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DISTRIBUTION OF EPIPHYTES ON TRUNKS OF THE ARBORESCENT FERN, *BLECHNUM PALMIFORME,* AT GOUGH ISLAND, SOUTH ATLANTIC

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ABSTRACT. A total of 25 species of epiphyte was recorded from trunks of the arborescent fern, *Blechnum palmiforme,* on Gough Island; many of these also occurred on other hosts and/or on the ground. Number of species of epiphytes was positively correlated with trunk height, whereas their total percentage cover showed no such relation. There were no significant vertical or radial differences in size of patch for any of the species abundant enough to be tested. Ferns were the dominant group; bryophytes and lichens also were important, but angiosperms were of minor significance. Frequencies of trunks occupied differed with trunk height for many species, but did not differ radially.

Microdistributional patterns included (a) species characteristic of the bottom of the trunk, (b) those found primarily near the top, and (c) those more uniformly distributed; some species favored certain sides of the trunk over others. Patterns of individual species variously canceled or enhanced each other and collective total cover of some larger taxa maintained significant vertical (bryophytes) or radial (ferns) differences; lichens as a group tended to be sparsely but uniformly distributed.

Distributional patterns of organisms, on whatever scale, usually form a complex kaleidoscope reflecting the interaction of many separate environmental influences. Individual species respond differently to the various components of the environmental milieu and different geometries result. These, in turn, may be modified by biotic interaction with other species. Community structure may vary with spatial alterations in either the number and kinds of component species, or variation in the representation of particular ones. For example, a given density of vegetation may result from a lush growth of one species, an accumulation of many sparse ones, or various intermediate combinations. Like other plants, epiphytes exhibit these distributional complexities (see review, Chapters 7, 8, in Benzing 1990).

One of the problems in analyzing distributions is that on a broad scale, there are few replications with the same history and pool of available species. On the microdistributional level, however, greater replication is possible, but often those replicates provide limited vertical or horizontal scope, or they contain few species.

The present study analyzes the distributional patterns in the assemblage of epiphytes on the trunks of the arborescent fern, *Blechnum palmiforme* (Thouars) C. Char. on Gough Island, South Atlantic. This system has two advantages: (1) Many of the host ferns were similar in size (and presumably age); thus temporal, successional, and host-size differences were minimized. Each individual fern was a replicate of the epiphytes' environment, including a vertical component (with its attendant gradients in light, temperature and moisture) and an exposure component (different quadrants of the trunk). (2) There was a rich epiphytic flora, including lichens, bryophytes, ferns and angiosperms. Many previous studies of species-rich epiphytic assemblages have been conducted in tropical or subtropical regions (Benzing 1990). The present one provides a valuable comparison with a cool temperate/sub-Antarctic flora, the first of its kind analyzed in detail.

STUDY AREA

Gough Island is a volcanic island rising 910 m above the southern Atlantic Ocean at 40°19′19″S latitude and 09°53′42″W longitude (Roux 1981). Tristan da Cunha and its satellite islands of Nightingale and Inaccessible lie 370 km to the north-northwest. Otherwise the nearest land is southern Africa about 2,800 km away; Antarctica and South America both are more than 3,000 km distant.

Although the island is technically in the sub-Antarctic zone, its climate approaches maritime, cool, wet temperate, with a mean annual rainfall of 3,225 mm at the coast, increasing at higher elevations (Holdgate 1960). Mean monthly temperatures on the coast are between 10°C and 15°C year-round (extremes 1°–24°C) with lower temperatures and seasonal snow at higher elevations.

The vegetation is essentially temperate (Wace 1960), but with some sub-Antarctic elements (Roux 1981). It is zoned altitudinally. Beginning at the sea, Tussock Grassland gives way interiorly to Fern Bush and thickets of the composite tree, *Phylica arborea* Thouars. These are replaced at successively higher elevations by Wet Heath and Peat Bogs, Moorland, Feldmark and Montane Rock communities (Wace 1961). The

FIGURE 1. The study site, a fern savannah of *Blechnum palmiforme* (upper) and a fern showing epiphytes on its trunk (lower).

present report treats only the Fern Bush habitat.

The study site was an open savannah of the arborescent fern, *Blechnum palmiforme*. Some trunks were procumbent for part of their length and partly buried in peat, but most were vertical with ascendant trunks up to 1.6 m tall (FIGURE 1). The savannah was located immediately inland from the South African weather station at

Gonçalo Alvarez on the eastern coast. It was sheltered from the sea wind by a belt of *Phylica arborea*. Ground vegetation of the sampled stand consisted of a nearly continuous layer, primarily of the ferns *Elaphoglossum succisifolium* (Thouars) Moore and *Asplenium obtusatum* Forst. f., various herbs, and scattered hummocks of sedges. Wace (1961) studied the vegetation of three *Blechnum* stands at various localities and elevations and noted differences in trunk height and cover, and composition of the ground layer.

Materials and Methods

The epiphytic flora on the trunks of the ferns was sampled at three levels, (1) an upper level 10 cm below the base of the fronds, (2) a basal level 10 cm above the ground and (3) a central level half way between the upper and basal ones. The last was omitted if the distance between upper and basal levels was less than 20 cm.

At each level a string was wrapped around the trunk, then divided into four quadrants, northeast (NE), northwest (NW), southwest (SW), and southeast (SE). The lengths of the string intersecting each species of epiphyte or bare trunk, was measured and totaled for each quadrant and then expressed as percentage cover. Live and dead epiphytes were tallied separately. Epiphyllic plants on the leaves of epiphytes were not recorded. After sampling was completed for a particular fern, its height was measured and its trunk examined; any epiphtyic species present but which did not occur in the line transects were recorded.

Field work was conducted in September 1986. Beginning at the point where a pre-existing path first reached the savannah, all ferns were systematically sampled as the investigator proceeded through the study area; sampling was continued on each day weather was favorable from the initiation of the project until the expedition ended. The only selectivity exercised was that procumbent trunks and trunks that were in contact with other trunks and not amenable for individual sampling were ignored; only six such ferns were bypassed and 37 were sampled. On the last day, a large number of unsampled ferns was searched for epiphytes.

Frequency and cover were analyzed separately and by methods appropriate to each. Frequency was expressed as the number of tree ferns occupied by each species; data were tallied separately by level and by quadrant. First, a 4×2 contingency table, with columns representing the four quadrants and rows representing occurrence (number of ferns with epiphytes and the number of ferns without epiphytes) was set up for the upper level and the null hypothesis of no difference between quadrants tested by a chi-square test. Then the middle level and basal level each were similarly tested individually. Following that, a 3×2 contingency table of level and occurrence was constructed and tested as above (rejection level 0.05%; 13 of 17 significant tests, $P < 0.005$). These tests permitted assessing whether or not for a given quadrant there were differences in frequency of a particular species of epiphyte at different levels, and conversely whether at a particular level there were differences among quadrants. Interaction of level and quadrant was not assessed by this procedure.

Percentage cover values by individual species and total percentage cover for all species were arcsine transformed and analyzed by analysis of variance (ANOVA) using repeated measures (quadrants: NE, NW, SW, SE) within levels (top, center, basal). Only the 28 ferns tall enough to have all three height levels were used. Later, however, the upper level of that group was compared to the upper level of shorter ferns that lacked transects from central and/or basal levels.

Individual measurements of line intercept are related to patch sizes of epiphytes inasmuch as when there are large patches (either large individual plants and/or large groups of conspecific plants in direct contact) intercepts are larger than when patches are smaller. Consequently, length of line intercept was used to assess patch size. Patches that straddled a boundary between quadrants were assigned to the quadrant containing the largest portion of the intercept. A factorial analysis of variance was used to compare patch sizes in different quadrants and at different levels for all species that had at least five patches in each quadrant and level category. Where this was not obtained, comparisons were made between different quadrants separately for each level at which the requirements were fulfilled. Where quadrants could not be compared because some had less than five patches, differences between quadrants were ignored and comparisons made directly between all levels for which there were five or more patches at every level.

Because intercepts do not always go directly through the middle of a patch, they are not accurate indications of absolute size of patches but afford a relative measure only. The term "patch size" is used subsequently to refer to such intercept values.

In the field, different species of hepatics were not distinguished and only when voucher specimens were identified was it realized that individual collections were mixtures of three species rather than composed of only one. Consequently, in the data analyses all three species had to be lumped into the collective term "hepatics" and treated as a single "species" rather than as three. Also, mosses often occurred as very small, sterile

plants and consequently their allocation to species during field measurements should be considered as more tentative than for other taxa.

Results and Discussion

Habitats of Epiphytic Species

The epiphytic habits and microdistribution of some of the species of the present study have been commented upon previously. *Asplenium alvarezense,* the two *Hymenophyllum, Thuidium curvatum, Hypnum elatum* and *Elaphoglossum succisifolium* were listed by Wace (1961) and Wace and Holdgate (1958) as epiphytic on *Blechnum* and/or *Phylica* on Gough Island, and in some cases, Tristan da Cunha. *Hymenophyllum aeruginosum* also was an epiphyte on grass tussocks. The two *Hymenophyllum* were noted to extend to the ground where there were no other understory plants, and the rest of the above species commonly occurred on the ground as well as on trunks. Wace and Holdgate (1958) recorded *Thuidium* growing on the upper trunks of *Blechnum,* just below the older fronds, and on the ground. *Hypnum,* found primarily on the lower parts of *Blechnum* trunks in the present study, also occurs on the lower parts of *Phylica* trunks (Wace 1961). *Brachythecium* cf. *rutabulum,* here tentatively placed as a basal to central epiphyte was noted by Wace (1961) on the ground and as an epiphyte on the lower portion (<1 m) of *Phylica* trees. Ireland (1982) listed its habitat as "bases of trees, humus, rocks and soil over rock in moist shady places." *Leptotheca gaudichaudii* was recorded from the ground layer and as an occasional epiphyte on *Blechnum* by Wace (1961); Magill (1987) gave its habitat as rock. In the present study it occurred as an epiphyte only twice. The lichen *Pseudocyphellaria* sp. was found at mid-trunk level in some quadrants of the present study; on Tristan da Cunha *P. intricata* was found on the bases of the main stems of *Phylica* (Wace & Dickson 1965).

Some of the species found as rare epiphytes in the present study were listed only as ground-layer plants by Wace (1961). These included *Histiopteris incisa, Asplenium obtusatum* and *Acaena.* However, he does mention that *Acaena* "scrambles over the outspread fronds and upper trunk" of *Blechnum.*

Roux (1981) in a review of the ferns of Gough Island, listed seven of the 26 species as epiphytic as well as terrestrial or lithophytic, and of those he specifically mentioned *Hymenophyllum aeruginosum, H. peltatum* and *Asplenium alvarezense* as common on the stems of *Blechnum palmiforme.* He indicated that depauperate forms of *Vittaria vittaroides* (Thouars) C. Chr. was epiphytic on *Blechnum,* but only in a restricted part of the island, away from the location of the present study. He also listed *Blechnum penna-marina* (Poiret) Kuhn as epiphytic on tree fern trunks, as did Wace (1961); it did not occur as such in the present study. All of the epiphytic ferns of the present study were included in Roux's (1981) list of epiphytes except *Asplenium obtusatum* and *Histiopteris incisa,* both of which he considered to be terrestrial.

It is clear that, except possibly for the lichens, the epiphytic flora on *Blechnum* trunks is not one that is restricted to that habitat but rather is a subset assembled from species occupying other sites as well, including terrestrial ones.

Even predominantly epiphytic species, such as the two *Hymenophyllum,* were not restricted to *Blechnum* in their epiphytic habit. The tree *Phylica* also bears a rich epiphytic flora that includes many of the species found on *Blechnum.* In some literature mention is merely made that certain species are epiphytic in fern-bush, a type of vegetation containing both *Phylica* and *Blechnum.* Consequently, it is not always possible to ascertain the extent to which these plants share epiphytic species. The information available, however, suggests that each species has a large proportion of epiphytes exclusive to it. On Tristan da Cunha Wace and Holdgate (1965) listed 14 epiphytes for *Phylica* and nine for *Blechnum.* Only one species, the hepatic *Lepidozia procumbens* was common to both.

On Gough Island, collective lists from Wace (1960, 1961) and Roux (1981) yielded 30 species epiphytic on *Phylica* and 33 as epiphytic or "trunk epiphytes & ground layer" for *Blechnum.* There were only 13 species shared.

The 25 species of epiphyte recorded from *Blechnum* in the present study is probably not a complete list. In particular, there are probably more hepatics. No distinction was made between hepatic species in the field. Vouchers contained three species but more may have been present. Wace and Dickson (1965) stated that a feature of the flora of Tristan da Cunha was the large number of leafy hepatics epiphytic on the trunks of *Blechnum palmiforme* and *Phylica arborea*; in particular, there were 29 species of *Lophocolea,* most of which are epiphytic. Many of the Tristan da Cunha species of hepatics may also occur on Gough, and even allowing for the fact that a number of them may occur only on *Phylica,* or other species, it is likely that further study will expand the list for *Blechnum.*

The epiphytic flora varied with different exposures and elevations (Wace 1961). The combined list of 33 species on *Blechnum* from Wace (1960, 1961) and Roux (1981) included multiple localities and was larger than the list of 25 species found from a single stand of *Blechnum* in the

TABLE 1. Occurrence of epiphytes on trunks of ferns on Gough Island.

	Ferns							Bryophytes							
Tree no.	*Asplenium alvarezense*	*Hymenophyllum peltatum*	*Hymenophyllum aeruginosum*	*Elaphoglossum laurifolium*	*Elaphoglossum succisifolium*	*Asplenium obtusatum*	*Histiopteris incisa*	*Thuidium curvatum*	*Hypnum elatum*	*Brachythecium rutabulum*	Unidentified moss sp. 1	Unidentified moss sp. 2	Unidentified moss sp. 3	*Leptotheca* cf. *gaudichaudii*	Hepatics*
1	+	+	+					+							
2	+	+	+					+	+	+					
3	+	+						+							
4	+	+						+	+						
5	+	+	+	+	+			+							
6	+	+	+	+				+	+						
7	+	+	+	+				+	+				+		
8	+	+		+				+	+	+					
9	+	+		+				+	+	+		+	+		
10	+	+	+					+	+						
11	+	+	+	+				+	+		+				
12	+	+	+	+				+							
13		+	+					+							
14	+	+	+	+				+							
15	+	+		+				+	+						
16	+	+	+	+	+			+	+		+				
17	+	+		+				+	+						
18	+	+	+	+				+	+	+	+				
19	+	+	+	+				+	+	+		+			+
20	+	+	+	+					+	+	+				+
21	+	+	+	+						+	+				+
22	+	+	+	+					+		+			+	+
23	+							+							
24	+	+	+						+	+	+				
25	+							+	+					+	
26	+	+							+	+					
27	+	+	+	+		+			+		+				+
28	+	+							+		+				+
29	+			+	+			+							
30	+	+	+	+				+							
31	+	+						+							
32	+	+	+	+				+	+						
33	+	+													
34	+	+					+	+	+	+					
35	+	+						+	+	+	+				+
36	+							+	+	+	+				+
37	+	+						+	+						
Total	36	33	20	20	3	1	1	29	25	12	11	2	2	2	8
% of trees	97.3	89.2	54.1	54.1	8.1	2.7	2.7	78.4	67.6	32.4	29.7	5.4	5.4	5.4	21.6
			37 (100%)								36 (97%)				

* At least three species: *Adelanthus bisetulus* (Stephani) Grolle; *Lepidozia laevifolia* (Hook. f. *et* Tayl.) Gott. *et al.*, *Drepanolejunea tristaniana* S. Arn.

TABLE 1. Extended.

Lichens					Angiosperms		No. of species					
Cladonis sp.	*Hypotrachyra* sp.	*Usnea* sp.	*Pseudocyphellaria* sp.	Unidentified lichen sp. 1	*Scirpus bicolor*	*Acaena sanguisorbae*	Ferns	Bryo-phytes	Lichens	Angio-sperms	Total	
							3	1	0	0	4	
+	+	+					3	3	3	0	9	
+	+	+					2	1	3	0	6	
+	+						2	2	2	0	6	
	+	+	+				5	1	3	0	9	
+	+	+	+				4	2	4	0	10	
+		+	+				4	3	3	0	10	
+		+	+				3	3	3	0	9	
+		+	+			+	3	5	3	1	12	
	+		+		+		3	2	2	1	8	
		+					4	3	1	0	8	
+	+						4	1	2	0	7	
+	+	+					2	1	3	0	6	
+	+						4	1	2	0	7	
+	+	+	+				3	2	4	0	9	
+	+	+	+				5	3	4	0	12	
							3	2	0	0	5	
+		+	+		+		4	4	3	1	12	
+		+	+				4	5	3	0	12	
+	+	+	+				4	4	4	0	12	
+	+	+					4	3	3	0	10	
+	+	+	+				4	4	4	0	12	
							1	1	0	0	2	
	+			+			3	3	2	0	8	
+							1	3	1	0	5	
+							2	2	1	0	5	
+	+		+				5	3	3	0	11	
+	+						2	3	2	0	7	
							3	1	0	0	4	
+			+				4	1	2	0	7	
							2	1	0	0	3	
+	+		+				4	2	3	0	9	
		+					2	0	1	0	3	
+							3	3	1	0	7	
+	+		+				2	5	3	0	10	
+		+	+				1	5	3	0	9	
+			+		+		2	2	2	1	7	
27	19	18	18	1	3	1	3.1	2.5	2.2	0.1	7.9	$\bar{x}$/trunk
73.0	51.4	48.7	48.7	2.7	8.1	2.7	0.18	0.22	0.21	0.05	0.47	SE
		32 (87%)			4 (11%)		44	31	44	5	36	% of total species-pool

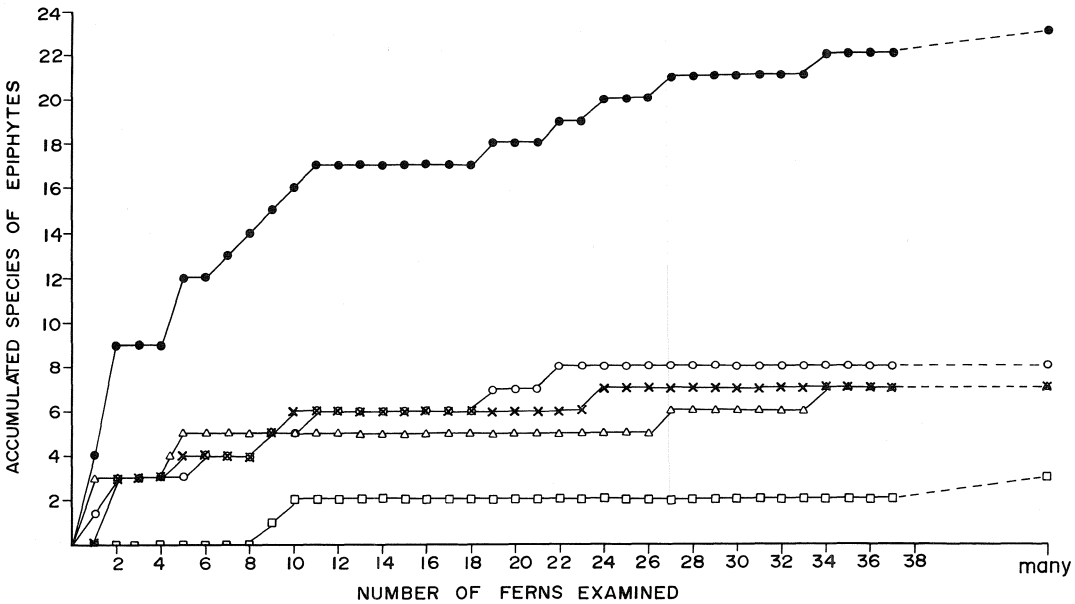

FIGURE 2. Cumulative number of species of epiphytes on *Blechnum palmiforme* trunks at Gough Island. Dots = all species; circles = bryophytes; x's = lichens; triangles = ferns; squares = angiosperms. Solid line indicates species on trunks of sampled ferns (either in transects or elsewhere on the trunk); dotted lines additional species found on non-sampled trunks. Bryophytes include three species of hepatics lumped as one "species"; see text.

present study (see below). The present list has 11 species not present in their collective lists (excluding unidentified species on the present list that may have been on their lists), whereas they had 19 species not on the present one. Combining the two gives a minimum of 44 species known to be epiphytic on trunks of *Blechnum palmiforme* on Gough Island (and if all my four unidentified ones are species not included on their lists, the total is raised to 48).

Species Richness

The sampled fern trunks contained seven species of ferns, seven species of mosses, five species of lichens, three species of hepatics and two species of angiosperms for a total of 24 epiphytic species (TABLE 1). Twenty-one of these occurred in the transects and three occurred on the same trunks (but only outside transects). The accumulated number of species had reached an asymptote for all groups before the end of sampling (FIGURE 2). Inspection of many additional fern trunks in the study area and elsewhere on the island uncovered only one species not found on the sampled ferns. It was the angiosperm *Empetrum rubrum* which, although a common plant on the ground, was observed only as one single epiphytic individual. Thus, the total recorded species of epiphytes was 25.

No fern trunk was completely bare of epiphytes, and the number of species per trunk ranged from 2 to 12 with a mean of 7.9 (TABLE 1). Ferns contributed the greatest mean number of species per trunk (3.1), with bryophytes and lichens also well represented (2.5 and 2.2 species per trunk respectively) but angiosperms poorly so (0.1 species per trunk).

On the average, on any one fern trunk there were slightly less than half the total species of ferns and lichens recorded from the transects, but less than a third of the available species of bryophytes and only five per cent of the flowering plants (TABLE 1).

All of the sampled ferns had at least one species of epiphytic fern, and all but one had at least one species of bryophyte. Lichens were less often represented in that only 87% of the fern trunks had them; only four of the 37 ferns had epiphytic angiosperms (TABLE 1).

Taking into consideration the total number of species, mean number of species per trunk, and the number of trunks occupied, it is clear that ferns are the dominant taxon of epiphytes, with bryophytes and lichens also important but angiosperms relatively unimportant.

Species richness of epiphytes was greater on the tall ferns than on shorter ones. This was true not only for total epiphytes, for which the correlation with height was significant ($r = 0.513$; $t = 3.54$; $0.005 > P > 0.001$), but also for ferns ($r = 0.505$; $t = 3.46$; $0.005 > P > 0.001$) and

TABLE 2. Number of quadrants containing individual species of epiphytes at each sampling level. $N = 37$ for the upper level, 28 for the central level and 33 for the basal level.

Level	Quadrant	*Asplenium alvarezense*	*Hypnum elatum*	*Hymenophyllum aeruginosum*	*Elaphoglossum laurifolium*	*Cladonia* sp.	*Thuidium curvatum*	*Hypotrachyra* sp.	*Hymenophyllum peltatum*	Unidentified moss sp. 1
Upper	NE	34	0	1	1	7	9	2	18	0
	NW	33	0	1	0	1	8	1	19	1
	SW	32	0	3	2	1	11	0	18	1
	SE	32	1	6	0	4	8	1	20	1
Central	NE	5	8	5	4	1	5	1	15	3
	NW	6	8	4	4	3	6	4	17	4
	SW	5	11	10	4	0	4	3	21	2
	SE	8	12	11	3	1	3	1	19	2
Basal	NE	10	8	14	12	1	4	1	18	1
	NW	8	6	12	11	0	5	2	20	6
	SW	5	11	16	6	0	3	2	20	3
	SE	6	10	16	8	1	1	0	16	3

lichens ($r = 0.465$; $t = 3.11$; $0.005 > P > 0.001$) taken individually. The correlation for bryophytes also was positive ($r = 0.276$) but was not significant ($t = 1.70$; $0.10 > P > 0.05$). There were too few angiosperms for meaningful analysis to be made.

Frequency of Occurrence

Some species were present on most of the trunks sampled; others were less commonly present and some were represented on only a few ferns. The most commonly represented species was the fern *Asplenium alvarezense* which occurred on all but one of the sampled trunks. Four other species (another fern, *Hymenophyllum peltatum,* two mosses, and one lichen, *Cladonia* sp.) occurred on two thirds or more of the ferns. Only eight species (36%) occurred on half or more trunks; nine species (41%) were found on less than 10% of the trunks (TABLE 1).

Frequency of occurrence on different parts of trunks also varied, and the pattern was different for different species. For particular quadrants the different levels were occupied at significantly different frequencies. There were some species that were more frequently represented at the central or basal levels than at the upper one (TABLE 2). For *Hypnum elatum* the differences among levels were highly significant for each quadrant. For *E. laurifolium* and *H. aeruginosum* differences in level were significant except for the SW and SE quadrants respectively. *Usnea* sp. and *Brachythecium* had a similar pattern of microdistribution but were in low frequencies overall and were not tested statistically.

Asplenium alvarezense displayed the opposite pattern in that it occurred on a greater number of trunks at the upper level than at the central or basal one (TABLE 2); the differences were highly significant for all quadrants. *Cladonia* sp. and *Thuidium curvatum* also seemed to favor the top level but differences were significant only for the NE and SE quadrants respectively.

There was only one species that was more often represented at mid-level than at either the upper or basal levels. It was *Pseudocyphellaria* sp. The difference was significant only for the SW quadrant. Two species, *H. peltatum* and Unidentified Moss species No. 1 showed no significant differences in frequency among levels and, from that standpoint, can be considered uniformly distributed. Other species were too rare for any microdistributional pattern to be detected.

By contrast, there were no statistically significant differences in frequency of occupancy of different quadrants at any of the three levels. In 27 chi-squared tests (nine species at each of three levels), P values were greater than 0.25 in 22 tests and greater than 0.10 in one; in only three did the values border on significance ($0.10 > P > 0.05$; *H. aeruginosum* upper and central levels; *Cladonia* upper level).

In summary, several species occurred on a greater number of trunks in the central and lower portions (lower-trunk specialists) than on the upper trunk. There was at least one upper-trunk specialist and possibly one mid-trunk specialist. None of the species clearly favored one quadrant over another.

Total Cover

The total epiphytic cover on fern trunks was extremely high and averaged 84.5%, with many values of 100% for individual transects (although some low ones occurred also).

Analysis of variance showed no significant dif-

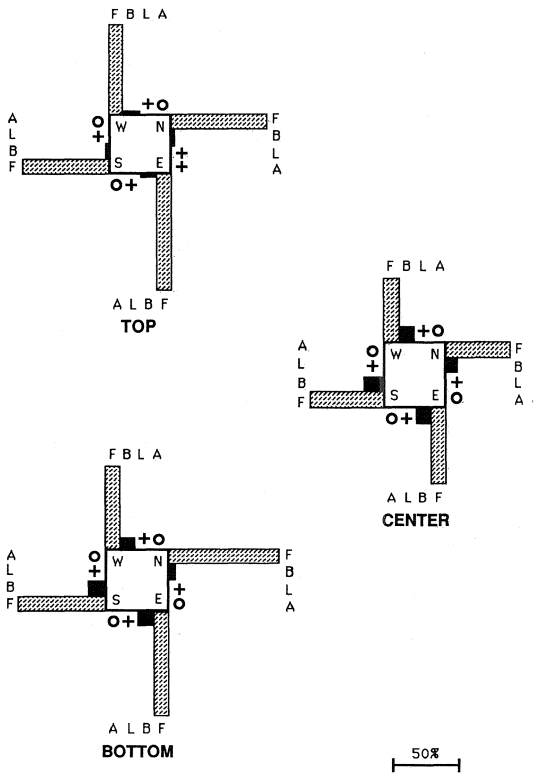

FIGURE 3. Mean percent cover of ferns (F), bryophytes (B), lichens (L) and angiosperms (A) on four quadrants at each of three vertical levels on trunks of *Blechnum palmiforme*. Letters in square indicate compass directions. Scale shows 50% cover. + indicates present but at values too low to show to scale conveniently. 0 indicates absence.

ferences in total epiphytic cover among the different levels ($F = 1.27$; $P = 0.29$), but there were significant differences among quadrants ($F = 6.41$; $P < 0.001$). The interaction term between level and quadrant was not significant ($F = 0.98$; $P = 0.44$) and therefore the differences among quadrants was consistent at all heights.

The above analysis included only those tree ferns tall enough to have all three levels (see methods section); nine short ferns were excluded. A separate analysis of variance comparing the upper level of the short ferns with that of the taller ones revealed that, at that level, there was no significant difference ($F = 0.23$; $P > 0.50$) between tree fern size classes in total epiphytic cover.

Ferns contributed by far the greatest component of total epiphyte cover in all quadrants and levels (FIGURE 3). Mean total cover of ferns was 67.1% with corresponding values of 15.7%, 1.6% and 0.1% for bryophytes, lichens and angiosperms respectively. Analysis of variance on arcsine-transformed data for ferns revealed significant differences among quadrants ($F = 5.51$; $P = 0.001$) but not among levels ($F = 1.93$; $P = 0.15$). For bryophytes differences among quadrants were at the border of significance ($F = 2.66$; $P = 0.05$) and those among levels were significant ($F = 4.17$; $P = 0.02$). Cover was heaviest on the middle and bottom two segments (FIGURE 3). For lichens, differences were not significant either among quadrants ($F = 1.06$; $P = 0.37$) or levels ($F = 2.06$; $P = 0.13$). The interactive terms were not significant for any of these comparisons ($F = 0.86, 0.61, 1.64$; $P = 0.52, 0.72, 0.14$, respectively). There were too few angiosperms for meaningful analysis.

Cover of Individual Taxa

Cover values of individual species varied from place to place on the fern trunks as indicated by analyses of variance with repeated measures. *Asplenium alvarezense* showed significant differences in percent cover both at different levels on the trunk and in different quadrants (TABLE 3), with the highest values being at the top of the trunk. The differences between quadrants was only at the upper level, the central and the basal ones having similar cover all round the trunk. Consequently, the interaction between quadrants and levels was significant.

Hymenophyllum aeruginosum had significantly greater cover on the bases of the trunks than at higher levels. There also were significant differences among quadrants with a tendency to favor the southern ones; the interaction between variables was not significant (TABLE 3).

For the moss, *Hypnum elatum,* there were marked, significant differences in mean cover at different heights, the top level being nearly bare of this species but with relatively high cover on the middle and basal parts of the trunk. There were also significant differences in mean cover among the quadrants, the highest values being in the southern quadrants. The interaction term was not significant (TABLE 3).

H. peltatum did not differ significantly in cover from one level of the trunk to another (TABLE 3), but there were differences among quadrants, with the southern quadrants being slightly favored over the northern ones; there was no significant interaction of level and quadrant.

Mean cover of *Thuidium* did not differ significantly from one level to another. It did show significant differences among quadrants, with the northwestern quadrant being favored. The interaction term was not significant.

Clearly, among the ferns and bryophytes there are upper trunk specialists, lower trunk specialists and possibly a mid-trunk specialist as well as those that were distributed evenly at all vertical levels. The contributions of two common

TABLE 3. Variation of cover of epiphytes in different quadrants and at different levels of tree fern trunks.

Species	Quadrant	Mean percent cover			Level		Quadrant		Interaction	
		Top	Middle	Basal	F	P	F	P	F	P
Asplenium alvarezense	NE	44.8	5.7	6.0	28.09	<0.001	6.77	<0.001	4.62	<0.001
	NW	30.7	6.8	5.7						
	SW	29.5	4.8	2.7						
	SE	31.3	6.3	4.7						
Hymenophyllum aeruginosum	NE	0	8.5	27.0	33.25	<0.001	6.94	<0.001	1.87	0.09
	NW	0	3.9	15.2						
	SW	1.1	8.5	22.4						
	SE	4.3	17.5	23.8						
Hypnum elatum	NE	0	8.2	6.7	8.95	<0.001	6.91	<0.001	1.82	0.10
	NW	0	8.4	6.8						
	SW	0	18.0	16.6						
	SE	0.9	14.4	9.8						
Thuidium curvatum	NE	7.5	4.5	1.1	2.47	0.09	3.44	0.02	0.17	0.99
	NW	9.6	6.4	5.1						
	SW	8.4	3.6	2.9						
	SE	5.9	2.5	0.9						
Hymenophyllum peltatum	NE	17.9	30.4	26.6	0.45	0.64	2.88	0.04	1.13	0.35
	NW	26.5	31.2	28.0						
	SW	28.9	37.3	26.1						
	SE	33.2	32.5	32.5						

ferns, one a top specialist (*A. alvarezense*) and the other a bottom specialist (*H. aeruginosum*) tended to cancel each other and ferns collectively showed no significant vertical differences in cover. The scarcity of one moss (*Hypnum elatum*) in the top layer was reflected in lower cover of bryophytes generally in that part of the trunk.

The uniformly distributed species, of course, did not cause regional variations in cover, and the rarer species collectively exerted only a minor influence on the collective pattern of larger taxa.

Equitability in Cover

The epiphytic assemblage on Gough Island tree ferns is a highly inequitable one (FIGURE 4). The fern *H. peltatum,* accounts on the average for almost a third of the total epiphytic cover and it and the two next highest species combined (*A. alvarezense* and *H. aeruginosum*) account for over 60%. Of the 24 epiphytic species on sampled trunks, seven (four ferns, three bryophytes) accounted for over 95% of total epiphytic cover. Thus, the assemblage is characterized by a few common to abundant species and many relatively rare ones.

"Patch Size"

Intercepts ranged from 0.1 cm to 60 cm for all species collectively. It was rare that intercepts covering even a whole quadrant occurred. Only 17 of the total 1,149 intercepts measured exceeded 15 cm (15 of these are treated specially below). Most were relatively small and mean values for all species ranged from 1.0 cm to 7.8 cm.

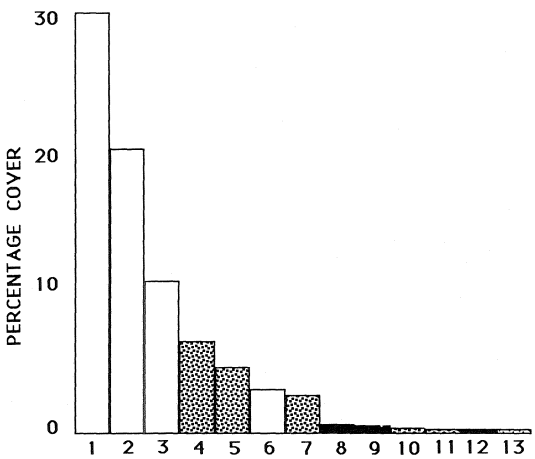

FIGURE 4. Equitability of cover of epiphytes on *Blechnum palmiforme* trunks. Open bars represent fern species, mottled ones represent bryophytes and black ones indicate lichens. 1 = *Hymenophyllum peltatum.* 2 = *Asplenium alvarezense.* 3 = *Hymenophyllum aeruginosum.* 4 = *Hypnum elatum.* 5 = *Thuidium curvatum.* 6 = *Elaphoglossum laurifolium.* 7 = Unidentified Moss No. 1. 8 = *Hypotrachyra* sp. 9 = *Cladonia* sp. 10 = *Brachythecium* cf. *rutabulum.* 11 = Hepatics. 12 = *Usnea* sp. 13= All other species combined.

Only two species, *Asplenium alvarezense* and *Hymenophyllum peltatum,* occurred in sufficient numbers of patches in all categories of quadrant and level for complete analyses of "patch size" to be made. A factorial analysis of variance revealed no significance differences attributable either to quadrant ($F = 0.56, 0.32$; $P = 0.64, 0.81$, respectively) or to level ($F = 1.17, 1.35$; $P = 0.31, 0.26$). These analyses excluded seven patches of *Asplenium* and six of *H. peltatum* that extended over two or more complete quadrants and could not be assigned to any particular one. When these were included and a one-way analysis of variance directly comparing levels was performed, again differences among levels was not significant ($F = 0.23, 2.18$; $P = 0.88, 0.12$). *Hymenophyllum aeruginosum* and *Hypnum elatum* were present in sufficient numbers for analysis by quadrant only on the central and basal portions of fern trunks. Neither species had significantly different "patch sizes" among different quadrants ($F = 1.96, 0.46$; $P = 0.13, 0.71$, respectively) or between central and basal levels ($F = 0.62, 0.47$; $P = 0.43, 0.50$). Lumping all quadrants at each level and including two large patches formerly excluded because they covered two or more complete quadrants, made direct comparison among all three levels possible for *H. aeruginosum.* The differences were not significant ($F = 1.89$; $P = 0.16$). A similar comparison could not be made for *Hypnum* because it occurred too infrequently at the top level.

Thuidium curvatum could be tested for differences among quadrants only at the top level and *Elaphoglossum lauratum* only at the bottom one. Neither species displayed significant differences among quadrants at these respective levels ($F = 1.57, 1.19$; $P = 0.88, 0.32$). Lumping all quadrants for a particular level for the former species and then comparing levels directly revealed no significant differences between levels ($F = 2.43$, $P = 0.09$); data were insufficient for a similar test on the latter species. Low numbers of patches in quadrants and levels prohibited testing of other species.

Regional differences in the epiphytic flora on different parts of trunks has been shown to reflect a lag in colonization and growth by epiphytes on the new surfaces produced by the growth of the host plant (Rogers 1988). Specifically, as the upper trunk extends upward, it may be slow to be colonized by new epiphytes and the patches there might be small. This hypothesis was rejected for the present study because patches on all parts of the trunk, either vertically or radially, had the same average size, and seemed to be in equilibrium. Consequently, explanation of distributional patterns on the trunks must involve factors other than lag in colonization and growth.

Number of Patches

Because average patch size did not vary among different levels or quadrants, it would be expected that number of patches of epiphytes and their cover would have similar patterns of variation on the fern trunks. That proved to be true in most cases. A chi-square analysis of number of patches of all species collectively, and of the various species individually, revealed nonrandom distributions on the fern trunks ($P < 0.01$ in all cases; same species as those analyzed for cover in TABLE 3). *Asplenium alvarezense* was confirmed as an upper trunk specialist and *H. aeruginosum* and *Hypnum elatum* as lower trunk ones. An additional species, *Elaphoglossum laurifolium* was tested. It showed significantly greater number of patches on the lower trunk than at higher levels (Number of patches: Top 1; Middle 15; Basal 56; $P < 0.001$) and favored northern quadrants (NE 22; NW 20; SW 12; SE 18; $0.05 > P > 0.02$). There were three differences between the analyses of cover and of number of patches: (1) *H. peltatum* had significantly more patches at the upper level ($0.05 > P > 0.02$) but not among quadrants ($P > 0.20$); it was the reverse for cover (TABLE 3). (2) All species collectively also showed a reversal with vertical differences in number of patches being significant ($P < 0.001$) but not those for cover (see above); there were significant differences among quadrants in cover (see above) but not in number of patches ($0.20 > P > 0.10$). (3) *Thuidium* displayed a significantly greater number of patches at the upper levels ($P < 0.001$) whilst its cover values did not show significant vertical differences (TABLE 3).

Mortality

Most of the epiphytes were alive and appeared in good health. Only six patches (0.5%) contained dead plants and these occurred only in two species (five patches of *H. peltatum* and one of *H. aeruginosum*). Two patches (one of each species) were exceptionally large (23.0 and 45.6 cm). The dead cover of these species was only 3.6%, and 7.1% of their total cover, respectively, and collectively accounted for only 2.4% of the total epiphyte cover.

Factors Affecting Microdistribution

Distributional patterns have been viewed above from several different taxonomic levels: (1) the total epiphytic flora, (2) the major higher taxa (ferns, bryophytes, lichens, angiosperms) and (3) individual species. Patterns differ with the hierarchical level examined, and depending on

TABLE 4. Summary of vertical and radial variation in epiphytes on trunks of *Blechnum palmiforme*. L (Level) signifies vertical variation, Q (Quadrant) indicates radial variation, + means differences are significant and − that they are not. ± means that vertical differences were significant for some quadrants but not for others. * means $P = 0.05$, at borderline of significance.

Taxon	Cover	Patch		Frequency of trunks occupied
		Number	Size	
All species	L− Q+	L+ Q−		
Ferns	L− Q+			
Asplenium alvarezense	L+ Q+	L+ Q+	L− Q−	L+ Q−
Hymenophyllum peltatum	L− Q+	L+ Q−	L− Q−	L− Q−
Hymenophyllum aeruginosum	L+ Q+	L+ Q+	L− Q−	L± Q−
Elaphoglossum laurifolium		L+ Q+	L− Q−	L± Q−
Bryophytes	L+ Q*			
Hypnum elatum	L+ Q+	L+ Q+	L− Q−	L+ Q−
Thuidium curvatum	L− Q+	L+ Q+	L− Q−	L± Q−
Unidentified moss #1				L− Q−
Lichens	L− Q−			
Cladonia sp.				L± Q−
Hypotrachyra sp.				L± Q−

the criterion used (cover, frequency, patch size, patch number) (TABLE 4).

There are several theoretical ways a given epiphytic species could be distributed on fern trunks: (1) It could occur everywhere (all levels, all quadrants) at the same frequency and cover values and thus be uniformly distributed. (2) It could be uniformly distributed in terms of frequency but not in terms of cover. This would happen if the species were represented as often at all levels and in all quadrants, but in certain situations occurred in larger patches than in others. (3) It could be uniformly distributed in terms of cover but not in frequency. This would happen if the species were found in large patches when rare but in small patches when common. (4) Finally, both frequency and cover could vary with level or quadrant. The actual situation was complicated by the fact that radial and vertical components showed different patterns; when there was uniform vertical distribution, radial distribution varied, or vice versa (TABLE 4).

There are a variety of environmental gradients that are potentially important in influencing the observed patterns. The texture of the upper trunk is fibrous whereas the middle and lower portions are smoother. The fronds shade the upper trunk more than the lower portions. Humidity may be higher near the ground or in close proximity to transpiring fronds than it is at mid-trunk. The climate varies altitudinally on Gough (Holdgate 1960) and there are weather differences from one locality to another. These may influence whether particular species are epiphytic or occupy other habitats and affect the mix of epiphytic species at particular localities.

Biotic factors also may be important (Rogers 1988). Abundant cover of early colonizers may preclude establishment of later arrivals. There may be successional changes with ruderals giving way to competitors. However, in the present study this source of variation was controlled by carrying out the primary analysis on a group of ferns of about the same size, and presumably age. Furthermore, these did not differ in cover from smaller ferns in those analyses in which the two groups could be compared.

Rogers (1988) found that the southern and western sides of tree trunks in Australia were more favorable for lichen growth than the northern or eastern ones. This group was too sparse in the present study for individual species' microdistributions to be analyzed in detail. However, collectively lichens were rather uniformly distributed on the trunks. Some ferns and bryophytes did favor the southwestern quadrant but it was not a general rule; some favored the northeastern one.

In conclusion, the epiphytic assemblage on *Blechnum palmiforme* trunks on Gough Island is a complex mixture of species of ferns, bryophytes, lichens and a few angiosperms, each with its own microdistributional pattern. Abundances of lower trunk specialists and upper trunk specialists cancel out each other among the ferns so that total fern cover does not show significant vertical differences. Radial differences persist to the higher taxonomic levels. Bryophytes also have vertical specialists and the collective result is for greater cover on the lower parts of trunks. Lichens are more uniformly distributed.

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