The diversity of hemi-epiphytic figs (*Ficus*; Moraceae) in a Bornean lowland rain forest

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The diversity and niche specificity of hemi-epiphytic figs in a lowland dipterocarp forest in Sarawak were investigated in 1998. Twenty-seven fig species (264 individuals, *c.* 120 ha) colonized a diversity of host taxa (35 families), but densities were very low and only 1.77% of trees >30 cm d.b.h. were occupied. There were no significant associations with host taxa or host-bark roughness but among 11 common species (≥9 individuals) the distributions of all other parameters (host-d.b.h., height and position of colonization, crown illumination, soil-texture and slope-angle) were significantly different, and we identified five fig guilds. The guilds corresponded to canopy strata, and appeared to reflect the establishment microsite requirements of different species. A fundamental trade-off within the hemi-epiphytic habit was revealed: Species colonizing larger hosts were rarer, because of lower host densities and more specific microsite requirements, but had better light environments and attained a larger maximum size. The single strangler species appeared to escape many of these constraints, and an important source of mortality caused by host-toppling, indicating the advantages of this strategy. Thus, the hemi-epiphytic figs in this community have come to fill a remarkable diversity of niches, despite low levels of competition, through the exigencies of a complex environment. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, **78**, 439–455

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'The forests abound with gigantic trees with cylindrical, buttressed, or furrowed stems, while occasionally the traveller comes upon a wonderful fig tree, whose trunk is itself a forest of stems and aërial roots . . . I believe that they originated as parasites, from seeds carried by birds and dropped in the fork of some lofty tree. Hence descend aërial roots, clasping and ultimately destroying the supporting tree, which is in time entirely replaced by the humble plant which was at first dependent upon it. Thus we have an actual struggle for life in the vegetable kingdom, not less fatal to the vanquished than the struggles among animals which we can so much more easily observe and understand.'

Alfred Russel Wallace (1869), *The Malay Archipelago*

INTRODUCTION

Hemi-epiphytes are a poorly known but fascinating group of plants. The growth-form has evolved several times and is recorded in at least 20 plant families, but

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by far the most important, with approximately 500 species, are the figs (*Ficus* L. spp., Moraceae) (Putz & Holbrook, 1986). Distributed throughout the tropics, hemi-epiphytic figs range in size from huge Banyans (*Ficus benghalensis* L.), whose crowns are reputed to reach over 150 m in diameter (King, 1888), down to small understorey shrub-like species that perch on the buttresses of canopy trees. A big strangler fig, with its intertwined aerial-roots wrapping around and encasing the remains of its one-time host, is an extraordinary sight (Wallace, 1869 (1986 facsimile edition); Dobzhansky & Murca-Pires, 1967) and the mystic and power attributed to these plants, and the fertility associated with their massive crops of fruit, have caused them to be venerated in traditional cultures around the world.

Figs are invariably one of the most species-rich genera in any tropical lowland forest, whether in the Neotropics, Africa or Melasia (Janzen, 1979b). They have a roughly pan-tropical distribution, with approximately 750 species in the genus (Berg, 1989), and in addition to the aforementioned hemi-epiphytes, include shrubs, small to large trees, bole climbers to those with thick cable-like lianas, and true epiphytes. However, in any particular locality hemi-epiphytic figs constitute from one third to over half the fig species and are often a critical component in the forest ecosystem, because of the large quantities of fleshy fruit they produce (Terborgh, 1986; Lambert & Marshall, 1991). Yet, despite this manifest importance, comparative studies on sympatric fig species are rare and generally restricted to studies of their specialized pollination system (e.g. Herre, 1996) or seed disperser assemblages (e.g. Kalko, Herre & Handley, 1996; Shanahan & Compton, 2001). How so many apparently ecologically similar plant species coexist is one of the most fundamental, and possibly least understood, questions in tropical ecology (e.g. Connell, Tracey & Webb, 1984; Hubbell & Foster, 1986; Condit *et al.*, 1996).

As with all primary hemi-epiphytes, the seeds of these figs germinate in the canopy of a host tree, and hence the plant exists initially as an epiphyte. From the seedling aerial-roots, which resemble stems more than normal terrestrial roots (Putz & Holbrook, 1986), grow down the host's trunk to the ground and thus the adult plant is connected to the forest floor. Hemi-epiphytes only utilize their host trees for physical support and many species remain dependent on their hosts throughout their life. The stranglers, however, produce anastomosing aerial-roots that eventually enclose and kill the host, leaving the fig free-standing (Dobzhansky & Murca-Pires, 1967). Few other plants exhibit such dramatic ontogenic change.

The fleshy fruits of hemi-epiphytic figs are eaten by birds, bats, and arboreal mammals (Shanahan *et al.*, 2001) and the drupes voided in the faeces. In some species secondary dispersal by ants may be important (Roberts & Heithaus, 1986; Kaufmann *et al.*, 1991; Laman, 1996b). Germination and early seedling survival appears to be dependent on microsites with good moisture retention, such as pockets of humus (Ramirez, 1976; Laman, 1995; Swagel, Bernhard & Ellmore, 1997), and several studies have suggested that host species offering such microsites are preferentially colonized (Guy, 1977; Todzia, 1986; Michaloud & Michaloud, 1987; Daniels & Lawton, 1991; Patel, 1996; Athreya, 1999; Doyle, 2000). Water stress is a critical factor during the epiphytic seedling phase, and substantial changes in leaf structure and water-relations occur in the transition from epiphytic to rooted stages (Putz, Romano & Holbrook, 1995; Holbrook & Putz, 1996a; Holbrook & Putz, 1996b), but in microsites with an accumulation of epiphytic humus nutrients may not be limiting (Putz & Holbrook, 1989). How fast hemi-epiphytic figs grow is unknown. However, plants in the epiphytic stage are always small, rarely, if ever, exceeding 1 m height before connecting to the ground (Ramirez, 1977; N. M. Holbrook, pers. comm.). And, at least, some species appear to grow very quickly, judging by the colossal proportions of individuals found on abandoned buildings (Dobzhansky & Murca-Pires, 1967; Perry & Merschel, 1987; R. D. Harrison, pers. observ.).

The tendency has been to regard hemi-epiphytic figs as equivalent and differences among species in terms of their growth-forms, the hosts they colonize, or the positions they occupy in the canopy, have rarely been examined. For example, it is generally assumed, especially in popular literature, that most or all hemi-epiphytic figs are stranglers, when in fact relatively few species adopt this habit (Corner, 1940; Todzia, 1986). Studies on epiphyte communities have shown that species specialize on different hosts or in different parts of the canopy (e.g. Zimmerman & Olmsted, 1992; Hietz & Hietz, 1995; Chettri & Rai, 1996). Hence, one might expect hemi-epiphytes to be similarly specific in their habits. Indeed, in the only such study to date, five hemi-epiphytic fig species in Indonesian Borneo were found to belong to two broad groups, one colonizing bigger trees and higher canopy positions relative to the other (Laman, 1996c).

Here we investigate the diversity of hemi-epiphytic figs in a lowland tropical rain forest in Sarawak, Borneo. We attempt to elucidate critical factors in the hemi-epiphytic niche and to what extent species can be segregated accordingly. Specifically, we examined the following hypotheses; hemi-epiphytic fig species (1) exhibit different habits with respect to size and growth-form, (2) differ in the taxa, size or bark roughness of the host trees they colonize, (3) occupy different sites on their host trees or different light

environments in the canopy, and (4) differ in their local distribution according to soil type and topography. Based on the results we obtained, we then attempted to identify and characterize fig guilds. We found hemi-epiphytic figs to be remarkably diverse, both with respect to species richness and the variety of niches they occupied, and we discuss these findings with respect to the hemi-epiphytic habit and the diversity of tropical forests.

METHODS

STUDY SITE AND SPECIES

Our study site was Lambir Hills National Park (LHNP, 40°20′ N, 1130°50′ E, 150–250 m a.s.l.), located 30 km south of the town of Miri in northern Sarawak, Malaysia. The national park is approximately 6500 ha of which two thirds are primary lowland dipterocarp forest. It experiences a perhumid climate with a mean annual precipitation of approximately 2700 mm, and monthly average precipitation ranging from 168 mm in July to 328 mm in November. However, infrequent minor droughts occur, most often in February–March, and occasional severe droughts, which last for two or more months, have also been recorded particularly during El Niño events (Walsh, 1996; Harrison, 2001).

All hemi-epiphytic and climbing figs were included in our survey. However, this paper is concerned only with species belonging to the monoecious subgenus *Urostigma*, the so-called strangler figs of popular accounts. The climbing figs of sections *Kalosyce* and *Rhizocladus*, and understorey hemi-epiphytes of section *Sycidium*, all in the dioecious subgenus *Ficus*, will be considered in a separate paper. Phylogenetic constraint and their very different ecological characteristics preclude meaningful comparison here. Hereon, fig or hemi-epiphyte refers to species of *Ficus* subgenus *Urostigma* (Corner, 1965).

In total we surveyed approximately 120 ha including the 52 ha Long-term Ecological Dynamics Plot (LaFrankie, Tan & Ashton, 1995), an 8 ha plot of the Canopy Biology Program (Inoue & Hamid, 1997), and trails around the park headquarters (*c.* 60 ha). In the trail areas both sides of the trail to a distance of approximately 40 m were surveyed and all individuals observed were included. No attempt was made to accurately measure the area covered and hence these results were not used in our density estimates. The plots were surveyed by two observers walking in parallel, 20 m apart, between marking posts and within sight of one another. Binoculars were used to aid identification of aerial-roots, especially on trees festooned with climbers and epiphytes. The aerial-roots of a hemi-epiphytic fig are distinctive, and recognizably

different from the lianas of climbers, even when quite small (<1 cm diameter). Aerial-roots are tapered from top down, which is especially noticeable immediately below the point of attachment, the periderm is flaky and has numerous lenticels, and they produce copious white latex when cut. We surveyed all individuals with aerial-roots connected to the ground, i.e. there was no minimum aerial-root diameter (smallest recorded, 0.3 cm). But, we did not attempt to include the epiphytic seedlings. To evaluate the efficiency of our surveys, 10 ha of the 52 ha plot were re-surveyed in the reverse direction. However, no new individuals were found.

The majority of individuals were identified in the field. From long-term studies in LHNP, including monthly phenological observations from October 1994 to November 1998 of the hemi-epiphytic figs in the trail area and 8 ha plot (R. D. Harrison, unpubl. data), the observers were already familiar with most species. Nineteen species had been previously collected and voucher specimens lodged in the field herbarium in LHNP and at the Sarawak Forest Department herbarium in Kuching (see Table 2, Results section). Species requiring more thorough examination were collected and compared with voucher specimens and collections in the Kuching herbarium. For eight species, only non-fertile specimens were collected, as none were found with fruit, and these were deposited at LHNP. Although clearly distinct species, the names assigned on the basis of non-fertile specimens should be regarded as provisional. The census work was conducted between January and October 1998.

HEMI-EPIPHYTE AND HOST ATTRIBUTES

Five attributes of each fig were measured: (1) the number of aerial-roots and their diameter at breast height (d.b.h), measured with diameter tape at 1.3 m; (2) position of colonization (trunk, branch crotch (branching of the main bole, numbered from the lowest upwards), or branch limb (including second order crotches)), being the point from which the aerial-roots descended and branches radiated out; (3) height of the position of colonization, measured using a clinometer; (4) crown-area, calculated from the maximum and minimum crown diameters measured with a tape at ground level; and (5) hemi-epiphyte canopy illumination index (HCI, relative illumination of the fig crown), assessed by the observer. For HCI, the index suggested by Clark & Clark (1992) could be applied with refinements pertinent to hemi-epiphytes as explained in Table 1. For individuals with multiple aerial-roots, d.b.h. was calculated from the sum of their cross-sectional area. However, for some very large figs with anastomosing aerial-roots, the d.b.h. had to be estimated from measurements of the largest roots.

Table 1. Hemi-epiphyte crown illumination (HCI) index values and their definitions. Adapted from Clark & Clark (1992)

Index value	Definition
5	Crown completely exposed: emergent crown of free-standing strangler or hemi-epiphyte on emergent host with >50% of crown-area extending beyond host's crown (i.e. not blocked by host's crown)
4a	High over-head light, lateral light partially blocked: free-standing stranglers in canopy layer with lateral light blocked; hemi-epiphytes in the canopy layer with >50% of crown-area exposed to direct over-head light (i.e. not blocked by host or neighbouring crowns)
4b	Full lateral light, over-head light partially blocked by host's crown: hemi-epiphytes on emergent trees with <50% of crown-area extending beyond host's crown
3	Some over-head light, high lateral light (crown lit laterally): hemi-epiphytes on canopy to subcanopy hosts with some over-head light but <50% of canopy area exposed to direct overhead light; high lateral light (i.e. neighbouring crowns not obscuring lateral light)
2.5	High lateral light: hemi-epiphyte with direct overhead light completely blocked but high lateral light
2	Medium lateral light: no direct over-head light and lateral light partially blocked by neighbouring crowns, not recorded for hemi-epiphytic figs
1	No direct light: not recorded for hemi-epiphytic figs

The growth forms of the aerial-roots and crown were also noted.

For each host: (1) bark roughness, scored as 1 = smooth or flaky, 2 = scaly, 3 = fine to medium fissured, and 4 = deeply fissured; (2) host diameter at breast height (host-d.b.h); and (3) host identification (host-ID) were recorded. For those individuals in the plots, host tag-numbers were noted and the host-d.b.h and host-ID obtained from the plot data sets (refer to LaFrankie *et al*., 1995 for standard plot methodologies). In the trail area host-d.b.h. was measured at 1.3 m, or above buttresses if present, and identification was made to the family level. For a small number of individuals, host data could not be obtained from the plot data sets, and some individuals of *F. kerkhovenii* and *F. stricta* were free-standing, having strangled their hosts. These individuals were not included in the analysis of host data.

The frequencies of potential-hosts were calculated from the plot data sets and based on the host-d.b.h. range of each fig species (potential-host frequency = frequency of stems within the observed host-d.b.h. range of the fig species concerned). A minimum of three individuals was used to estimate the host-d.b.h. range. In the 52 ha plot a survey of soil-texture and slope-angle, measured at the centre of each of 1300 20 × 20 m quadrats, was conducted in 1994. Soil was collected and assigned to one of four texture grades (Kimmins, 1987), according to the apparent sandiness, stickiness and slipperiness. These four classes were later calibrated in the laboratory for a subsample of quadrats by the dispersion and settling method using a LaMotte Soil Texture Unit (LaMotte Co., Chestertown, Maryland, USA) and the differences between classes were found to be strongly correlated to differences in sand content. Slope angle was measured with a clinometer and measuring-pole. Analysis of soil-texture and slope-angle were restricted to those individuals occurring in the 52 ha plot.

DATA ANALYSIS

Statistical comparisons in this paper were restricted to those species with nine or more individuals in total. For each variable we initially attempted to reject the null hypothesis that all fig species came from the same distribution. If rejected, *post hoc* tests (Scheffé *F*-tests or *G*-tests, Sokal & Rohlf, 1995) were carried out to obtain the homogeneous groupings. Categorical variables (host-ID, bark roughness, colonization position, HCI index and soil-texture) were examined by *G*-tests. For continuous variables, ANOVA was used when the homogeneity of variances was confirmed (host-d.b.h and colonization height), otherwise Kruskal–Wallis non-parametric ANOVA was used (slope-angle). For host-ID, host-d.b.h., soil-texture and slope-angle, actual distributions were examined against expected distributions, based on the occurrence of potential-hosts, soil-textures and slope-angles in the 52 ha plot. For host-d.b.h., HCI index, soil-textures and slope-angles we also examined the correlations (Kendall rank correlation) with fig size (aerial-root d.b.h) to investigate the influence of fig demography. Fig guilds were identified by cluster analysis (Ward's minimum variance method) and a canonical discrimination analysis (CDA) was conducted to test the significance between guilds. Analyses were conducted using SAS (SAS Institute Inc, 1985; Procedures FREQ, GLM, NPAR1WAY, CLUSTER, CANDISC).

RESULTS

SPECIES OF HEMI-EPIPHYTIC FIG

A total of 27 species of hemi-epiphytic fig were recorded among 264 individuals found during our survey (Table 2). Given these belong to a single subgenus (*Ficus* subgenus *Urostigma*) this indicates a very high level of α diversity, even by the exalted standards of lowland dipterocarp forests. However, hemi-epiphytic figs were rare, both in terms of the densities of individuals (range 0.02–0.42 ha^{-1}) and the occupancy rate of potential-hosts (range 0.01–0.42%). Only 0.41% of trees over 10 cm d.b.h and 1.77% of trees over 30 cm d.b.h. occurring in the plots (60 ha) were occupied by a hemi-epiphytic fig. Quantitative comparisons hereon are restricted to the 11

species with nine or more individuals recorded in the survey (Table 2).

SIZE AND GROWTH FORM

Hemi-epiphytic fig species clearly differed in size and growth form (Table 3). Aerial-roots often forked above the height (1.3 m) at which they were measured, inflating the numbers reported here. Only *F. kerkhovenii*, the single strangler among these species, commonly had more than one aerial-root descending from the point of attachment. *Ficus kerkhovenii* was also clearly the largest in terms of maximum aerial-root diameter, although for maximum canopy area it was only marginally larger than some other species (Table 3). Across all species, there

Table 2. Species of hemi-epiphytic figs (*Ficus* subgenus *Urostigma*) in Lambir Hills National Park, Sarawak. Taxonomic arrangement follows Corner (1965); *N* = number of individuals surveyed (area covered *c.* 120 ha); D = density of individuals occurring in two forest dynamics plots (60 ha); Host occupancy = percentage of potential hosts (defined as all stems within the host-d.b.h. range of the fig species, and estimated from a minimum of three individuals) in the plots (60 ha) colonized

Section and subsection	Species	*N*	D (ha^{-1})	Host occupancy (%)	Voucher specimen no.
Urostigma					
	F. caulocarpa Miq.	1	0.02	–	RDH 568
	F. virens Ait.	4	0.05	0.01	RDH 202
Conosycea					
Conosycea	*F. bracheata* Wall. ex Miq.	1	0.02	–	–
	F. consociata Bl. vs. murtoni	7	0.08	0.12	RDH 200
	F. cucurbinita King	12	0.10	0.19	RDH 089
	F. drupaceae Thunb.	1	0.02	–	–
	F. kerkhovenii Val.	22	0.27	0.03	Nagamitsu 531
	F. palungensis Weiblen	22	0.33	0.03	RDH 545
	Sp. D (undescribed sp.)	6	–	–	RDH 173
	F. stupenda Miq.	14	0.12	0.02	RDH 070
	F. subgelderi Corner	30	0.40	0.07	RDH 215
	F. subtecta Corner	1	0.02	–	–
	F. xylophylla Wall. ex Miq.	26	0.35	0.07	RDH 155
Dictyoneurone	*F. binnendykii* Miq. vs. latifolia	13	0.15	0.01	RDH 196
	F. delosyce Corner vs. obtusa	31	0.42	0.03	RDH 198
	F. dubia Wall. ex King	17	0.20	0.42	RDH 129
	F. glaberrima Bl.	2	0.02	–	RDH 549
	F. pellucido-punctata Griff.	4	0.05	0.03	–
	F. pisocarpa Bl.	13	0.08	0.03	RDH 518
	F. retusa L.	8	0.13	0.01	–
	F. sumatrana Miq.	4	0.03	0.03	RDH 180
	F. sundaica Bl.	3	–	–	–
Benjamina	*F. benjamina* L.	6	0.02	0.06	RDH 203
	F. callophylla Bl.	2	0.02	–	RDH 543
	F. subcordata Bl.	9	0.08	0.18	RDH 199
	F. stricta Miq.	4	–	–	–
	F. tristanifolia Corner	1	0.02	–	–
Total	27 species	264	2.99		

Table 3. The life forms of 11 hemi-epiphytic fig species (*Ficus,* subgenus *Urostigma*) at Lambir Hills National Park, Sarawak: mean number of aerial-roots (± SD), maximum aerial-root diameter at breast height (d.b.h), maximum crown area and the growth form. For description of growth form refer to text

Ficus species[1]	N	Mean number of aerial-roots	Maximum aerial-root d.b.h. (cm)	Maximum crown area (m²)	Growth form
F. kerkhovenii	22	1.7 ± 1.96	200	2990	Strangler
F. cucurbinita	12	2.1 ± 2.57	50	2200	Radial
F. subcordata	9	1.2 ± 0.44	25	2900	Radial
F. dubia	17	1.6 ± 2.18	25	1370	Radial
F. delosyce	31	1.2 ± 0.50	24	750	Radial
F. xylophylla	26	1.5 ± 0.71	23	790	Radial
F. stupenda	14	1.3 ± 0.47	20	2670	Radial
F. subgelderi	30	1.2 ± 0.38	20	1010	Radial
F. pisocarpa	13	1.4 ± 0.65	16	800	Radial
F. binnendykii	13	1.2 ± 0.60	13	910	Emergent
F. palungensis	22	1.3 ± 0.57	5	180	Vine

[1]In reverse size order

was over an order-of-magnitude difference in the maximum size attained.

We recognized four types of growth form (Table 3). The radial growth form is the typical hemi-epiphytic shape in which the branches of the figs crown arch out from close to the point of attachment. There may be a short trunk, but the vertical growth of the fig is limited and the fig's crown is largely below that of the host. *Ficus kerkhovenii* (strangler) had a similar growth form initially, but developed more massive aerial-roots, greater penetration of the host's crown and, of course, eventually progressed to a free-standing phase. A total of six out of the 22 individuals observed were free-standing. The only other strangler in the survey was *F. stricta* with three individuals, of which one was free-standing. *Ficus binnendykii* had an emergent growth form, with an extended vertical trunk ending in a narrow crown that poked out above the host's. The final growth form was that of *F. palungensis* which had a flexible vine-like stem that climbed from the point of attachment through the host's branches. Sometimes it extended to other host trees adopting a form of colonial growth as aerial-roots would descend from each host.

HOST CHARACTERISTICS

The 227 hemi-epiphytic figs for which the host family could be reliably identified colonized a total of 35 families (Table 4), or roughly half the families of potential-host trees found in LHNP. Dipterocarpaceae, however, accounted for 40% of all hosts. Host genus and species were only identified for figs in the two plots. One-hundred and eighty-one hemi-epiphytic figs colonized 73 genera and 107 species of host, or approximately 27% and 9% of potential-host taxa occurring in LHNP, respectively. Thus, it can be seen that as whole hemi-epiphytic figs colonized a very wide range of host taxa. The most common host species was *Whiteodendron moutlonianum* (Myrtaceae), which was colonized 12 times.

Among species there was a highly significant difference in the colonization rate on dipterocarps relative to other families (Table 5), but *post hoc* comparisons indicated a broad overlap between species. Moreover, none of the species were significantly more frequent than expected on dipterocarps, when the proportions of dipterocarps among hosts and potential-hosts were compared by size-class (Fig. 1, Wilcoxon two-sample test). More refined analyses were not possible because of small sample sizes even for the most common species.

Two host attributes, besides their taxonomy, were considered: host-d.b.h and bark roughness (Table 6). There was a highly significant difference across fig species in host-d.b.h and *post hoc* tests revealed a substantial segregation of species. Each species also showed a highly significant difference between actual host-d.b.h. distribution and that of potential host-d.b.h. (ANOVA, $P < 0.001$; Fig. 1). But aerial-root d.b.h. was significantly correlated with host-d.b.h. in only two species (*F. kerkhovenii*, $N = 16$, $\tau = 0.45$, $P < 0.05$; *F. subgelderii*, $N = 29$, $\tau = 0.44$, $P < 0.01$). Interestingly, there was no significant difference across species in bark roughness, and most species colonized the full range of bark types from smooth to deeply fissured.

These results suggest that host size is the most important host attribute, and four types of host-

Table 4. Families of host trees colonized by hemi-epiphytic figs (*Ficus,* subgenus *Urostigma*) at Lambir Hills National Park, Sarawak. Potential-host occurrence was calculated from plot (60 ha) data sets based on the host-d.b.h. range of all hemi-epiphytic figs

	Hosts		Potential hosts
	No.	%	%
Anacardiaceae	5	2.2	7.0
Annonaceae	2	0.9	3.0
Bombacaceae	2	0.9	0.7
Burseraceae	4	1.8	7.6
Celastraceae	1	0.4	0.7
Chrysobalanaceae	1	0.4	0.3
Clusiaceae	1	0.4	3.2
Dilleniaceae	4	1.8	0.9
Dipterocarpaceae	92	40.5	15.8
Ebenaceae	1	0.4	2.4
Euphorbiaceae	9	4.0	12.9
Flacourtiaceae	3	1.3	1.1
Lauraceae	12	5.3	3.3
Leguminosae	10	4.4	1.5
Linaceae	1	0.4	2.4
Melastomataceae	5	2.2	2.2
Meliaceae	3	1.3	1.4
Moraceae	17	7.5	2.1
Myristicaceae	5	2.2	4.6
Myrtaceae	20	8.8	4.7
Olacaceae	2	0.9	0.7
Oleaceae	1	0.4	0.1
Oxalidaceae	1	0.4	0.1
Polygalaceae	1	0.4	1.6
Rhizophoraceae	1	0.4	0.5
Rubiaceae	4	1.8	0.6
Sapindaceae	1	0.4	0.6
Sapotaceae	5	2.2	2.2
Simaroubaceae	1	0.4	0.0
Sterculiaceae	1	0.4	1.1
Theaceae	1	0.4	0.8
Tiliaceae	1	0.4	1.4
Thymelaeaceae	1	0.4	0.0
Ulmaceae	2	0.9	0.7
Verbenaceae	6	2.6	1.1
Others			10.7
Total	227	100	100

d.b.h. distribution can be recognized (Fig. 1). A right-skewed distribution (*F. binnendykii*, *F. delosyce*, *F. palungensis, F. pisocarpa* and *F. subgelderii*), indicating a predominance on smaller hosts within the host-d.b.h. range of a species. In these species the majority of individuals were recorded on hosts of <50 cm d.b.h. A left-skewed distribution (*F. dubia,*

F. kerhovenii and *F. subcordata*) indicating a predominance on larger hosts within the host-d.b.h. range of a species. An approximately normal distribution (*F. curcurbinita* and *F. xylophylla*) and an even distribution (*F. stupenda*) with hosts in every size-class.

COLONIZATION SITE AND LIGHT ENVIRONMENT

In terms of the site hemi-epiphytes occupied within the canopy of a host, two attributes were investigated: colonization height and position. Hemi-epiphytic figs demonstrated a highly significant difference in their height of colonization, and *post hoc* comparisons revealed considerable segregation of species (Table 7). For colonization position it was only possible to test between trunk and crotch positions, but the difference was also highly significant. Species with a low proportion of trunk positions also occupied few higher branch crotches. These species appear to be specialists on the large crotches at the base of a host's crown, while other species were relatively catholic with respect to the colonization positions they occupied. It is also clear that the former group colonized larger hosts and higher positions compared to the latter (Tables 6 and Table 7).

The HCI index, an estimate of the level of light reaching the fig crown, showed a highly significant differences across species (Table 8), although all species were relatively light demanding and no individuals were found in the lowest light environments (Table 1). In four out of the 11 species aerial-root d.b.h. was significantly correlated with HCI index, indicating larger individuals had better light environments (Table 8). Free-standing individuals of *F. kerkhovenii* were removed from the analysis of HCI index to control for the absence of a host crown.

SOIL TYPE AND TOPOGRAPHY

Analyses of the differences in distribution with respect to soil-texture and slope-angle were restricted to those individuals found in the 52 ha plot and there were only eight species with sufficient individuals for quantitative analysis. Nevertheless, there were significant differences across species for both parameters (Table 9), although only two species showed a significant association with soil-texture and one with slope-angle when compared with expected distributions. *Ficus xylophylla* show a preference for sandier soil (*G*-test $\chi^2 = 4.33$, $P < 0.05$), while *F. kerkhovenii* was strongly biased towards the clay rich soils (*G*-test $\chi^2 = 7.74$, $P < 0.01$) and steep slopes (ANOVA f = 13.0, d.f. = 1, $P < 0.001$). However, there were no significant correlations between aerial-root d.b.h and soil-texture and slope-angle for any species (Kendall rank correlation, $P > 0.05$).

Table 5. Proportion of dipterocarp and non-dipterocarp hosts colonized by 11 hemi-epiphytic fig species (*Ficus* subgenus *Urostigma*) at Lambir Hills National Park, Sarawak. The frequencies of dipterocarp and non-dipterocarp hosts are compared across species (*G*-test). Homogeneous groups are indicated by common letters

Ficus species	Frequency on dipterocarp hosts	Frequency on non-dipterocarp hosts	Groups	
F. subcordata	7	2	A	
F. dubia	10	7	A	
F. cucurbinita	6	6	A	B
F. stupenda	7	7	A	B
F. xylophylla	12	14	A	B
F. pisocarpa	5	8	A	B
F. binnendykii	5	8	A	B
F. subgelderi	10	20	A	B
F. kerkhovenii	6	12	A	B
F. palungensis	3	19	A	B
F. delosyce	4	27		B
	$\chi^2 = 25.9$	d.f. = 10	$P < 0.01$	

Table 6. Diameter at breast height (d.b.h., mean and standard deviation (SD)) and bark roughness (mean score and range) of host trees colonized by 11 hemi-epiphytic fig species (*Ficus* subgenus *Urostigma*) at Lambir Hills National Park, Sarawak. Host-d.b.h. was compared by ANOVA (f_{max}-test used to confirm homogeneity of variances). Bark roughness was compared by Kruskal–Wallis non-parametric ANOVA. Bark roughness class scores were: smooth or flakey = 1; scaly = 2; fine to medium fissured = 3; and deeply fissured = 4. Homogeneous groups for host d.b.h. are indicated by common letters

Ficus species	*N*	d.b.h. of host trees Mean (cm)	SD	Scheffe group					Host bark roughness Mean score	Range
F. subcordata	9	110	50.3	A					2.6	2–4
F. cucurbinita	10	97	30.9	A	B				2.2	1–4
F. dubia	16	96	27.0	A	B	C			2.2	1–4
F. stupenda	12	89	58.1	A	B	C	D		2.0	1–4
F. kerkhovenii	16	74	30.6	A	B	C	D	E	2.3	1–4
F. xylophylla	25	74	26.2	A	B	C	D	E	2.1	1–4
F. pisocarpa	13	67	29.6	A	B	C	D	E	2.1	1–4
F. subgelderi	29	53	28.9		B	C	D	E	2.2	1–4
F. binnendykii	13	48	24.3			C	D	E	1.9	1–3
F. delosyce	30	42	23.4				D	E	1.8	1–3
F. palungensis	20	32	17.3					E	2.0	1–4
Total	184									
		f = 9.21, d.f. = 10, 182							$\chi^2 = 8.8$	
		$P < 0.001$							$P > 0.05$	

HEMI-EPIPHYTIC FIG GUILDS

To investigate whether there were recognizable guilds of hemi-epiphytic figs in the canopy we conducted a canonical discrimination analysis. Variables found to be significant in the analyses above (host-d.b.h., colonization height and HCI index) were used, although colonization position as a binomial variable (trunk or crotch) could not be included. Potential guilds were identified by cluster analysis, so membership did not involve any a priori decision.

Among the 11 species of hemi-epiphytic figs investigated five guilds were identified (Fig. 2A, Wilk's Λ, $P < 0.01$). The first canonical variable (CAN1) and second canonical variable (CAN2) explained 87% and
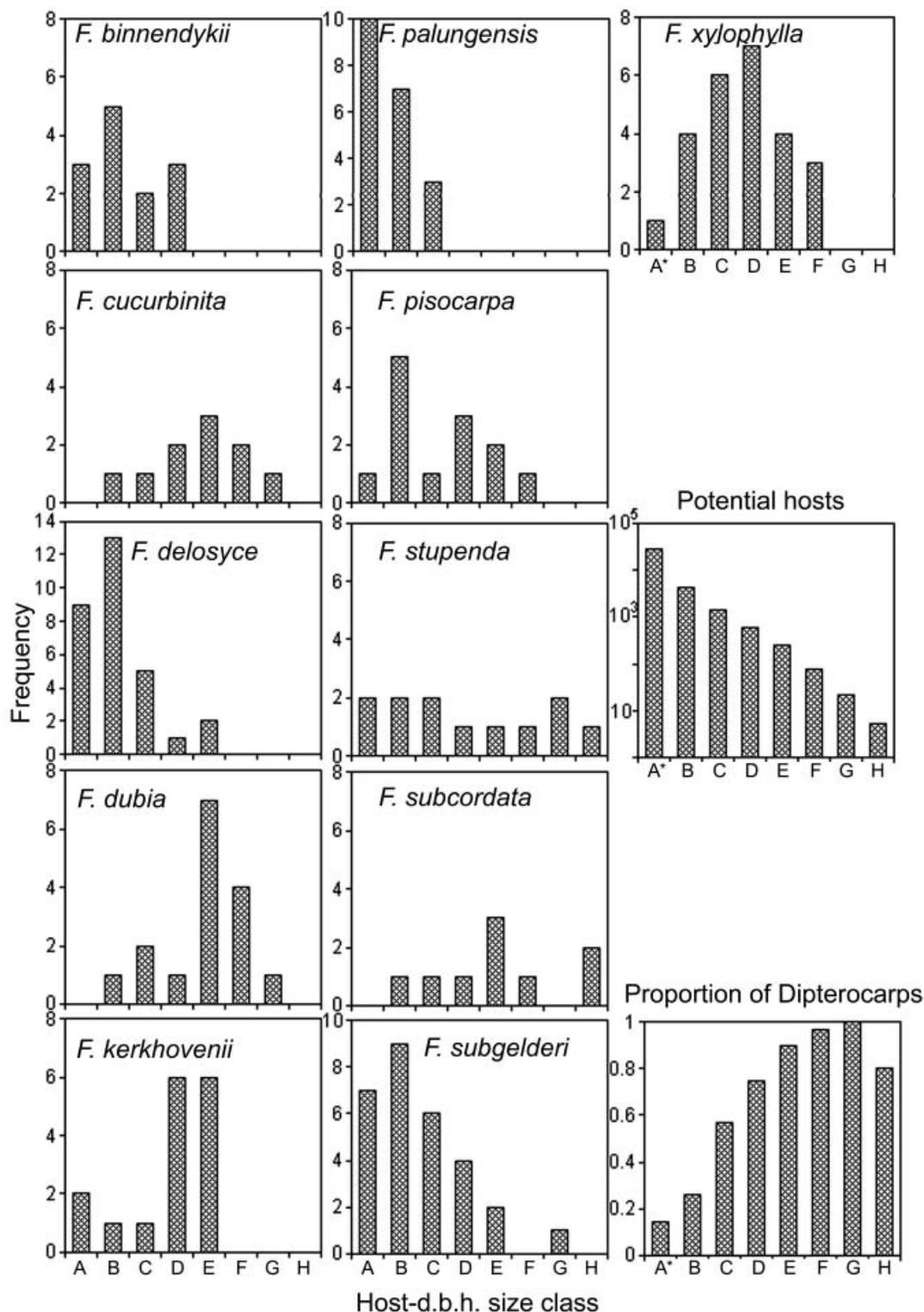
Figure 1. Frequency distributions of host-d.b.h. size classes for 11 hemi-epiphytic fig species (*Ficus* subgenus *Urostigma*) in LHNP (size classes, cm, A = <30 (A* = 10–30), B = 30–50, C = 50–70, D = 70–90, E = 90–110, F = 110–130, G = 130–150, H = >150). The frequency distribution of potential hosts (log scale) and the proportion of dipterocarps in each d.b.h. size class are also given (data from a 52-ha plot in LHNP). In all species, actual host-d.b.h. distributions were highly significantly different from potential host-d.b.h. distributions (ANOVA, *P* < 0.01).

Table 7. Height and position of colonization in the canopy of host trees by 11 hemi-epiphytic fig species (*Ficus* subgenus *Urostigma*) at Lambir Hills National Park, Sarawak. Colonization height/position was measured at the point from which roots descended and branches radiated out. For height the mean, standard deviation (SD) and Scheffe groups are given. For position the frequencies of different categories are given. Crotch refers to primary branch forks with the tree bole, numbered from the lowest upwards. Branch limb includes higher crotch positions and secondary branch forks. Colonization height was compared by ANOVA (f_{max} – test used to confirm homogeneity of variances) and position on host tree (trunk vs. crotch positions) by *G*-test. Homogeneous groups are indicated by common letters

| *Ficus* species | N | Height of colonization | | | | | | Position of colonization on host | | | | | |
		Mean (m)	SD	Scheffe group				Trunk	1st crotch	2nd crotch	Branch limb	Group	
F. subcordata	9	34.4	7.6	A				0	7	1	1	A	
F. dubia	17	29.5	7.7	A	B			2	13	1	1	A	B
F. cucurbinita	12	29.3	9.9	A	B			0	9	2	1	A	
F. pisocarpa	13	26.0	8.3	A	B	C		0	7	6	0	A	
F. kerkhovenii	22	25.9	6.0	A	B	C		2	13	2	1	A	B
F. xylophylla	26	25.8	6.2	A	B	C		0	14	9	3	A	
F. stupenda	14	25.6	7.2	A	B	C		2	5	3	4	A	B
F. binnendykii	13	21.3	9.4		B	C		3	3	4	3	A	B
F. subgelderi	30	20.7	8.2		B	C		11	8	6	5		B
F. delosyce	31	19.2	8.4		B	C		13	7	2	9		B
F. palungensis	22	15.7	7.3			C		8	11	2	1		B
Total	209							41	97	38	29		
		f = 7.79, d.f. = 10, 198						χ^2 = 35.2					
		$P < 0.001$						$P < 0.001$					

Table 8. Hemi-epiphyte canopy illumination (HCI) indexes of 11 hemi-epiphytic fig species (*Ficus* subgenus *Urostigma*) at Lambir Hills National Park, Sarawak. Differences between species were compared by *G*-test. The means, homogeneous groups, and the correlation with fig size (aerial-root d.b.h. and Kendall's τ) are given. Free-standing individuals of *F. kerkhovenii* were removed, when included *F. kerkhovenii* had a mean HCI index of 4.5. Homogeneous groups are indicated by common letters

| *Ficus* species | N | HCI index | | | vs. fig size |
		Mean	Groups		
F. kerkhovenii	22	4.4	A		0.44*
F. subcordata	9	4.4	A		0.17
F. stupenda	14	4.4	A		0.06
F. dubia	17	4.4	A		0.23
F. cucurbinita	12	4.2	A		− 0.07
F. xylophylla	26	4.1	A		0.33*
F. subgelderi	30	3.8	A	B	0.40**
F. delosyce	31	3.7	A	B	0.26
F. binnendykii	13	3.5	A	B	0.59**
F. pisocarpa	13	3.3		B	0.00
F. palungensis	22	3.1		B	0.03
	χ^2 = 65.2		$P < 0.001$		

*$P < 0.05$, **$P < 0.01$

Table 9. Soil and slope conditions beneath eight hemi-epiphytic fig species (*Ficus* subgenus *Urostigma*) in a 52-ha plot at Lambir Hills National Park, Sarawak. Soil texture grades (Kimmins, 1987) and mean and range of slope angle are given. Differences between species in soil texture grades were examined by *G*-test (clay-rich $1 + 2$ vs. sandy $3 + 4$) and for the slope angle by Kruskal–Wallis non-parametric ANOVA. Homogeneous groups are indicated by common letters

| *Ficus* species | *N* | Soil texture grade | | | | | | Slope angle | |
		1	2	3	4	Groups		Mean	Range
F. xylophylla	19	1	0	1	17	A		18.6	5–28
F. subgelderi	20	3	0	0	17	A		24.5	8–45
F. delosyce	24	2	2	0	20	A		19.9	5–46
F. dubia	9	1	1	1	6	A	B	18.9	10–28
F. binnendykii	8	0	2	0	6	A	B	24.3	2–40
F. palungensis	18	1	4	2	11	A	B	25.3	3–57
F. stupenda	7	1	1	2	3	A	B	19.7	10–40
F. kerkhovenii	11	2	5	1	3		B	33.1	18–50
		$\chi^2 = 15.8$						$\chi^2 = 18.9$	
		$P < 0.05$						$P < 0.05$	

13% of the variance between guilds, respectively. Each guild was also significantly different from all others ($P < 0.05$; Mahlanobis distances). The standardized canonical coefficient of each attribute is a measure of its relative contribution to the overall canonical variable (Fig. 2B). Host-d.b.h and colonization height contributed most to CAN1, while colonization height (negative sign) and HCI index contributed most to CAN2. All three attributes were significant correlated (Host-d.b.h.–Colonization height: $r^2 = 0.59$, $P < 0.001$; Host-d.b.h.–HCI: $r^2 = 0.43$, $P < 0.001$; Colonization height–HCI: $r^2 = 0.51$, $P < 0.001$).

Three of the guilds, with three species each, corresponded to hemi-epiphytic fig species colonizing emergent hosts, canopy hosts and subcanopy hosts, respectively (Fig. 2A). *Ficus palungensis* formed a separate guild of its own on smaller hosts, lower positions and lower light levels, while *F. pisocarpa* was found on canopy hosts but at lower light levels than the other species in that group.

DISCUSSION

SPECIES OF HEMI-EPIPHYTIC FIG

The community of hemi-epiphytic figs at LHNP was very diverse. However, this level of species richness is by no means unusual in figs and is comparable to other sites in the region (Laman & Weiblen, 1999). Perhaps more remarkable are the extraordinarily low densities of individuals in each species (0.02–0.42 ha^{-1}), especially with respect to potential hosts (0.01–0.42% occupancy). However, like high species richness, low density appears to be a common characteristic of hemi-epiphytic figs in natural forest (Corner, 1940; Todzia, 1986; Michaloud & Michaloud, 1987).

Such low densities might result from a rarity of microsites, or from an inability to reach them, or both. On roadsides in India, where seed rain was artificially high, Patel (1996) found up to 18 hemi-epiphytes growing in different positions on the same host. So, given the extraordinarily low rates of host occupancy here, microsites would not appear to be limiting, even considering that some species may have more stringent microsite requirements. Indeed, from measurements of seed rain in the canopy, Laman (1996a) suggested that, despite the production of huge quantities of seed, microsites were very under-saturated. The mortality of rooted individuals caused by their hosts toppling also appears quite high (Harrison, 2001) and so may contribute to the low densities observed.

A consequence of these low densities is that hemi-epiphytic figs rarely compete. In this study, only 0.41% of trees >10 cm d.b.h and 1.77% of trees >30 cm d.b.h. were colonized by a hemi-epiphyte, and no instances of two figs on the same host were recorded. Epiphytic seedling densities may be higher, but low rates of seed saturation will limit competition for the same microsite.

The low densities of hemi-epiphytic figs also have significant implications for their species-specific pollinators. Pollinating fig wasps have very short lifespans (Kjellberg, Doumesche & Bronstein, 1988) and are unable to reproduce outside the fig inflorescence. In hemi-epiphytic figs crops of inflorescences are usually highly synchronous, so pollinating wasps emerging from a ripe inflorescence, with their load of pollen, must disperse to another fig with inflorescences at the
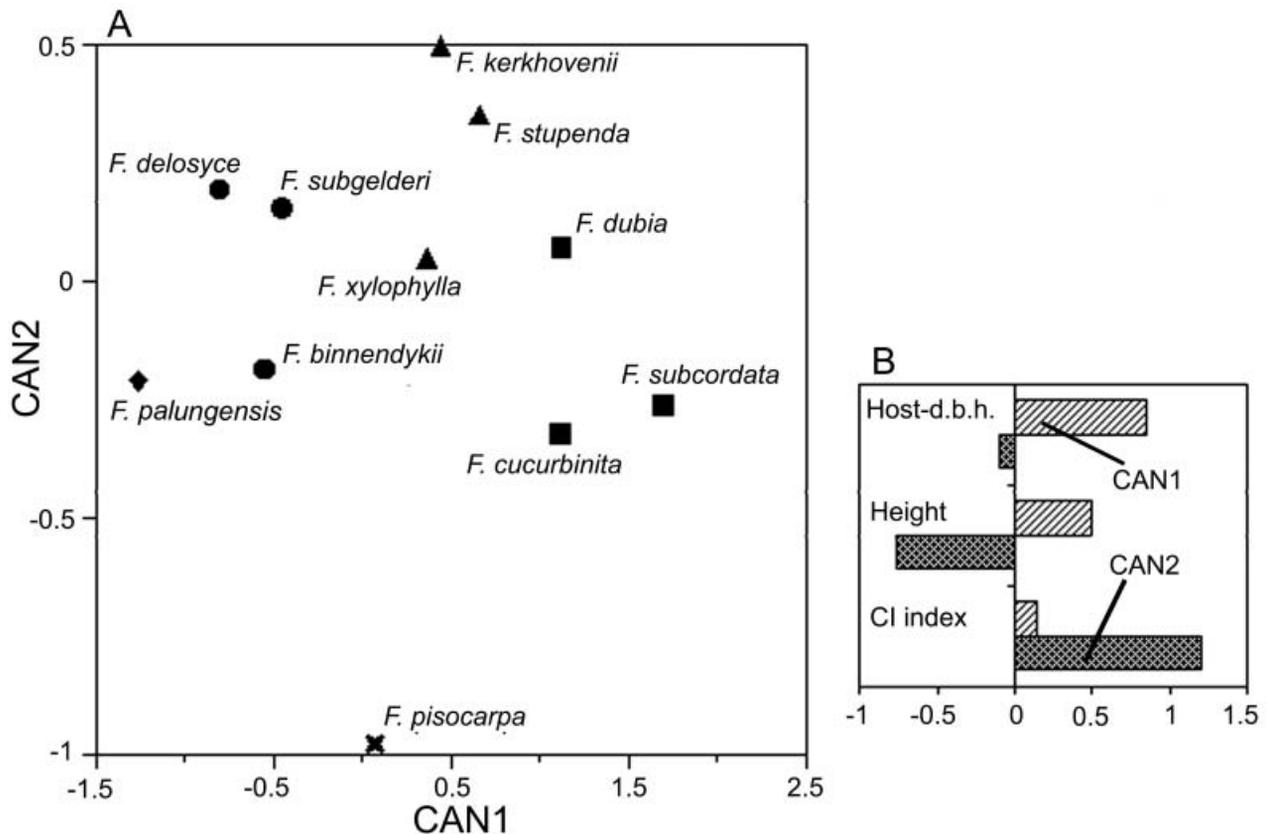
Figure 2. Canonical discrimination analysis of five guilds among 11 hemi-epiphytic fig species (*Ficus* subgenus *Urostigma*) in LHNP according to host-d.b.h., colonization height and HCI index. (A) Plot of species by the means of their first (CAN1) and second (CAN2) canonical variables; ■ emergent guild, ▲ canopy guild, ● subcanopy guild, × *F. pisocarpa*, and ◆ *F. palungensis*. All guilds were significantly segregated from one another ($P < 0.05$; Mahlanobis distances). (B) The contribution of each variable to the CAN1 and CAN2 according to their standardized canonical coefficients.

receptive stage (Galil & Eisikowitch, 1968). Cohorts of pollinators therefore cycle from plant to plant and, at the population level, figs must flower continuously to maintain their pollinator populations. The low flowering frequency typical of hemi-epiphytic figs means that fig populations must be very large (Bronstein *et al*., 1990) and, when combined with such low densities, means that the pollinators must disperse huge distances (Nason, Herre & Hamrick, 1998). It is therefore interesting that in Borneo only two out of 44 species of hemi-epiphytic fig are endemic, while in other sections of the genus endemism varies from 30% to 65% (Corner, 1965).

SIZE AND GROWTH FORM

Our first hypothesis, that hemi-epiphytic figs differ with respect to size and growth form, is clearly born out (Table 3). For want of an appropriate allometric model for hemi-epiphytes and the small sample sizes of

some species, we simply compared the maximum sizes observed. However, the sample sizes of the smaller species were reasonable and hence the differences are unlikely to be anomalous. In hemi-epiphytes crown area probably correlates closely to potential fecundity, given the greater leaf area available and the proximal use of assimilates for fruit production (Herre, 1996). The growth-form categories were subjectively designated, but reflect substantial differences in the habits of these plants, and are corroborated by results of other objectively measured parameters.

HOST CHARACTERISTICS

Interestingly, host attributes other than size did not appear very important. As a whole hemi-epiphytic figs colonized an extraordinary diversity of host taxa (Table 4) and the majority of host species were colonized just once. Dipterocarps, which account for approximately 80% of the canopy and emergent trees

in these forests (Fig. 2), constituted 40% of hosts but were not occupied more often than expected. Host bark roughness was also not found to be significant and most species also colonized the full range of bark types. There were, however, highly significant differences across species in host-d.b.h and in all species actual host-dbhs deviated significantly from potential host-d.b.h. distribution (Table 6, Fig. 2).

Superficially, the lack of any preference for particular host taxa does not appear to agree well with the results of other studies. *Ficus crassiuscula* in Costa Rica, for example, was much more abundant on certain host species than expected from their relative trunk area (Daniels & Lawton, 1991). While in Panama (Todzia, 1986), West Africa (Michaloud & Michaloud, 1987), India (Patel, 1996; Athreya, 1999) and Australia (Doyle, 2000) hemi-epiphytes were found to colonize some host species more frequently than expected based on their densities. Finally, in Indonesian Borneo, Laman (1996c) found significant differences among the five species he studied in bark-roughness and the proportion colonizing dipterocarps. However, he concluded that these could be accounted for by differences in host-d.b.h. In fact, with the exception of *F. crassiuscula*, which has an unusual growth-form, host-d.b.h. emerges as the most consistently important host attribute in all these studies. That figs are capable of colonizing a very wide variety of host taxa is not surprising. In very diverse forests, with many rare species, specializing in one or a few species of host would be paramount to committing evolutionary suicide.

COLONIZATION SITE AND LIGHT ENVIRONMENT

Our hypotheses that the distributions of hemi-epiphytic figs within the canopy differ according to colonization site and light environment were supported (Tables 7 and 8). Clearly, the location of suitable microsites is important for germination and seedling establishment and colonization sites on bigger trees tend to be higher and have higher light levels. However, the relationship is not so straightforward. The fig species in this study that were found on larger hosts also had a distinct preference for branch crotches, as opposed to trunk positions, and were found most frequently on the lowest, and therefore biggest, branch crotch (Table 7). In many canopy trees this basal branch crotch forms a broad bowl in which detritus collects, puddles form, and other epiphytes gain a purchase: all of which are factors that contribute to creating a suitable microsite for the establishment of a hemi-epiphytic fig. Moreover, in the rare instances of trunk establishment, large knot holes – which provide similar microenvironments (Laman, 1995) and may

also permit the roots of the hemi-epiphytic access to the rotten interior of older trees – appear to be important (Galil, 1984; Michaloud & Michaloud, 1987; Athreya, 1999). Such sites also provide a solid platform from which a hemi-epiphyte is less likely to be dislodged in high winds or torrential rain and which are strong enough to support the weight of a large individual. Conversely, the fig species that showed a preference for smaller hosts were also less particular about their colonization position and were found on small branch crotches, limbs and trunks (Table 7). These species were also clearly able to colonize trunk positions, and branch limbs, without knot holes through a different method of attachment. Instead of simply descending straight to the ground, the aerial-root in these species wound tightly around the host's trunk near the point of attachment and then in a gradually expanding helix as it descended (R. D. Harrison, pers. observ.). Clearly, the larger the host the less efficient this method of attachment. The epiphytic seedlings of species on smaller hosts, being lower in the canopy, may also suffer less from severely dehydrating conditions and strong winds, and the aerial-roots have a shorter distance to grow. Hence, they may not require the same quality of microsite as those on canopy or emergent hosts.

SOIL TYPE AND TOPOGRAPHY

Topography and soil types are often important axes in the distribution of tree species in dipterocarp forests (Whitmore, 1984), and climbers are known to segregate according to local topography in LHNP (Putz & Chai, 1987). Hence, it is perhaps not surprising to find that at least two species of hemi-epiphytic figs revealed preferences for different soil types and topography in LHNP, especially as Laman (1996c) found that species in Indonesian Borneo showed preferences for different forest habitats. For example, *F. xylophylla* was associated with the alluvial habitat, which would tend to agree with the correlation with sandier soil here. Also, although most hemi-epiphytic fig species are widely distributed, assemblages differ substantially between sites (Corner, 1965; Laman & Weiblen, 1999) suggesting large scale habitat associations. However, how soil and topography can affect the distributions of plants that start life in the canopy of a tree is not immediately obvious, and there was no significant correlation in any of the species between aerial-root d.b.h and soil-type or slope angle, indicating there was no evidence that these parameters affected the growth or survival of the rooted phase. Moreover, finding a rooted hemi-epiphyte that has died standing is extremely rare (R. D. Harrison, pers. observ.), suggesting mortality is low. Hence, at a large

scale uneven distributions may simply be stochastic, reinforced by subsequent differences in seed production, while at a local scale may correlate with other factors, such as higher light environments on steeper slopes.

HEMI-EPIPHYTIC FIG GUILDS

We were able to identify five guilds among the 11 species examined (Fig. 2A). The first three, with three members each, corresponded to the main canopy strata, while the other two guilds reflected the idiosyncratic characteristics of their single member. *Ficus pisocarpa* was essentially a canopy guild species that was found in lower light environments, while *F. palungensis* with its vine-like growth form was an unusual species found low in the canopy. Superimposing other fig attributes on these groupings is revealing in what it teaches us about the hemi-epiphytic niche.

Of these species, densities were lowest for those on emergent hosts and highest in the subcanopy, but the occupancy rate of emergent hosts was highest (Table 2). Thus, although species on emergent hosts were rarer overall, reflecting the lower densities of such large trees, they appeared to be more efficient at reaching their hosts. The fruits of these species are also larger (*c.* 30 mm long) than those of subcanopy species (≤15 mm long), and are fed on by a guild of specialist long-range dispersers, particularly hornbills (Shanahan & Compton, 2001).

Subcanopy hemi-epiphytic figs had smaller maximum canopy areas than figs on canopy or emergent hosts, as one might intuitively expect. Trees in the subcanopy usually have a narrow, monopodal crown as they exploit small gaps in the canopy and high levels of lateral light, and lower light levels may also be expected to limit growth in these species. However, the ability to colonize a greater variety of positions on a host presumably increases the chance of seedlings establishing.

WHAT FACTORS INFLUENCE THE DISTRIBUTION OF HEMI-EPIPHYTES WITHIN THE CANOPY?

Seed rain appears to be a major limiting factor in hemi-epiphytic fig recruitment, so we might expect factors which attract seed dispersers to have a strong influence on the distribution of individuals, and associations may also exist between hosts and ants that predate on the seeds or young seedlings (Roberts & Heithaus, 1986; Laman, 1996b). In southern India, Patel (1996) found a positive association between figs and animal dispersed hosts, and in this study *Arteocarpus* spp. (Moraceae) and *Whiteodendron moutlonianum* – animal dispersed, subcanopy to canopy species – were relatively common hosts. We also found some figs in mixed-species clumps, suggesting that the proximity of one fig increases the probability that seeds from others will be scattered nearby, and the higher occupancy of emergent trees might reflect the selective use of these as perches by hornbills. However, with respect to species specializing on different canopy strata, the influence of such factors seems unlikely to be important. Hemi-epiphytic fig seeds are scattered very widely with the majority of seeds falling through the canopy to the forest floor (Janzen, 1979a; Laman, 1996a), and Shanahan & Compton (2001) found that the seed dispersers of subcanopy species were also active in the canopy. So the combined effects of gravity and seed dispersers should tend to redistribute hemi-epiphytic fig seeds throughout the vertical structure of the forest.

Another possible factor is the growth of hosts after establishment of their hemi-epiphyte, especially if combined with interspecific differences in the growth rates of aerial-roots. In a survey of rooted individuals, such as this, a species might appear to show preferences for canopy or emergent hosts when in fact their distribution resulted from colonizing fast growing hosts. However, no preferences for host taxa were detected in this study and it is difficult to envisage how species could select hosts according to growth rate. Moreover, if hosts grew substantially following colonization one would expect correlation within species between aerial-root d.b.h and host-d.b.h. Only two species showed such a relationship and neither of these were specialists on large hosts. Hence, it seems unlikely that the growth of hosts after establishment of their hemi-epiphyte has much influence.

Microsite quality has been shown to be important for germination and seedling establishment in at least one species (Laman, 1995) and several other authors have demonstrated its likely importance (Todzia, 1986; Michaloud & Michaloud, 1987; Putz & Holbrook, 1989; Patel, 1996; Athreya, 1999; Doyle, 2000). So it seems probable the habitat preferences of hemi-epiphytic figs revealed here result from the variation in microsite conditions between canopy strata and different environmental requirements for germinate and seedling establishment among species.

WHY STRANGLE YOUR HOST?

Strangling one's host is a drastic measure, involving considerable investment in aerial-roots to convert them from simple conduits to supporting structures capable of holding up not just the fig crown but also the weight of the dead host, until the latter has rotted away. However, judging from its phylogenetic distribution and the variety of ways in which hosts are killed, strangulation appears to have evolved several times. For example, *F. kerkhovenii* usually produces three

massive aerial-roots on different sides of its host, and then a band connecting them immediately below the point of attachment constricts the host. Actual strangulation takes just a few months (R. D. Harrison, pers. observ.). Other species wrap their host in a lattice work of aerial-roots (Laman & Weiblen, 1999), or completely encase them (Daniels & Lawton, 1993), and at least one species relies on splitting rather than strangling (Galil, 1984).

Several authors have suggested that hemi-epiphytes evolved from plants that colonized rocky areas, as an adaptation to escape the dull interior of the forest floor and access high light environments in the canopy (Dobzhansky & Murca-Pires, 1967; Ramirez, 1977; Putz & Holbrook, 1986), and subsequent studies support this view (e.g. Todzia, 1986; Laman, 1995). But access to high light levels from the time they are seedlings, and escaping the need for heavy investment in structural support, is compensated by the difficulties of recruitment. In fact, the attributes of species in the different guilds in this study suggest a fundamental trade-off within the hemi-epiphytic habit: Colonizing positions higher in the canopy, with better light environments and potential to attain a larger size, commits species to relative rarity because of the lower densities of suitable hosts and a requirement for higher quality microsites for seedling establishment.

Moreover, there are penalties for dependence on a host tree. In LHNP all natural mortality of rooted hemi-epiphytic figs (8% per year) under phenological observation was as a result of the host toppling (Harrison, 2001). In fact, it has been suggested that hemi-epiphytes preferentially colonize injured hosts because of the high quality of establishment microsites associated with damage sites and rotting wood (Galil, 1984; Michaloud & Michaloud, 1987; Athreya, 1999). But in this study the majority of hosts did appear to be healthy, and clearly hemi-epiphytes that colonize healthy hosts should have a longer life-expectancy. Indeed, comparable to the concept of reduced virulence in parasites, the growth of hemi-epiphytes must be constrained by the need to ensure the continued vitality of their hosts. Hemi-epiphytes tend to be small relative to their hosts and, crucially, they must avoid over-shading of the host's crown. All the hemi-epiphytic species in this study colonized positions at, or close to, the base of their host's crown, and thereby were at least partly shaded by it, but only four species showed evidence of improving their crown light environment through growth (Table 8). *Ficus subgelderii* and *F. xylophylla* grew out sideways beyond the cover of their hosts, while *F. binnendykii* grew upwards and eventually emerged above the host's canopy, but the crown of this species was always very small. And, *F. kerkhovenii* strangled their hosts.

Ficus kerkhovenii colonized subcanopy to canopy hosts, but showed a preference for larger individuals in its host range. It had the highest crown light environment and achieved the largest maximum canopy area of the species in this study. It was also one of the more common species. Thus, strangling one's host appears to release a species from many of the constraints of the hemi-epiphytic habit.

CONCLUSIONS

This study has demonstrated substantial differences in the habitat preferences (Bazzaz, 1991) of hemi-epiphytic figs in the canopy of a tropical rain forest, and elucidated the factors likely to be responsible for these patterns. Tropical forests are typified by large numbers of rare species, and proponents variously expound niche specialization driven by high levels of competition (e.g. Ashton, 1988) or stochastic processes with large numbers of ecologically equivalent species (e.g. Hubbell & Foster, 1986) to explain this high diversity. However, the diverse community of hemi-epiphytic figs at LHNP would appear to be an example where low levels of competition and specialized niches exist together. The canopy is an extremely complex environment, over-stretching the ecological plasticity of any one species, and, combined with a severe weeding-out imposed by the difficulties of recruitment, appears to restrict species to certain viable niches within a multifarious hemi-epiphytic habit.

From a physiological point of view hemi-epiphytes are a fascinating group of plants (Putz & Holbrook, 1986) and, with the ecological diversity demonstrated in this study, are a topic ripe for further investigation. In particular, the patterns shown here need to be studied with respect to the germination requirements, seedling establishment and early growth of different species. Apart from its intrinsic value, such knowledge would benefit wildlife conservation given the importance of figs in the diets of many vertebrates. Fig populations could be artificially enhanced to help compensate for the small size of many reserves and in urban environments, where figs are often planted, a greater diversity of species, particular of those species with larger fruit, could be cultivated to feed a wider community of frugivores.

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