Colonisation and diversity of epiphytic orchids on trees in disturbed and undisturbed forests in the Asian tropics

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ABSTRACT. Orchids are the most diverse group of epiphytes with more than two thirds of all their species being epiphytic, yet they are comparatively little studied. Colonisation, diversity and distribution of epiphytic orchids and their phorophytes (supporting trees) at 72 sites in disturbed and undisturbed natural forests of south-eastern Bangladesh were studied within a 21,070 km^2 area. No evidence of phorophyte specificity was found, but some phorophyte species were preferred. Most phorophytes (76%) bore only a single species of orchid in one clump. Both orchid and phorophyte species were diverse but 30% of epiphytic orchid species were restricted to a single tree. Larger trees and trees in richer orchid areas accumulated more orchids. Colonisation by an epiphytic orchid is a rare and random event, the presence of one orchid neither attracting nor repelling others on the same phorophyte. The data suggest that the frequency of colonisation by epiphytic orchids is primarily a function of the age of the phorophyte (with greater age allowing both more time and more surfaces to accumulate seeds on them) and the existing orchid richness of an area (allowing for a higher colonisation rate from local seed input). Selective logging of the oldest trees in an area would therefore cause a decline in epiphytic orchid abundance and further loss in orchid richness of the area.

Keywords. Colonisation, diversity, epiphytes, orchids, tropical forests

Introduction

It has been estimated that 24,000 or more vascular plant species are epiphytes (Kress 1986). Epiphytes predominantly occur in tropical and subtropical regions (Benzing 1986). According to Huda et al. (1999), there are 106 epiphytic and 56 terrestrial orchids in Bangladesh and later on, it was estimated 116 epiphytic, 60 terrestrial, one saprophytic and one amphibious species of orchid were found (Huda 2007). Orchids are the most diverse group of epiphytes, about 70% of their species being epiphytic (Gentry & Dodson 1987, Gravendeel et al. 2004).

The availability of suitable phorophytes (supporting trees) is believed to have a strong influence on orchid distribution (Withner 1974). Orchid populations are generally small and composed of scattered or clustered individuals (Ackerman 1986). The numbers of orchids based on the number of different clumps on phorophytes have been studied by Johansson (1974) and Catling et al. (1986) but they did not consider the size of the clump or the height at which they grew. Phorophyte age and area available for colonisation may also affect epiphyte abundance and community composition (Catling et al. 1986). Moreover, phorophyte architecture such as canopy structure, branching pattern, leaf size, etc., may have strong influences on the germination and establishment of epiphytes (Benzing 1986). More recently, Werneck & Espirito-Santo (2002) and Garcia-Suarez et al. (2003) studied the structure, distribution and abundance of vascular epiphytes at different heights and in relation to the 'diameter at breast height' (dbh) of the phorophyte. However, the height of epiphytic orchids on phorophytes may be an important factor related to pollinator visitation. Some publications have specifically studied the richness and distribution of epiphytic species (Madison 1977, Cardelus et al. 2006) but while these studies include some orchids, to our knowledge, no recent detailed studies of epiphytic orchids have been reported. Several other researchers have included some orchids in general studies of epiphytes (Lebrun 1937, Johansson 1974, Catling et al. 1986, Michaloud & Michaloud-Pelletier 1987, Benzing 1990, Bogh 1992, Zimmerman & Olmsted 1992, Tremblay et al. 2006). Among the most detailed studies of epiphytic orchids are those of Went (1940), Hosokawa (1957) and Johansson (1974) in the forests of Indonesia, Micronesia and West Africa, respectively. The distribution, colonisation and association of epiphytic orchids in Belize were studied by Catling et al. (1986), and orchid-phorophyte relationships in a forest watershed in Puerto Rico were studied by Migenis & Ackerman (1993).

The aims of the present work were to detail the diversity and distribution of epiphytic orchids over a wider geographical area in both disturbed and undisturbed natural forests and to determine their colonisation pattern and the diversity of phorophytes.

Materials and methods

Study sites

The study area extends over 21,070 sq. km and a general field survey was conducted in 72 different sites of Chittagong, Cox's Bazar, Rangamati, Bandarban and Khagrachari districts of south-east Bangladesh. Occurrences on roadside trees were excluded in this study. Three different forest types were also specially studied. One of the forests (Sitapahar reserve forest in Rangamati district) was a natural mixed-species forest, while the others have been replanted after logging. Dariardighi in Cox's Bazar district was planted in the 1940s and Perachar in Khagrachari district was planted in the 1980s; both these sites also had some residual mature trees from before the last logging. In both forests, trees were being logged since the last replanting.

Methods

Epiphytic orchid diversity and frequency of occurrence were generally studied in 72 sites, as well as three different one-hectare quadrats in south-east Bangladesh. Epiphytic orchid species were recorded from orchid-bearing trees at all sites. The studied sites were selected on the basis of the number of reserved forests and relatively undisturbed vegetation units in the respective districts, which resulted in uneven sample sizes. Both big areas with less studied sites (e.g., Bandarban) and smaller areas with more studied sites (e.g., Cox's Bazar) were included.

Access to tree crowns was achieved with a ladder or by climbing the trees with help of local tree climbers. Inaccessible branches were also examined with the help of binoculars. Specimens of all orchid species were collected from the study areas during fieldwork. Collected specimens were identified by consulting the literature and known specimens available at K, E and ABD. Due to difficulties in determining sterile specimens, small samples were taken from each and grown in the Orchidarium of Chittagong University until flowering. Voucher specimens of all species were deposited in the Herbarium of Chittagong University (HCU). The epiphytic orchid-bearing phorophytes (supporting trees) were identified in the field and specimens of unidentified phorophyte trees were collected for later identification.
The epiphytic orchid diversity index for a particular area was calculated by using the following formula, following the IUCN/SSC Orchid Specialist Group (1996):

$$\text{Orchid diversity index} = \frac{\text{Total number of orchid species}}{\text{Total area (sq. km)}} \times 1000$$

Numbers of clumps / individual phorophyte and clump sizes of epiphytic orchids were recorded in the field. Due to the irregular structure and size of the different orchids, clumps were also divided into three groups, 1) small clumps of 1–5 pseudobulbs or stem shoots, 2) medium clumps of 6–20 pseudobulbs or stem shoots, and 3) large clumps of more than 20 pseudobulbs or stem shoots (Huda 2000). Even very large 1–2 m spreading clumps were considered as a single large clump when all parts remained connected.

The clump height on the phorophyte tree above the forest floor and diameter at breast height (dbh) were also recorded for each individual phorophyte. Clump height of orchids was measured by using a clinometer. The lower portion of the clump was considered in measuring the height. In hilly areas, metre-graduated bamboo sticks were used to measure height above the ground. The dbh was measured using diameter tape.

In the three one-hectare quadrats, all trees >5 m tall were sampled. Within each quadrat, all trees and orchid species were identified either in the field or in the laboratory. The number of clumps / individual phorophyte, clump size, height of orchid clumps above the ground and dbh for trees within the quadrats were also recorded from all three forest areas.

Analyses

Statistical analyses including the χ^2 test, Yates correction, Poisson distribution, t-test, correlation and ANOVA by Post hoc test (LSD and Tukey test) were performed with Microsoft Excel and SPSS version 13.

Results

Distribution of epiphytic orchids

A total of 41 different epiphytic orchid species were recorded from the 72 sites. The scientific name authorities of orchids are given in Fig. 1, those of phorophyte tree species in Fig. 3. The distribution of the study sites, the total number of different epiphytic orchids encountered, and the orchid diversity index of each district are presented in Table 1. In spite of uneven sample sizes, Cox's Bazar was the richest area for epiphytic orchids with the highest diversity index and was much more diverse than the average for the whole region; whereas Khagrachari (a slightly bigger district with a similar number of sites studied) was the poorest area with the lowest diversity index. This may give some indication that the richness sampled has not been unduly influenced by area or number of study sites.

Orchid diversity and colonisation

The 41 orchid species were found on a total of 287 trees in the 72 studied sites. Most orchid species are infrequent in their occurrence on phorophytes. *Aerides odoratum, Cymbidium aloifolium* and *Bulbophyllum lilacinum* were the most frequently encountered on 66, 59 and 39 phorophytes, respectively, and 12 orchid species were found to be present on only one individual phorophyte (Fig. 1). Only 8% of the orchid species were found on less than 10 phorophyte trees. Among them, *Aerides odoratum* and *Cymbidium aloifolium,* are the commonly occurring species.

The distribution of number of epiphytic orchid clumps per tree among the phorophyte trees is illustrated in Fig. 2. Most phorophytes bore only a single orchid

Table 1. Total number of epiphytic orchid species found to occur in the 72 studied sites in 5 different districts of south east Bangladesh. The epiphytic orchid diversity index was calculated according to the IUCN/SSC Orchid Specialist Group (1996).

Parameters	District name					Total
	Chittagong	Cox's Bazar	Rangamati	Bandarban	Khagrachari	
Total no. of orchid species	22	26	17	16	07	41
Total area (sq. km)	5283	2492	6116	4479	2700	21070
No. of sites studied	14	13	22	11	12	72
Epiphytic orchid diversity index	4.16	10.43	2.78	3.57	2.59	3.42

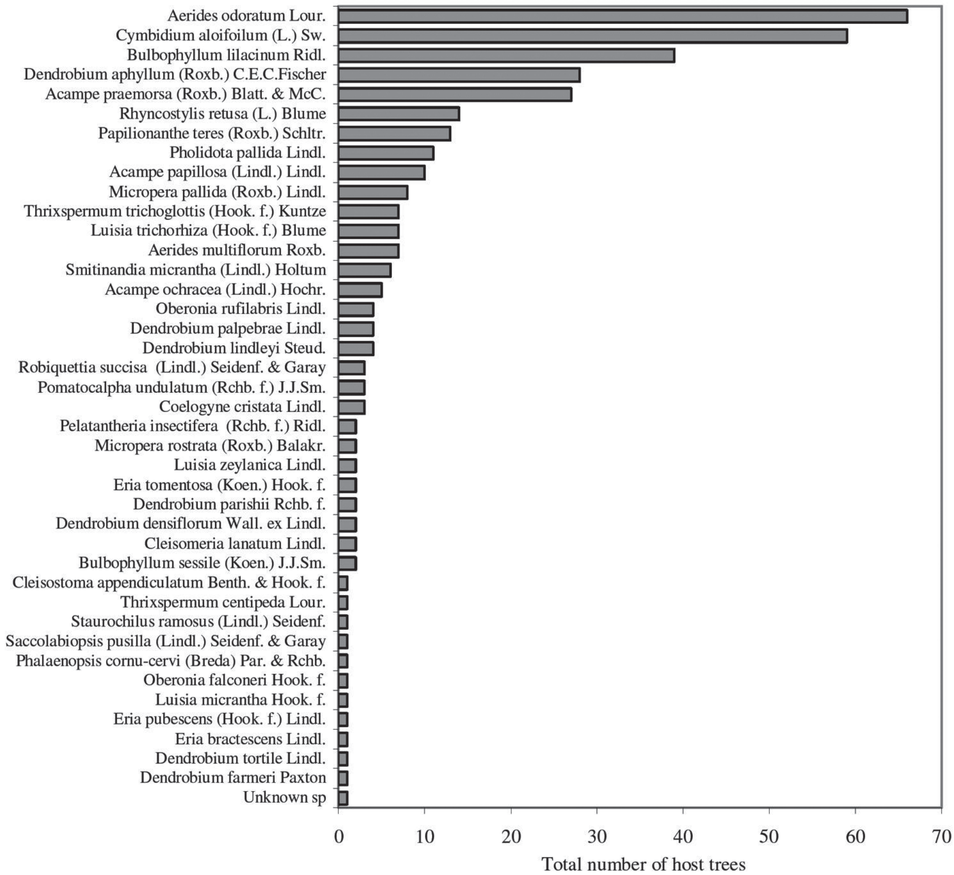

Fig. 1. Number of phorophyte trees associated with the different epiphytic orchid species.

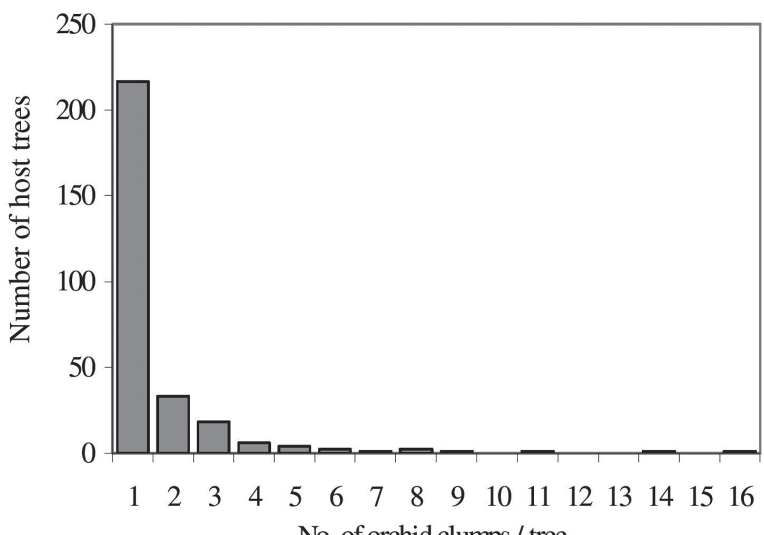

Fig. 2. Distribution of number of epiphytic orchid clumps per tree among the phorophyte trees.

clump. Only seven trees had more than seven clumps, and the maximum number of clumps recorded on a single phorophyte was 16.

Phorophyte diversity

A wide diversity of phorophyte species were colonised by epiphytic orchids. Both native (51 species) and exotic (6 species) phorophyte trees were recorded and phorophytes can be either evergreen (35 species) or deciduous (15 species) or semi-evergreen (5 species) but orchid density on evergreen phorophyte species was greater than deciduous (t=2.12, df=16, P=0.008 for quadrats, and t=2.01, df=48, P=0.05 for 72 sites). Orchids were found on 287 phorophytes of 57 different species (Fig. 3). A total of 30 different phorophyte species were recorded only once. The most frequently encountered phorophytes were *Mangifera indica* (49 trees) followed by *Artocarpus heterophyllus, Syzygium grandis, Tectona grandis* and *Lagerstroemia speciosa*.

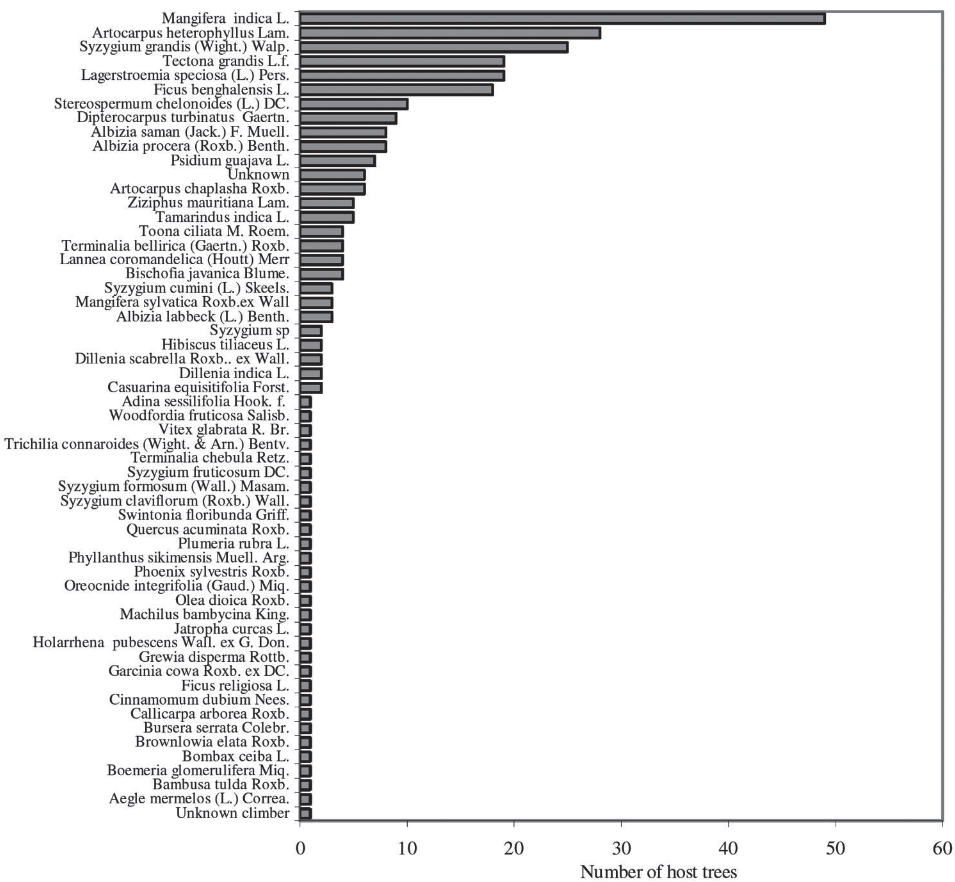

Fig. 3. Number of orchid-bearing trees per phorophyte tree species, ranked by abundance.

Orchid colonisation and phorophyte specificity

Number of orchid species and phorophyte tree density were positively correlated (r=0.902, df=55, P<0.001). A scatter plot of this data with 99% confidence intervals showed that the diversity of epiphytic orchids on the majority of phorophyte species was within expectation of the frequency of occurrence of the phorophyte (Fig. 4). Three native species *Syzygium cumini, Stereospermum cheolonoides* and *Syzygium grandis* had a wider diversity of orchids on them than expected indicating heterogeneity. No phorophyte species had lower levels of heterogeneity indicating an absence of phorophyte specificity. There was no indication of a levelling off in the relationship between phorophyte tree density and orchid diversity, indicating that saturation point had not been reached.

Colonisation pattern

The total number of orchid clumps recorded on an individual phorophyte species was correlated with the number of phorophytes of that species (r=0.944, df=55, P<0.001). Two phorophyte species, *Albizia procera* and *Albizia saman* supported more clumps than expected (Fig. 5) indicating increased suitability as phorophytes. The greatest number of clumps was recorded on *Mangifera indica.*

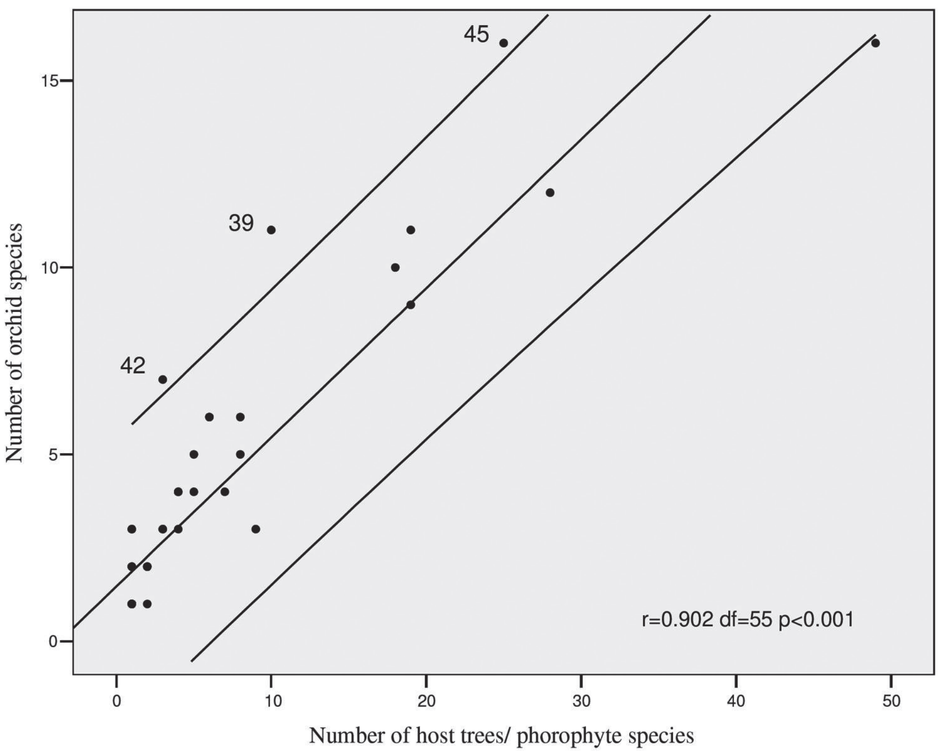

Fig. 4. The relationship between number of orchid species and phorophyte tree density. The regression line is fitted with 99% confidence intervals; 39: *Stereospermum chelonoides,* 42: *Syzygium cumini*, 45: *Syzygium grandis*.

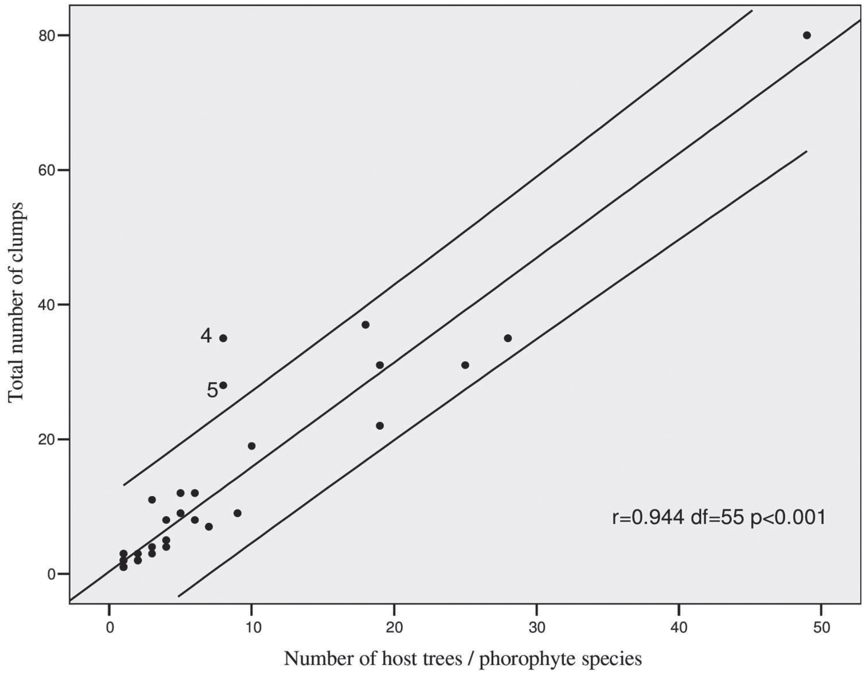

Fig. 5. The relationship between total number of epiphytic orchid clumps found and phorophyte tree density. The regression line is fitted with 99% confidence intervals; 4: *Albizia procera*, 5: *Albizia saman*.

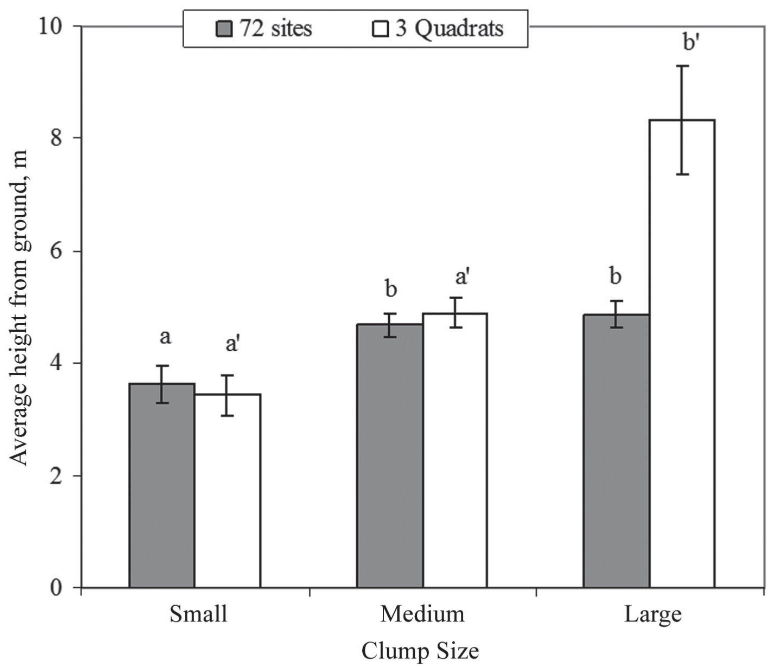

Fig. 6. Relative distribution of small, medium and large orchid clumps at different heights from the ground (mean+ SE).

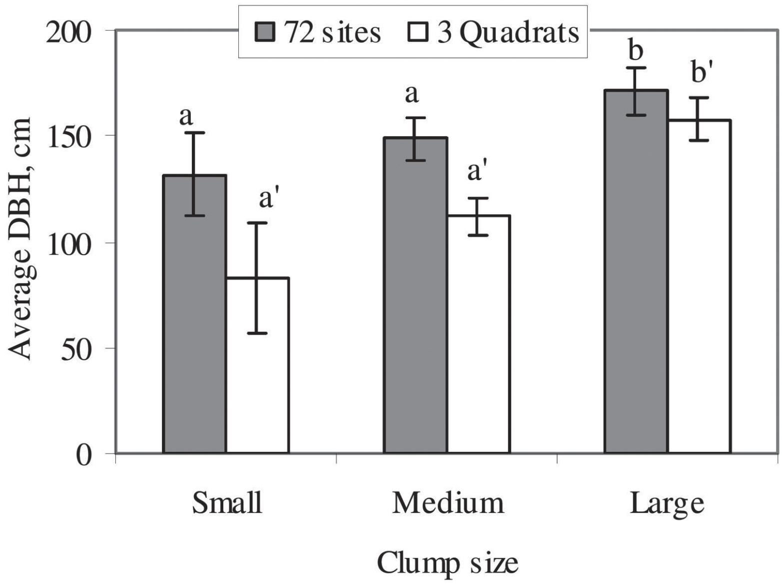

Fig. 7. Relative distribution of small, medium and large orchid clumps on phorophyte trees of different dbh sizes (Mean+SE).

The average height of occurrence of orchid clumps of different sizes is shown in Fig. 6. Small clumps are found at lower heights than medium or large clumps of epiphytic orchids (F=5.637, df=314, P=0.004; LSD and Tukey test showed significant differences between small and medium + large) in the 72 sites, and also at lower heights in the forest quadrats compared with large clumps (F=8.353, df= 41, P=0.001; LSD and Tukey test showed significant differences between large and small + medium clumps).

Clump sizes and average dbh of phorophytes were not significantly different among the 72 sites (F=2.143, df= 226, P=0.12) but in the forest quadrats the dbh of trees with large clumps was significantly higher than those for smaller and medium clumps (F=8.389, df=38, P=0.001; LSD and Tukey test showed difference between large and small; Fig. 7).

Colonisation of orchids in disturbed and undisturbed forest quadrats

Colonisation of trees by epiphytic orchids, phorophyte characteristics and area orchid diversity for the three forest quadrats were studied. A test of association between orchid presence on phorophytes and forest quadrats showed that orchids occur more frequently on trees in the quadrat sited in the more orchid-rich district than those from a quadrat in an area of lower orchid diversity index (χ^2 =11.43, df=2, P=0.003; Fig. 8).

Within the forest quadrats, average dbh was associated with orchid occurrence (3×2 contingency table for large, medium and small dbh of trees with orchid presence, χ^2=6.04, df=2, P=0.049). There was an association between clump size (large, medium and small) and forest quadrats (χ^2 =7.41 df=2, P=0.0246) indicating that more large clumps were found on trees at Sitapahar than expected (Fig. 9).

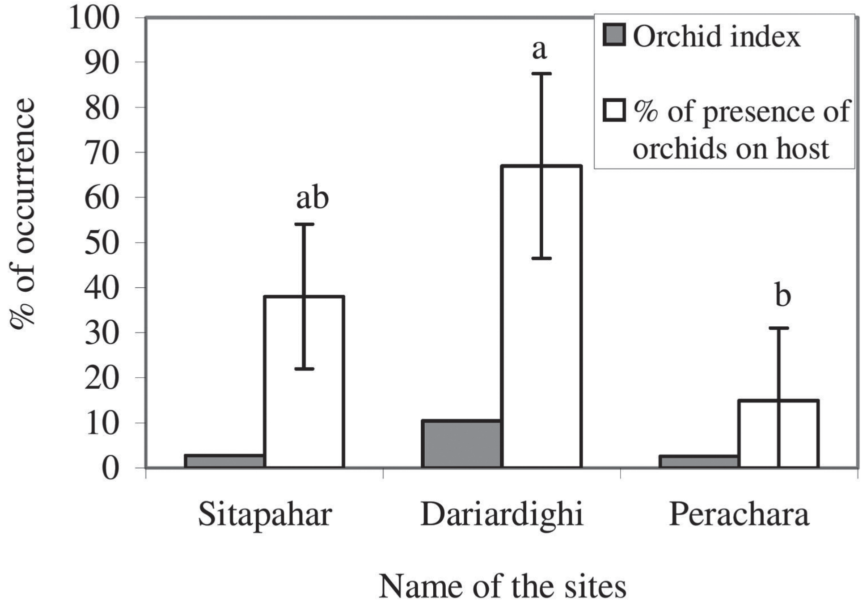

Fig. 8. The orchid diversity index and relative commonness of orchids on phorophyte trees, compared for the three 1-ha quadrat study sites; the latter with 95% confidence intervals shown.

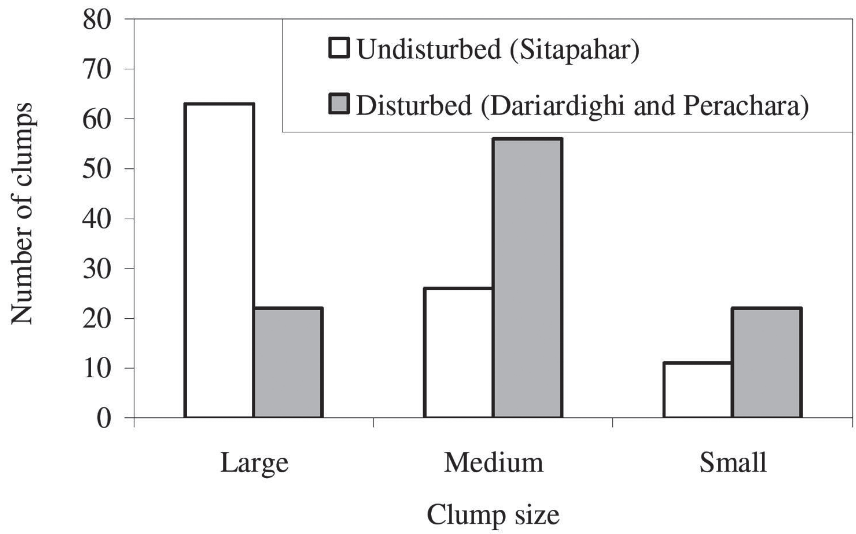

Fig. 9. Clump sizes of epiphytic orchids in the two different forest types.

Orchid colonisation in each of the forest quadrats follows the Poisson distribution (Table 2) indicating that Orchid colonisation is a rare and random event and one epiphytic orchid species does not attract or repel others on that phorophyte.

Table 2. Distribution of orchid clumps on trees above 5 m in height in 3 hectare forest quadrats and the χ^2 values obtained from a test of goodness of fit to values based on a Poisson distribution.

Places	Trees with no orchids	1 clump	2 clump	3 clump	4 clump	χ^2 values	df	P -values
Sitapahar	22	10	3	1	0	0.22	2	0.9
Dariardighi	7	10	3	0	1	1.09	3	0.78
Perachara	17	3	0	0	0	0.02	1	0.89
Total	46	23	6	3	1	0.47	3	0.93

Discussion

Epiphytic orchid diversity and distribution on phorophytes

The total number of epiphytic orchid species recorded during this project accounted for 39% of the total epiphytic orchid flora of Bangladesh. But considering the size of the study area (15% of Bangladesh), the epiphytic orchid species diversity of south-east Bangladesh is therefore reasonably diverse. In India, 14 epiphytic orchid species have been recorded from a tropical evergreen forest at Varagalaiar, Western Ghats (Annaselvam & Parthasarathy, 2001) and 26 species from a moist lowland forest of Eastern Himalaya (Padmawanthe et al. 2004). A total of 101 epiphytic orchid species were recorded from West Africa rain forest (Johansson 1974), 41 epiphytic orchid species from South Africa (Harrison 1972), 11 from a forest watershed of Puerto Rico (Migenis & Ackerman 1993), 232 from West Tropical Africa (Hepper 1968) and 414 from Zaire (Nihoul et al. 1969). The epiphytic orchid species diversity in south-east Bangladesh therefore appears to be only moderately rich in comparison with these other forest areas.

Orchids were found infrequently on trees throughout the 72 sites with the majority of species present in only one clump per phorophyte. A maximum of 16 clumps was found on an old tree of *Ficus benghalensis*. Thirty-six of the 41 epiphytic orchid species were found on less than 14 phorophytes. Epiphytic orchid occurrences on trees in south-east Bangladesh are therefore infrequent or rare and most do not form tree populations of more than one clump.

Phorophyte diversity

Most studies of epiphytes have concentrated on the epiphytes themselves and not on the phorophytes that support them. We have documented all the phorophytes for the epiphytic orchids in this study, together with a record of some of their characteristics. The 41 species of epiphytic orchids were found on 57 different phorophyte species of wide taxonomic diversity. The epiphytic orchids were found on both shrubby and small trees as well as very large trees, bamboos and date palms. The two most frequently encountered phorophytes were *Mangifera indica* (Mango) and *Artocarpus* *heterophyllus* (Jackfruit) and we found 16 and 12 different species of orchids on them, respectively. These phorophytes are very common, especially near to forest villages, as tree poachers do not cut these fruit-bearing trees.

Most of the epiphytic orchids were found on evergreen rather than deciduous tree species. However, further examination of this discrepancy in the forest quadrat showed no association between leaf persistency and orchid presence on the trees, indicating that there is no preference for one type of tree. Nevertheless epiphytic orchid density was greater in evergreen species than in deciduous ones, indicating that leaf persistence may influence secondary colonisation. This might result from the continuous presence of moisture throughout the year promoting seedling growth and/or shade effects, which maintain the growth environment and microclimate. Large openings in the canopy have been shown to reduce the abundance, distribution and diversity of shade-requiring epiphytes (Hietz 1999). Conversely, Annaselvam & Parthasarathy (2001) found that epiphyte density was greater on deciduous species in India than on evergreens. Architecture may play a critical role in determining phorophyte suitability (Migenis & Ackerman 1993).

Most individual phorophytes bore only one epiphytic orchid species on them. This agrees with Annaselvam & Parthasarathy (2001) who showed that most phorophytes supported only a single epiphyte on them. Benavides et al. (2005) found one phorophyte carried an average of 2.2 epiphytic individuals and 1.8 epiphytic species in the rain forests of Colombian Amazonia.

Phorophyte specificity and heterogeneity

No phorophyte specificity was found in the present study. Increase in the number of phorophytes of a single species was correlated with numbers of native species and exotic trees in line with expectation. Further, low levels of occurrence of epiphytic orchid species per native phorophyte supported the lack of specificity. Although *Thrixspermum trichoglottis* occurred most frequently on an exotic, *Psidium guajava,* this species also occurred on three native species. Orchids also showed no phorophyte specificity in the Bisley watershed (Migenis & Ackerman 1993). However, epiphytes often exhibit a certain degree of phorophyte preference, often on trees shared by co-occurring epiphytes, indicating the suitability of a tree for epiphyte colonisation (Benzing 1990). Phorophytic preference is also a common phenomenon in Puerto Rico and elsewhere in the Neotropics, but specificity is not common (Ackerman et al. 1989, Allen 1959, Zimmerman & Olmsted 1992). Phorophyte specificity has been shown, or at least surmised, for some Indonesian, Philippine and Puerto Rican orchids (Went 1940, Sanford 1974, Tremblay et al. 1998) but as in many other tropical forests (Johansson 1974, Todzia 1986, Zimmerman & Olmsted 1992) there was no evidence of phorophyte specificity exhibited by orchids in the present study.

There was also no indication of a levelling off of the relationship between phorophyte frequency and orchid diversity, suggesting that no species saturation had been reached. The total number of orchid clumps found on most phorophyte species increased with more records of the host in line with expectation. Two species of *Albizia procera* and *Albizia saman* supported more clumps than expected, indicating some preference for, or ease of, colonisation. These results are similar to those of Zimmerman & Olmsted (1992) who showed that commoner phorophytes bore more epiphytic species.

Colonisation pattern

Our data show that large clumps were found at greater height on the phorophytes, which might be expected as orchids age and increase in clump size with the growing tree. However, it might indicate habitat preferences for different epiphytic orchids within the phorophyte. No similar data directly match our findings due to lack of previous work on epiphyte clump size. Werneck & Espirito-Santo (2002) reported a higher abundance of epiphytes at intermediate heights on the phorophytes, but different epiphytic species showed very contrasting vertical distributions. Benavides et al. (2005) reported that epiphytic diversity was highest in the branches of crowns and lowest on the stem bases.

Werneck & Espirito-Santo (2002) found that epiphytic species differed significantly in their distribution along branch diameters of the phorophyte and our data showed that larger clumps were found more frequently on trees with larger dbh in the forest quadrats. Orchids tend to be restricted to larger phorophytes because of their preference for larger diameter supports (Zimmerman & Olmsted 1992). Prosperi (1998) also found a highly significant positive correlation between the rate of colonisation and host diameter above 50 cm, and according to Flores-Palacios & Garcia-Franco (2006) epiphytic communities are unsaturated, as the number of species increases with tree size and do not reach a ceiling in Guyana.

Colonisation of orchids in disturbed and undisturbed forests

Our data illustrate that forests in areas of richer epiphytic orchid diversity can have higher colonisation rates (even though disturbed) than forests in orchid-poor areas, even when undisturbed. This suggests that epiphytic orchid-rich areas therefore provide potential recruitment for all types of forests within that zone. However, our data suggest that throughout all forest types orchid colonisation is a random and rare event, with no attraction or repulsion shown by the presence of a single clump on a tree. Larger trees within the forests accumulate more epiphytic orchids and more large clumps, and undisturbed forests also have larger clumps. Our data suggest that logging of the most mature trees in a forest selectively modify the epiphytic orchid flora by combining the decimation of both the largest clumps of orchids, and the trees with the greatest colonisation, which may have accumulated over many years of growth.

The occurrence of epiphytic orchids tends to be biased towards the larger phorophytes, a pattern to be expected if large trees are more likely to accumulate epiphytes, as a result of increased branch area or increased time available for epiphytic colonisation (Zimmerman & Olmsted 1992). The rate of illegal felling of large trees has probably already drastically affected the epiphytic orchid flora.

The data presented here show that the diversity of epiphytic orchids is now based on a fragile phorophyte system because most orchids occur only singly on a tree. In addition, a large number of epiphytic orchid species have been found only once (30%). So, careful management is essential to conserve the larger phorophytes as well as the epiphytic orchids, otherwise one third of all the epiphytic orchids will experience severe decline.

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