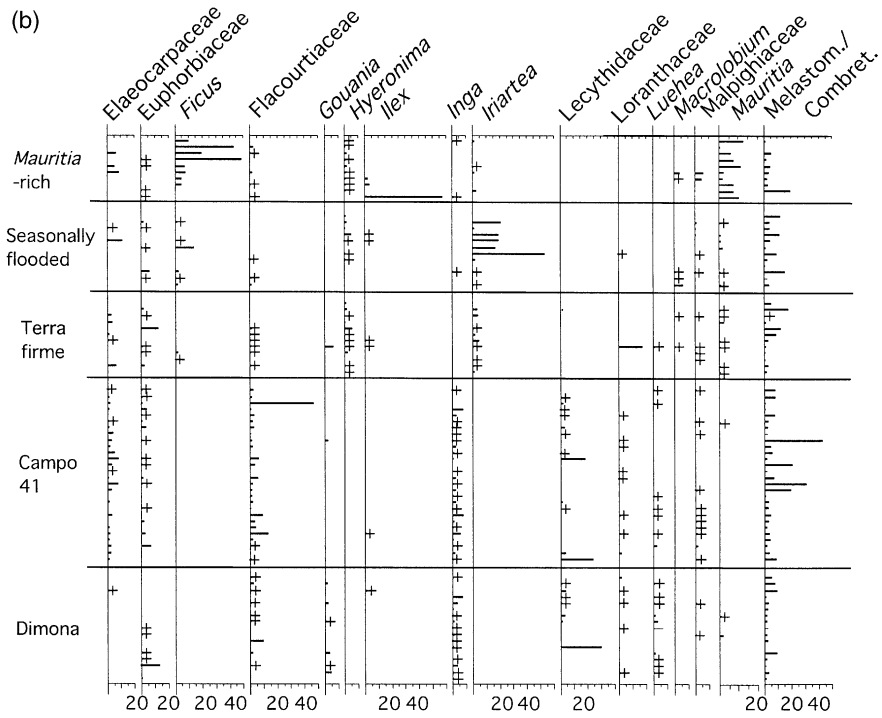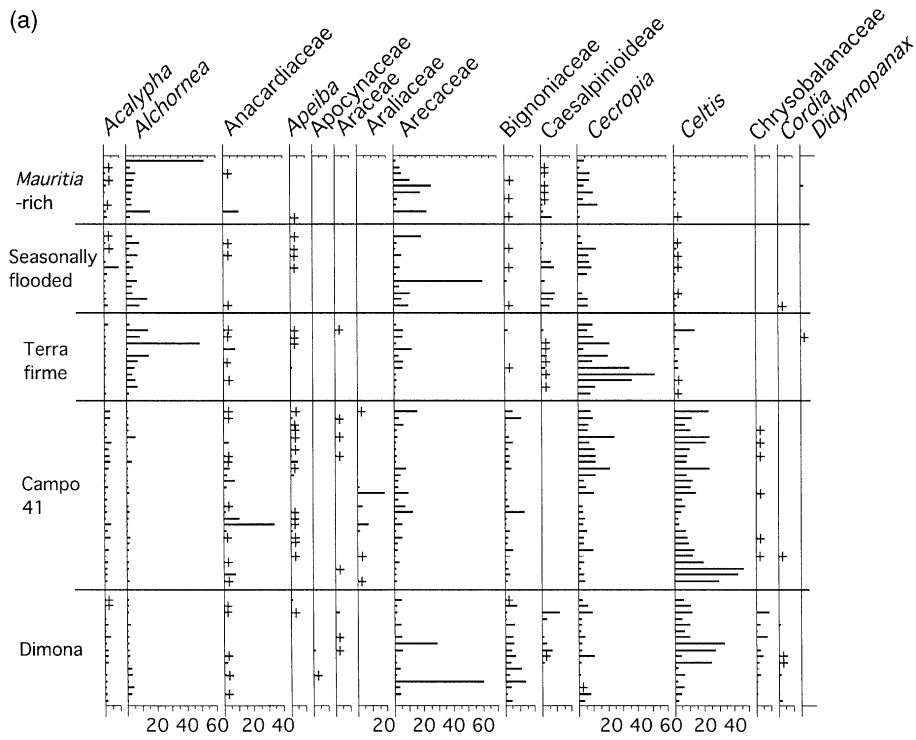


Figure 3. DCA results of ordinating 30 pollen taxa in the modern pollen rain from Cuyabeno, Campo 41 and Dimona. Data for each taxon represent the mean percentage of the total pollen rain collected in 2 years of trapping (1991–1993). Data were normalized by log transformation and rare species were downweighted. Axis 1 eigenvalue 0.23, Axis 2 eigenvalue 0.08.
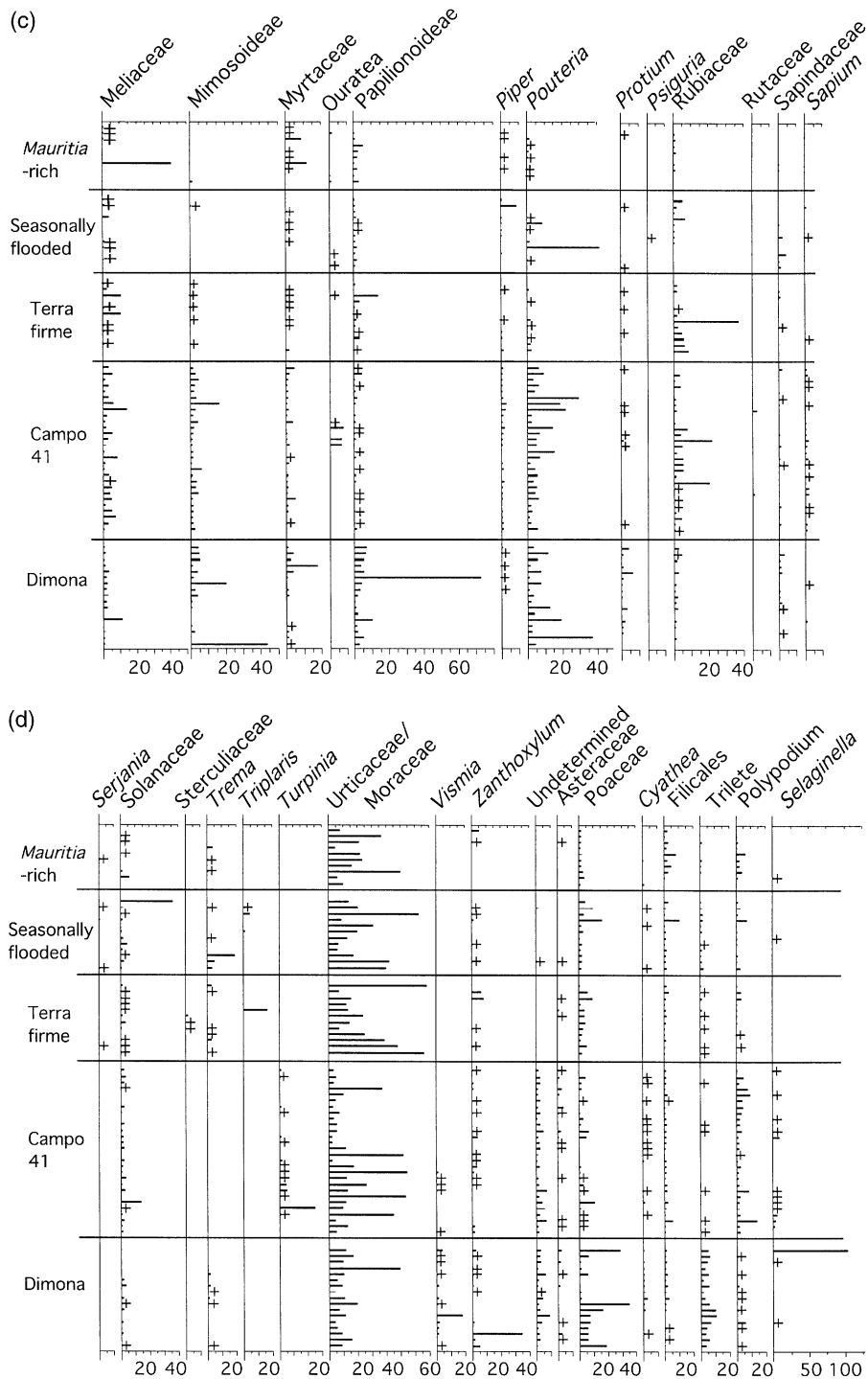
(a)



(b)

Figure 4.   Per cent pollen representation of 55 common pollen types and five spore types in modern pollen spectra from Cuyabeno, Campo 41 and Dimona. The pollen sum includes all arboreal and herb elements. Family totals exclude any separately plotted genus that is a member of that family. Spore sums were calculated as a percentage of the pollen sum. + indicates < 3% of the pollen sum.

result consistent with previous pollen trap studies (Behling *et al*. 1997, Bush 1991).

The ordination of the data produced a strong separation of the three sites (Figure 2). As the DCA axes are expressed in standard deviations of species turnover × 100, they are scaled to reflect β-diversity (Hill 1979a). But a note of caution needs to be introduced as Birks (1985) observed that pollen data do not conform exactly to the community model on which DCA was founded. Consequently, with pollen data the axial scores should be used as a guide rather than an absolute value (Birks 1985). Reducing the data set from 183 to 30 taxa would be predicted to reduce variation, but if the basic separation of sites is robust the resulting ordination pattern will appear similar to that of the full data set. If, however, it is only inconsistencies in identification that generate the ordination pattern, the grouping of sites will be altered. As predicted, when the 30-taxa data set is ordinated, the reduced variance between samples results in a tighter clustering of samples, but the groups of data points are virtually unchanged (Figure 3). Given that both analyses are consistent, we are confident that observer error is not significantly biasing these results. To test whether anemophilous taxa were causing the observed patterns in this data set we removed all anemophilous taxa from the data prior to conducting another DCA ordination. The overall pattern was unaffected with Campo 41, Cuyabeno and Dimona separating cleanly.

For the remaining presentation of results and discussion we will adopt the results of the run of 183 taxa. Figures 4a–c are summary diagrams of the 60 most abundant taxa found in the samples (full data are available from the Latin American Pollen Database).

To determine the strength of habitat separation at the level of β-diversity, a further ordination was performed on the Cuyabeno data alone. The Cuyabeno data were drawn from terra firme, seasonally inundated and *Mauritia*-rich forest and pollen spectra from these habitat types were analysed using DCA. With untransformed percentage data, the first axis of the ordination reflects increasing moisture (Figure 5) with the seasonally flooded forest occupying intermediate positions between the terra firme and *Mauritia*-rich forest. Log-transformed data produced no interpretable pattern from which we conclude that it is abundance rather than occurrence of pollen types that determines this pattern.

## DISCUSSION

Hypothesis 1: γ-diversity has a stronger influence than β-diversity on pollen spectra. There is no doubt that this hypothesis has been upheld. The terra firme sites of Dimona, Campo 41 and Cuyabeno are clearly distinguishable. These data convincingly demonstrate that γ-diversity is strongly reflected in pollen spectra whereas β-diversity is relatively weakly manifested. In both our study of pollen rain, and the analyses of Gentry (1990) and Terborgh &
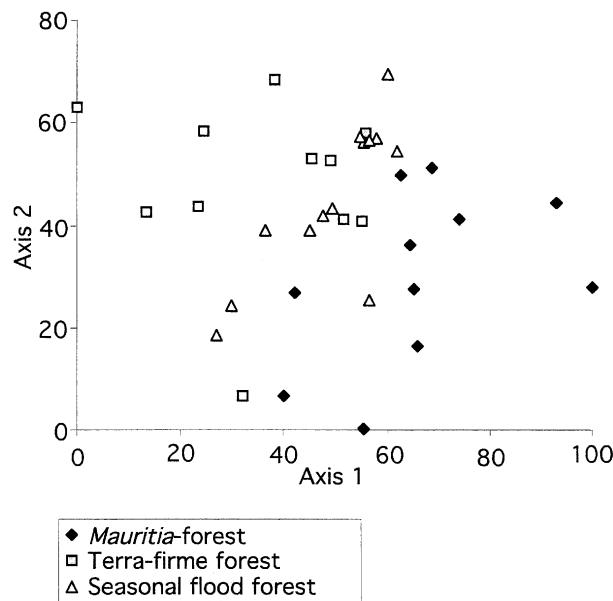
Figure 5. DCA results of ordinating 111 pollen taxa in the modern pollen rain from Cuyabeno. Data for each taxon represent the mean percentage of the total pollen rain collected in 2 years of trapping (1991–1993). Data were normalized by log transformation and rare species were downweighted. Axis 1 eigenvalue 0.26, Axis 2 eigenvalue 0.16.

Andresen (1998), regional differences outweighed local differences in forest composition at the family level. This pattern was true, even when local habitat types were as different as *Mauritia* forest versus terra firme forest.

Indeed, the observation that γ-diversity was stronger than β-diversity also applies to Dimona and Campo 41, for, although we have treated those as uniform forest types, considerable intra-site variation existed. Canopy gaps, steep slopes, well-drained areas, and soggy bottomlands all provided β-diversity at the floristic level, but this was not reflected in the pollen spectra. Yet, all of the samples showed a stronger affinity with nearby sites than apparently more similar habitats at a greater distance. These data are entirely consistent with the study of pollen spectra from Barro Colorado Island, Panama, where the only statistically significant difference between samples within a mature forest was where canopy gaps allowed *Cecropia* and *Miconia* to flower profusely (Bush & Rivera 1998).

Hypothesis 2: Pollen spectra of forests growing under different hydrological regimes within the same climatic regime can be reliably distinguished from one another.

This hypothesis was tested using the data from Cuyabeno. The ordination of pollen rain data from three forest types, each with different hydroperiods, provides a first axis that is interpretable. This axis represents an ecological gradient of increasing flood duration with end members of the terra firme

forests at the negative extreme and *Mauritia*-rich forest at the positive extreme of Axis 1. As might be expected, the habitats of intermediate flood duration were located in the centre of the axis. However, some of the terra firme and *Mauritia*-rich forest samples also plotted in the centre of the axis.

These data reflected diffuse ecotonal boundaries between neighbouring forest types. For example, although *Mauritia* clearly characterized the flooded forest type in the field, in the pollen spectra (Figure 4), the representation of *Mauritia* pollen did not overwhelm that of other taxa, and was entirely consistent with the 6–16% documented in *Mauritia* swamps in Central Brazil (Ferraz-Vincentini & Salgado-Labouriau 1996). Indeed, in the Cuyabeno data the combined pollen influx (grains $cm^{-2}\,y^{-1}$) of elements common to both *Mauritia* and terra firme forest, e.g. *Alchornea, Cecropia, Celtis* and Urticaceae/Moraceae pollen, was always greater than the *Mauritia* pollen influx.

Taxa that appeared to characterize the different forest types were *Ficus, Iriartea* and *Alchornea*. In the *Mauritia*-rich forest *Ficus* was locally very abundant. *Ficus* is cleistogamous and so its presence in the samples probably reflects either defecation by frugivores or the direct input of figs falling onto the traps (Horn & Ramirez 1990). It is possible that parrots (e.g. some species of macaws), which commonly nest in *Mauritia* trunk cavities, were a significant source of faecally deposited *Ficus* pollen. The best single indicator of the presence of seasonally flooded forest was the abundance of *Iriartea*, whereas terra firme forests were characterized by high values of *Alchornea* and a high diversity of relatively rare components. The overlap of the habitats in ordination space is not an artefact of the pollen rain, but reflects the real, diffuse, boundaries and the many shared species found in neighbouring habitats (Pitman *et al*. 1999). These data suggest that identifying extreme representative members of swamp forest, *Mauritia* forest, and terra firme forest is feasible. However, the intermediate samples, where there is a large overlap of taxa at the genus level, do not separate easily, and will prove more problematic in palaeoecological interpretations.

The message that emerges from this study is that strong regional differences can be detected across the Amazon basin in the pollen spectra from comparable forests. Presently, it is not known if this γ-diversity is the product of finely tuned adaptation to different climate and soils, or whether it is simply a function of scale (Terborgh & Andresen 1998). In terms of palaeoecological interpretation, these data suggest that pollen spectra would respond to the large scale replacement of one terra firme flora with another. Similarly, the local replacement of habitat types along a moisture gradient would also be detectable, though the diffuse ecological boundary between community types plus the longevity of individuals would serve to blur such change in high resolution (annual to decadal) records.

Finally, these data indicate that great caution must be used in selecting modern analogues to aid in the interpretation of lowland tropical fossil pollen records unless the analogues are collected close to the sampling site.

## CONCLUSIONS

The principal finding of this study is that in closed-forest settings, intra-site habitat variability in Amazonian pollen spectra is less than inter-site variability. The γ-diversity of Amazonian forests 1000 km and 25 km apart provide a surprisingly strong separation between terra firme sites. Whether the γ-diversity is caused by ecological factors such as climate or soil type, or whether it is simply a function of the vastness of Amazonia cannot be discerned.

β-diversity along the continuous gradient of hydrological change within a forest, produced identifiable end-members but, as might be predicted, left a lot of intermediate samples that could not be reliably attributed to a given habitat type. Consequently, in Amazonian palaeoecological reconstructions the changes in habitat type will appear muted, not only because of the longevity of trees, but also because of the diffuse change in community composition from one habitat to another. It seems probable that the commonest taxa in the pollen rain are likely to dilute signals of ecological change as they are less specialized and more widespread than previously supposed (Pitman *et al*. 1999). Identifying indicator taxa, and improving the recognition of distinctive, but unknown pollen types becomes a priority.

Our data also provide a caution that the collection of modern analogue data should, to the greatest extent possible, be constrained to the geographic vicinity of the palaeoecological site to which they are applied.

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