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RESEARCH LETTER

Reproductive ecology and pollen representation among neotropical trees

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ABSTRACT

Three years of pollen trapping data from Barro Colorado Island, Panama, are compared with local vegetation inventories. Two hypotheses relating pollen representation to 'messy' pollination and flower form are tested. Dioecious taxa were found to be over-represented in pollen spectra compared with their occurrence in local forests. Similarly, anemophilous and 'messy' pollination types were found to be over-represented. While anemophilous taxa were the best dispersed pollen types, zoophilous taxa were also well-represented in dispersal classes of 20–40 m and > 40 m. Thus pollen arriving to lake sediments is most likely to be from anemophilous species or those zoophilous species exhibiting 'messy' pollination syndromes. Pollination mechanisms will predictably bias the fossil record against certain flower morphologies. These data are of significance to those using the fossil pollen record to reconstruct the timing and sequence of angiosperm evolution. These data help prioritize plants to be included in modern pollen reference collections and to focus the search for 'unknown' types on most-likely candidate families.

Key words anemophily, Barro Colorado Island, dioecious, hermaphroditic, monoecious, Panama, pollen representation, pollination syndrome, tropical rain forest.

INTRODUCTION

The description of pollination syndromes (Faegri & van der Pijl, 1979) pairs floral characteristics and likely pollinators. In temperate regions anemophilous taxa are well represented in pollen spectra while zoophilous species are not (Regal, 1982). Anemophilous species are commonly 70–100% of the arboreal flora of temperate forest, but are usually just 2–3% of neotropical rain forest floras (Bawa & Opler, 1975; Croat, 1978), while the remainder of the flora is primarily zoophilous.

Analysis of pollen trap data from New Guinea, Ecuador and Panama (Flenley, 1979; Bush, 1991, 2000; Bush & Rivera, 1998) reveals that tropical lowland pollen influx is similar in amount to that of temperate forests. Given the paucity of anemophilous species in the lowland tropics, and the high diversity of pollen in tropical pollen rain, it is probable that an unexpectedly large proportion of pollen is coming from zoophilous taxa.

It is important to note that the pollen in a lake sediment or a pollen trap is wasted pollen, i.e. it failed to reach a stigma. Pollination strategies can range from those that produce and waste little pollen to those that produce and waste vast amounts. It is the release of such wasted pollen that Horn referred to as 'messy pollination' (Horn & Ramirez, 1990). Zoophily is often the product of co-evolution of the plant and its pollinator and such specialization, at least among temperate species, results in less pollen being produced than in anemophilous counterparts (Faegri & van der Pijl, 1979). Remarkably, despite being dominated by zoophilous species, tropical forests seem to produce similar amounts of 'wasted' pollen as temperate forests.

Determining a pattern in pollen representation sheds some light on the relationship between

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floral structure and pollinators (Bawa *et al.*, 1985a, 1985b; Renner & Feil, 1993) and helps to direct the construction of modern pollen reference collections toward the taxa most likely to be encountered in fossil pollen sequences.

Pollination syndromes and flower structure

A correlation has been suggested between dioecy and pollination systems in lowland tropical forest plants (Bawa, 1974, 1994; Bawa & Opler, 1975; Bawa *et al.*, 1985a, 1985b; Ibarra-Manriquez & Oyama, 1992). Bawa & Opler (1975) noted that most dioecious species have small, white or yellow-green flowers with an open structure, and suggested that this open structure shows no co-evolution with a particular pollinator. From this observation, it was suggested that such flowers were pollinated by small diverse insects and small bees (collectively small generalist insects; Bawa & Opler, 1975). In an analysis of pollination records for such open-structured flowers, Renner & Feil (1993) found considerable pollinator fidelity, with moths pollinating 25% of zoophilous dioecious species, bees 22.5%, beetles 20%, flies 12.5% and diverse insects just 10%. Renner & Feil (1993) noted that despite the appearance of allophily (adapted to pollination by any visitor) in these flowers, they were, in most cases, euphilic (adapted to a particular pollinator). Unlike Bawa & Opler (1975), who contended that pollen dispersal by small generalist insects was strictly local, Renner & Feil (1993) found the pollinators of these flowers to be highly motile.

Stelleman (1984) has suggested that the open structure of these zoophilous dioecious flowers and their protruding stamens leads to a great deal of pollen being blown from the flower. Indeed, he conjectured that many of these plants may shed so much pollen into the air as to be secondarily anemophilous; he therefore refers to such taxa as ambophilous.

For the purposes of this paper, the actual mode of pollination is of secondary importance to the observation that plants with these open floral structures are likely to release significant amounts of pollen that fail to reach a stigma. It is these wasted pollen grains that are most likely to be found in pollen traps and lake sediments.

On the basis that each of the following hierarchies represents a trend from greater to lesser potential 'messiness', we offer two testable hypotheses:

1 Pollen representation should follow the probability of outcrossing: *dioecy* > *monoecy* > *hermaphroditic self-incompatible* > *hermaphroditic selfers* > *cleistogamy* (anthers and styles totally enclosed within flower).

2 The more open the flower structure, the more likely the plant is to exhibit 'messy' pollination: i.e. anemophilous taxa often have fully exposed stamens dangling in the air, zoophilous open-flowered taxa have exposed stamens, while taxa pollinated by birds, bats, butterflies and moths often have stamens hidden deep in a corolla tube.

As a preliminary test of the first of these hypotheses, Bush (1995) compiled information from 16 lowland neotropical pollen records. The relative percentages of taxa that were dioecious, monoecious or hermaphroditic were computed, as were percentages for different pollination systems. When these frequencies were compared with the expected occurrence of dioecious, monoecious and hermaphrodites (derived from Bawa *et al.*, 1985a), dioecy was found to be over-represented among common pollen taxa. Those data also supported the suggestion that the more open the flower structure, the greater the probability of representation.

The present study compares 3 years of pollen rain data collected on Barro Colorado Island, Panama, with forest inventory data to determine the relative representation of floral types. Specifically, we wanted to test the model proposed by Bush (1995) that sexual mechanism and pollination syndrome were important determinants of the representation of neotropical pollen.

METHODS

Twenty-one pollen traps (Bush, 1991) spaced 100 m apart were set in the mature forest of the 50 ha permanent vegetation plot on Barro Colorado Island (Hubbell & Foster, 1990). Each trap was left in the field for a year and replaced on the day of collection. Data were gathered continuously from 1991 to 1994. Of a possible 62 traps (one was only run for 2 years), 56 were recovered and processed (Bush & Rivera, 1998).

In the laboratory, pollen was washed free of the rayon trap fibres, spiked with *Lycopodium* spores, and processed following the methods of

Faegri & Iversen (1989). The final residues were suspended in glycerine. Pollen identification was carried out using a Leitz Dialux light microscope at 400× and 1000× (for a more detailed discussion of methods see Bush & Rivera, 1998).

Richard Condit of the Smithsonian Tropical Research Institute provided data on all woody plants (> 1 cm d.b.h.) within a 40-m radius of each trap. The list of species found within 40 m of the traps was divided by sexual type (dioecious, monoecious or hermaphroditic) and their pollination systems (Bawa, 1974; Croat, 1978; Bawa *et al.*, 1985a, 1985b; Renner & Feil, 1993). When a species potentially had more than one pollination system, each potential system was weighted equally. Renner & Feil (1993) re-analysed the pollination data for a range of neotropical zoophilous dioecious taxa and concluded that some of the species thought previously to have been pollinated by small-generalist insects had specific pollinators. However, their analysis only included two groups that are important in the pollen rain of Barro Colorado Island: Arecaceae (pollinated by beetles) and *Cordia* (pollinated by small diverse insects; Renner & Feil, 1993). In the absence of detailed pollination data this group of small, green or white, open-flowered species, are characterized simply as 'open-flowered'. The basal areas of each floral form and pollination category at each trap site were also computed and expressed as a percentage of basal area.

The pollen data from each trap were categorized according to floral type and pollination mechanism. A mean pollen influx value for each species at each location was calculated. Seven locations were based on 2 years of data, while 14 locations were based on 3 years of data. Thus, for each combination of variables, the following statistics for each trap were calculated: percentage of flora, percentage of basal area, mean percentage of pollen flora and mean percentage of pollen influx. The ratio of pollen influx to basal area (signified 'R-rel' after Davis *et al.*, 1973) was used to estimate the degree of over- or under-representation for each of these taxa. The significance of this statistic is assessed using an ANOVA of 21 paired samples of basal area and pollen influx data for each trap location.

Pollen dispersal distances are based on the minimum source distance to the trap, i.e. all pollen is assumed to have come from the nearest potential source (Bush & Rivera, 1998).

RESULTS

The pollen traps yielded 118 pollen types of woody taxa. The percentages for the representation of sexual mechanisms are remarkably consistent for tree types, pollen types and basal area percentages (Table 1). Among these three data categories, it is evident that monoecious species have a disproportionately high percentage of basal area compared with their proportion in the flora. This high value may be due to a few very large trees, such as *Ficus* spp. and *Hura crepitans* (L.), dominating the basal area statistics at some locations. In contrast to the similarity between proportions of basal area, tree diversity and pollen taxa diversity, the pollen influx data look quite different. The representation factor for pollen influx percentages shows that dioecious taxa and monoecious taxa are over-represented (R-rel factors of 2.6 and 1.3, respectively) in the overall pollen rain, while hermaphroditic taxa have an R-rel of only 0.5.

Again, it is the pollen influx data that stand out as being different from the other categories in the analysis of pollination syndromes (Table 2). The only over-represented group is that of anemophilous taxa, while open-flowered and moth-pollinated species almost reach parity in terms of

Table 1 The representation of sexual mechanisms in the tree and pollen floras of Barro Colorado Island, Panama. R-rel = % mean pollen influx/% basal area

Floral form	% Tree types (*n* = 169)	% Pollen types (*n* = 118)	% Basal area	% Pollen influx	R-rel
Dioecious	18.93	20.4	14.44	37.75	2.6
Monoecious	13.31	13.13	24.64	31.95	1.3
Hermaphroditic	67.75	66.5	62.54	30.23	0.5

Table 2 The representation of pollination syndromes in the tree and pollen floras of Barro Colorado Island, Panama. R-rel = % mean pollen influx/% basal area

Pollination syndrome	% Tree types (n = 169)	% Pollen types (n = 118)	% Basal area	% Pollen influx	R-rel
Anemophilous	5.33	2.54	5.74	38.08	6.6
Bat	1.48	5.5	5.32	1.17	0.2
Bee	41.72	45.76	31.23	14.31	0.5
Bird	2.07	1.7	2.39	0.17	0.1
Butterfly/moth	5.03	8.47	14.37	11.61	0.8
Fig-wasp	1.78	0.85	3.52	0.13	0.04
Open-flowered	42.6	36.86	39.05	34.47	0.9

Table 3 Combined analysis of representation of trees and pollen on Barro Colorado Island, Panama, according to floral form and pollination syndrome. R-rel = % mean pollen influx/% basal area for the sum of all sites across all years. ANOVA statistics based on comparison of percentage mean pollen influx and percentage basal area for 21 sample sites

Floral form	Pollination	% Tree types (n = 169)	% Pollen types (n = 118)	% Basal area	% Pollen influx	R-rel	Fs (variance)	P <
Dioecious	Anemophilous	3.3	0.9	0.4	13.4	33.5	16.9	0.001
Monoecious	Anemophilous	2.1	1.7	5.3	24.7	4.7	16.9	0.001
Dioecious	Open	14.2	15.3	13.1	23.8	1.8	4.2	0.05
Monoecious	Bee	1.8	2.1	0.7	0.5	0.7	0.1	
Hermaphroditic	Butterfly/moth	4.4	6.8	14.0	11.4	0.8	0.1	
Dioecious	Bee	0.9	2.5	0.6	0.4	0.7	0.3	
Dioecious	Butterfly/moth	0.6	1.7	0.4	0.2	0.5	0.7	
Hermaphroditic	Bee	39.1	41.1	30.0	13.4	0.5	11.9	0.005
Monoecious	Open	7.7	8.5	15.1	6.6	0.4	5.2	0.05
Hermaphroditic	Open	20.7	13.1	10.9	4.1	0.4	17	0.001
Hermaphroditic	Bat	1.5	3.8	5.3	1.2	0.2	6.0	0.025
Hermaphroditic	Bird	2.1	1.7	2.4	0.2	0.1	4.4	0.05
Monoecious	Fig-wasp	1.8	0.9	3.5	0.1	0.03	1.6	

R-rel. Bird- and wasp-pollinated species are very strongly under-represented, with R-rel values of < 0.1.

Table 3 is an analysis of floral form and pollination syndrome that is ranked by R-rel values. The percentage of pollen influx is significantly different from percentage of basal area in eight of the 13 categories. Dioecious anemophilous pollen types are massively over-represented, with an R-rel value of 33.5%. Also significantly over-represented are monoecious anemophilous taxa and dioecious open-flowered taxa. Among hermaphroditic taxa the only one that is not significantly under-represented is the moth/butterfly pollinated group. The group with the lowest R-rel value is the fig-wasp-pollinated (*Ficus* spp.) taxa. *Ficus* pollen is always rare in this study (although this is not always the case: see Horn & Ramirez, 1990) but, as might be suspected, the occurrence of pollen is matched by a fig tree growing close by. Consequently, the comparison of *Ficus* pollen representation with that of *Ficus* trees has an insignificant variance.

The 20 most common pollen types account for 87% of total pollen influx, and 30% of the basal area of trees within 40 m (Table 4). An analysis of the flower form and pollination syndrome of these 20 pollen taxa reveals that 45% are dioecious, 40% hermaphroditic and 15% monoecious. The representation of pollination syndromes is: 52.5%

Table 4 Floral form and pollination syndrome, and representation of the 20 most common pollen taxa trapped on Barro Colorado Island, Panama. R-rel = % mean pollen influx/% basal area for the sum of all sites across all years

Pollen taxa	Flower type	Pollination	% Pollen	% Basal area	R-rel
Moraceae	Dioecious/Monoecious	Anemophilous	46	3.28	14
Cecropia	Dioecious	Anemophilous	10	0.64	15.6
Hyeronima	Dioecious	Open-flowered	5.9	0.58	10.2
Zanthoxylum	Dioecious	Open-flowered	3.9	0.73	5.3
Alseis blackiana	Hermaphroditic	Butterfly	3.7	3.94	0.9
Pouteria	Dioecious	Open-flowered/bee	2.5	1.12	2.2
Melastomataceae	Hermaphroditic	Bee	1.5	0.87	1.7
Arecaceae	Mono	Beetles	1.4	2.12	0.7
Casearia	Hermaphroditic	Open-flowered	1.3	0.56	2.32
Alchornea	Dioecious	Open-flowered	1.3	0.26	5.0
Faramea	Hermaphroditic	Moth	1.3	4.25	0.3
Trichilia	Dioecious	Open-flowered	1.2	5.41	0.2
Solanaceae	Hermaphroditic	Bee	1.2	0.02	60
Luehea	Hermaphroditic	Moth	1.1	1.39	0.8
Malpighiaceae	Hermaphroditic	Open-flowered	1.1	0.01	110
Trema	Monoecious	Open	1	0.02	50
Cordia	Dioecious	Open	0.9	0.65	1.4
Lecythidaceae	Hermaphroditic	Bee	0.7	1.16	0.6
Tetragastris	Dioecious	Open	0.6	2.75	0.2
Acalypha	Dioecious/Monoecious	Anemophilous	0.5	0.07	7.1

have open-flowers, 17.5% are pollinated by large- or medium-sized bees, 15% are anemophilous and 15% are moth- or butterfly-pollinated.

DISCUSSION

Hypothesis 1: Pollen representation should follow the hierarchy of: dioecy > monoecy > hermaphroditic self-incompatible > hermaphroditic selfers > cleistogamy

This hypothesis was supported by all tests and the importance of floral arrangement to pollen representation was shown to be separate from anemophily.

Dioecy favours representation in the pollen record and, to a lesser extent, so does monoecy. Hermaphroditic species are generally strongly under-represented in pollen spectra.

Hypothesis 2: Pollination systems correlated with 'messy' pollination will be over-represented in the pollen rain

To test this hypothesis, the observed and expected (Bush, 1995) sequence of pollination mechanisms represented in the pollen rain may be compared (Table 5). In general, there is good agreement between the predicted and observed values. Anemophilous and open-flowered taxa were over-represented while all other categories were under-represented. The match was not perfect as moth- and butterfly-pollinated taxa were better represented than expected, while bat-pollinated taxa were rare. No immediate explanation is apparent why butterfly/moth-pollinated species should be so well represented, other than that the initial

Table 5 Ranking of pollination syndrome according to R-rel, from highest to lowest. Expected ranking is based on Bush (1995)

Expected ranking	Observed ranking of influx
Anemophily	Anemophily
Open flower structure	Open flower structure
Bats	Large/medium bees
Large/medium bees	Moths/butterflies
Moths/butterflies	Bats
Birds	Birds
Fig-wasp	Fig-wasp

assumption that bat-pollination is more likely to be 'messier' than moth/butterfly pollination may be incorrect.

When the floral classes are subdivided into pollination classes a somewhat different pattern emerges, however. Whereas anemophilous dioecious and monoecious pollination classes had the highest R-rel values, zoophilous dioecious and monoecious taxa were generally under-represented. The exception to this pattern was among dioecious open-flowered taxa where there was a high R-rel value. The super-abundance of anemophilous pollen in the traps is an understandable function of wind pollination, especially among dioecious taxa. Vast amounts of pollen must be released by the male tree to ensure that some pollen will reach a female flower. Very little of that pollen reaches a female and this may be viewed as the ultimate 'messy' pollination process. Among monoecious taxa, it may be argued that less pollen is needed, as fertilization of flowers on neighbouring twigs may be all that is required. Nevertheless, the pollen release must still be relatively massive (e.g. *Quercus* or *Pinus* in a temperate system), especially if the plant is sequentially monoecious, or self-incompatible. Very few data are available to indicate the frequency of these latter traits among tropical monoecious trees. Thus, monoecious anemophily is a 'messy' form of pollination, but perhaps not as wasteful as dioecious anemophily.

Open-flowered dioecious taxa have lain at the centre of a debate among pollination specialists. One view was that the allophilous appearance of this group indicated that the most likely pollinators were small generalist insects (Bawa & Opler, 1975; Bawa, 1994), while Renner & Feil (1993) noted that many of these species in fact have specific co-adapted pollinators. Stelleman (1984) and Bullock (1994) suggested that some of these taxa may have a primary insect pollinator, but that so much pollen is blown free of the flower that they may be considered secondarily anemophilous. Testing whether the grain that pollinates a female flower arrived on a bee or a breeze is going to require more research, but from this study we can make some observations about pollination in these open-flowered taxa. To have an open flower structure alone does not guarantee over-representation. Note that both hermaphroditic and monoecious open-flowered taxa are strongly under-represented. The dioecious open-flowered taxa are clearly different from these other floral forms in their pollen liberation. Compared with truly anemophilous dioecious taxa, open-flowered dioecious taxa release about 5% the amount of pollen relative to basal area (R-rel of 33.5 vs. 1.79, respectively). This relatively low output suggests that anemophily is relatively unimportant to this group as a whole. However, another observation is that 'open-flowered' is a highly artificial grouping, reflecting a lack of autecological knowledge rather than any ecological affinity (see Renner & Feil, 1993). It is likely that within this class, individual species can be found to represent many different forms of zoophily and ambophily. Nevertheless, as a class the open-flowered dioecious taxa still produce twice as much pollen relative to basal area as any other zoophilous class. The enforced outcrossing combined with exerted anthers apparently leads to substantial pollen wastage.

Monoecious and dioecious, large- or medium-sized bee-pollinated taxa, and moth- and butterfly-pollinated taxa do not have significant variance between proportions of pollen trapped and basal area in the surrounding forest. The strong representation of hermaphroditic moth- and butterfly-pollinated taxa is surprising and no explanation is offered. The three taxa that contributed most pollen in this category were *Alseis blackiana* Hemsl., *Faramea occidentalis* (L.) A. Rich. and *Luehea* spp. All three taxa were abundant close to the traps and *Alseis* had a heavy flowering season in 1992–93 (Bush & Rivera, 1998).

The group with the lowest R-rel value is that of monoecious, fig-wasp-pollinated species. In these samples, this group is comprised of *Ficus* species, which are cleistogamous and monoecious (generally). *Ficus* pollen is documented from lake sediments (Bush & Colinvaux, 1988; Horn & Ramírez, 1990) and is a very abundant component in some pollen samples trapped in Ecuadorian flood forests (Bush, unpublished data). A combination of frugivore defecation or direct input of fallen figs to lakes is the most likely explanation of these occurrences. In the present study, *Ficus* pollen were rare and only found in samples with nearby *Ficus* trees. As would be expected of a cleistogamous flower, the pollen was not a regular component of airborne pollen.

Hermaphroditic taxa were all significantly under-represented (with the exception of moth/butterfly-pollinated species, above). The specialized flower structure, and possibility of self-fertilization may be important factors in reducing the amount of 'messy' pollination. Perhaps the most surprising class to be under-represented are the monoecious open-flowered taxa. Certainly, many of the species within this class are familiar components of pollen records from the neotropics, e.g. most of the Euphorbiaceae, but they show low R-rel values. It is possible that this class is again heterogeneous in terms of pollen production and wastage. Within this class some species may be heavy pollen producers, while others may produce only small amounts of pollen. For example, taxa that are sequentially monoecious are likely to be as 'messy' with their pollen as dioecious species, while others that are self compatible may release as little pollen as a self-fertile hermaphroditic species.

Among the most common pollen types, anemophilous taxa such as Moraceae (seven species combined), *Cecropia* and *Alchornea* are strongly over-represented (Table 4). Surprisingly, however, the most over-represented taxa are the zoophilous groups: Malpighiaceae, Solanaceae and *Trema*. These species did not overhang the traps, and unless the pollen comes from undocumented herbaceous species (which is unlikely), the high representation cannot be attributed to whole flowers falling into the traps.

Solanaceae and Melastomataceae, although hermaphroditic, have a 'messy' system of pollination and this may account for their substantial over-representation in this dataset (Table 4). These plants are frequently 'buzz'-pollinated (Mabberley, 1992). The vibrations from the wings of a visiting bee result in a cloud of pollen grains being expelled into the air. The pollinator is thereby coated with pollen, but the remaining pollen is free for capture by pollen traps.

Only two species of Malpighiaceae were documented within 40 m of the traps, *Malpighia romeroana* Cuatr. and *Spachea membranacea* Cuatr., and in most cases pollen appears to have been derived from a distance of more than 40 m. One possibility is that the pollen reflects the presence of fertile vines with stems too small to be included in the floral dataset. Eleven of 19 species of Malpighiaceae on Barro Colorado Island are vines or lianas (Croat, 1978). At present we can offer no further explanation for the over-representation of Malpighiaceae.

Casearia is another hermaphroditic genus that occurs in the top 20 pollen types. This genus may be over-represented in the pollen rain due to self-incompatibility. If species are capable of selfing, their pollen need never leave the flower. On this basis, one might predict that selfing species are less likely to be 'messy' with their pollen than are obligate outcrossers. Of the five species of *Casearia* near the traps at least one, *Casearia arborea* (L.C. Rich.) Urban, is known to be self-incompatible (Bawa *et al.*, 1985a). *Casearia corymbosa* H.B.K. is also self-incompatible, although it does not occur on Barro Colorado Island (Croat, 1978; Bawa *et al.*, 1985a).

Aspects of pollen dispersal

The modal minimum pollen dispersal distance (Fig. 1) of all taxa is between 20 m and 40 m. Anemophilous taxa could be biasing this dataset by inflating the longer dispersal categories. If anemophilous taxa are excluded, and only zoophilous arboreal species are considered (leaving 62% of the total pollen influx), the clear modal peak in the 20–40-m category is replaced by a

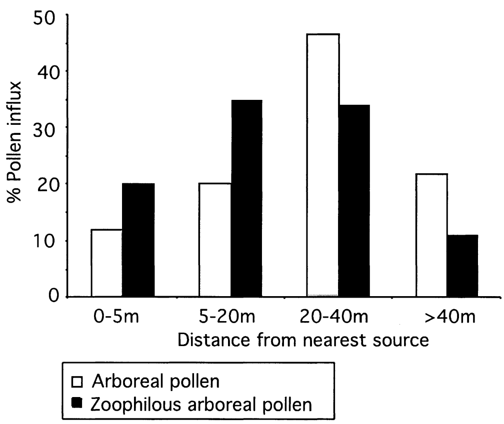

Fig. 1 Contrasting the minimum dispersal distances of arboreal- and zoophilous-arboreal pollen to pollen traps. Percentage refers to percentage of pollen influx for arboreal and zoophilous arboreal pollen, respectively. Arboreal pollen was 97% of total pollen influx and zoophilous pollen accounted for 62% of total arboreal pollen influx. For this analysis all pollen of a given taxon was assumed to have come from the nearest potential source individual (for full review of these data, see Bush & Rivera, 1998).

broader, flatter curve with no significant difference between the 6–20-m and 20–40-m dispersal categories. However, notions that zoophilous taxa are poorly dispersed are not supported by the observation that more than 40% of this pollen came from beyond 20 m.

Beyond the various 'messy' dispersal systems that can introduce zoophilous pollen to the air, the most likely correlate would be the distances travelled by different groups of pollinators and the average amount of pollen carried by each. Renner & Feil (1993) suggested that even open-flowered taxa are pollinated by highly mobile organisms (contra Bawa & Opler, 1975). In accordance with Renner & Feil's (1993) expectation, open-flowered dioecious species had strong pollen dispersal. For example, *Hyeronima* and *Zanthoxylum* were two of the most abundant pollen types found, occurring in most pollen traps. The basal area data reveal that trees of these genera were not found within 40 m of the traps, with only three exceptions. Even *Cordia* pollen, which is suspected to be pollinated by diverse small insects (Renner & Feil, 1993) was found to disperse between 20 m and 40 m (Bush & Rivera, 1998).

Although this is not a study of pollination, there seems to be no a priori reason to suggest that the pollen of dioecious, open-flowered taxa disperses less than that of monoecious or hermaphroditic open-flowered species.

The hypotheses reviewed

Taxa pollinated by wind or dioecious taxa with a very open structure were over-represented by pollen influx to the traps, all other pollination systems were under-represented. To explain the observed pattern, it is worth considering whether a pollination mechanism is likely to be 'messy' in the sense that excess pollen is spilled into the air. Anemophily is the shotgun approach to fertilization. Vast quantities of pollen are released and very little actually hits its target. This is the ultimate in 'messy' pollination and thus is best represented in pollen records. Dioecious flowers with an 'open' floral structure have anthers that are exposed or protruding. This openness, combined with relatively high pollen production, ensures that a substantial proportion of the pollen is blown free of the flower into the atmosphere (Bullock, 1994). Although not as 'messy' as anemophily, these open or ambophilous flowers are over-represented in pollen records.

CONCLUSIONS

Pollen records from the lowland tropics are characterized by highly diverse pollen floras (150 + pollen taxa are to be expected) and high proportions of unknown taxa (10–40% would be average). Much of the potential information in the record is lost among the 'unknowns' and our general lack of understanding of the proportional representation of species. This paper provides a prediction of which species are most likely to be represented in a neotropical pollen rain. For palynologists interpreting pollen diagrams it is very important to understand systematic biases, such as the degree of over-representation of anemophilous taxa. It is also important to understand which groups of taxa are likely to be silent in the pollen record. These same patterns are likely to have held true since angiosperms first evolved and interpretations of the rate of evolution of floral morphologies, if based on pollen representation, should take into account these potential biases. A major obstacle to refining neotropical palynology is dealing with the sheer diversity of pollen types. Studies such as this help to concentrate attention on the taxa that are most likely to occur in the fossil record, and thereby help guide the palynologist to new identifications of presently unidentified palynomorphs.

Pollen representation in lowland neotropical forests is strongly influenced by reproductive strategy. Plants that waste pollen are more likely to be found in the pollen rain than those that have neater pollination strategies. Indeed the predicted sequences, that went from most likely to be 'messy' to least likely to be 'messy' for both flower structure and pollination mode, were supported by the data. Anemophilous species were strongly over-represented relative to basal area. Dioecious open-flowered species were also over-represented and their pollen was commonly deposited more than 40 m from the point of origin.

Where hermaphroditic zoophilous species were found to be strongly represented, a correlation could often be suggested with an unusual pollination strategy or with self-incompatibility. Self-incompatibility requires the liberation of pollen from the flower, and in so doing increases the inherent likelihood that some pollen will be lost in the transfer. Consequently, hermaphroditic plants that routinely self-pollinate are probably the least likely to be found in pollen records.

A single study over a 3-year period cannot provide a definitive hierarchy. The ranking of sexual mechanisms and pollination syndromes is likely to be robust for those types that were either very strongly or very weakly represented. Classes that were statistically insignificant in terms of variance are especially likely to vary in importance according to local conditions. Further studies at other tropical locations are needed to refine this model and more research is needed into tropical pollination systems and the autecology of species.

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