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DOI

[10.1007/BF00045096](https://doi.org/10.1007/BF00045096)

Publication date

1994

Published in

Vegetatio

[Link to publication](#)

Citation for published version (APA):

Wolf, J. H. D. (1994). Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio*, 112, 15-28. <https://doi.org/10.1007/BF00045096>

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Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes

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Accepted 29.3.1993

Keywords: Canonical correspondence analysis, Canopy, Heterogeneity, Host specificity, Priority, Suspended soil, Tolerance

Abstract

The epiphytic vegetation on host trees along an altitudinal transect on the west slope of the Central Cordillera in Colombia was sampled. Bark-type restricted sampling comprised four full-grown forest trees, not necessarily four species, at altitudinal intervals of c. 200 meters from 1000 to 4130 m a.s.l. and included the canopy. Both vascular and non-vascular epiphytes, the latter often more abundant in the montane rain forest, were included in the analyses. Using a method of direct gradient analysis, canonical correspondence analysis, the variation explained by various environmental variables could be discriminated from a great amount of variation that seemed not related to any ecological factor. To a large extent, the randomness in propagule supply appears to determine the floristic composition on branch/trunk segments. The grouping of relevés in a phytosociological analysis concurred with a clustering of samples in an ordination diagram of the first two extracted constrained axes. The sample scores on these two axes were strongly correlated with the complex variables 'altitude' and 'height within the host tree'. Specialists and generalists with respect to the two variables were defined based on tolerances provided by the canonical correspondence analysis as was the position of species on the gradients involved. Independently from any of the other variables entered, a relation between the epiphytic vegetation and host species was detected, particularly in the case of *Brunellia occidentalis*, a fast growing tree species of higher altitude. No relation between chemical characteristics of suspended soil in the Upper Montane Rain forest and its supporting species could be demonstrated.

Nomenclature: Churchill, S. P. 1989. Catalogo Nuevo de los musgos de Colombia. *J. Trop. Bryology* 1: 95–132. Gradstein, S. R. & Hekking, W. H. A. 1979. A catalogue of the Hepaticae of Colombia. *Journ. Hattori Bot. Lab.* 45: 93–144. Sipman, H. J. M. 1989. Lichen zonation in the Parque Los Nevados Transect. In: van der Hammen, T., Diaz P., S. & Alvarez V., J. (eds) *Stud. Trop. Andean Ecosyst.* 3. Cramer, Berlin-Stuttgart. Or the latest taxonomic works, when available.

Introduction

Biogeographical and ecological studies on epiphytic bryophytes, lichens and vascular plants in the tropics indicate that two of the major environmental variables that species respond to are position within the host tree and altitude (Cornelissen & ter Steege 1989; Frahm 1987, 1990; Gradstein & Frahm 1987; Johansson 1974; Kürschner 1990; Richards 1952; Schimper 1888; Went 1940; Wolf 1993 a, b). However, quantitative ecological studies in tropical montane rain forests, characterized by a massive presence of epiphytes, are still rare, in particular studies that include non-vascular epiphytes and where full attention is paid to the vegetation in the canopy.

The environmental gradients involved are complex, reflecting simultaneous changes of ecological factors such as moisture availability, temperature and light intensity. In addition, bark characteristics apparently exert an influence on the establishment of epiphytes. The classical study by Barkman (1958) on epiphytic cryptogams still provides one of the most comprehensive discussions of these factors to date.

A common feature in tropical wet and cool montane forests is the accumulation of often great amounts of organic soil on slanting branches and in tree forks. Nutrient concentrations of suspended soils in the study area varied widely and pH values in the forests at altitudes above 2460 m ranged from 2.5 to 4.8 (Wolf 1993 b). A relationship between the spatial distribution of vascular epiphytes and the soil in which they are rooted has been postulated (Lesica & Antibus 1991).

The investigation of the relative importance of ecological factors is hampered by the lack of microclimatological data and by the often high correlation between separate factors. Moreover, the species-environment relationship is obscured by the observation that epiphytic communities may differ greatly in their floristic composition at apparently identical habitats. For example, Johansson (1974) observed that while some *Parinaria excelsa* trees (10 m or taller) carried 22 species of vascular epiphytes, other individuals were devoid of epiphytes. Also at a smaller scale, i.e. on branch

or trunk segments, similarity between relevés taken within the same community-type may be low (e.g. Barkman 1958). In this study, 20 community-types had on average a mean internal similarity between relevés, using the Similarity Ratio as index, of 15.6% only (Wolf 1993 a, b). Accidental species, i.e. those having frequencies less or equal than 10%, were excluded in the calculations.

In correlative response studies of epiphytes to environmental variables, one solution to this problem of great heterogeneity is to combine data from several sample-units to an average value, accepting loss of information and risking prejudice. In contrast, Oksanen (1988) demonstrated the value of a canonical ordination technique, canonical correspondence analysis (CCA), for heterogeneous epiphytic vegetation in Finland. Here, I apply this approach too. CCA was designed to detect patterns of variation in species data that can be explained by the environmental variables recorded (ter Braak 1986).

Aim of this paper is to determine the relative importance of certain environmental variables for understory and canopy epiphytic vegetation, including bryophytes, lichens and vascular plants, in an altitudinal transect. Specialists, *i.e.* those species having a narrow amplitude on an environmental gradient, are identified, as are generalists. The occurrence of host specificity will be examined.

Methods

Fieldwork was carried out during 1985, 1986 and 1988 in an altitudinal transect on the west slope of the Central Cordillera, Colombia, ca. 4° 50' N 75° 30' W. Van der Hammen *et al.* (1983, 1989 and in press) provided a detailed description of the transect.

At each of 15 sites, located at altitudinal intervals of approximately 200 meters from 1000 m up to 4130 m a.s.l., the epiphytic vegetation of four adult host trees was sampled according to the Braun-Blanquet approach in phytosociology (Westhoff & van der Maarel 1973). Trees having

an extremely coarse, smooth or sloughing bark were avoided. About 10 relevés, ranging from a few to over 20 dm², were laid out per tree from the tree base up to the twigs in the outer canopy. Rope climbing techniques were used for sampling (ter Steege & Cornelissen 1988). Species cover, in percentages, was estimated relative to the surface area of the upper half cylinder of branch/trunk segments.

At each relevé site, hemispherical photographs were taken to estimate diffuse site factors (Anderson 1964). The diffuse site factor is the percentage of total diffuse light at a given site compared with total diffuse light in the open. The percentages were ²log transformed and scaled on a 1–6 scale. When available, suspended soil was collected for chemical analysis. pH-values, conductivity of solutions (1:10) and the concentrations of the macronutrients N, P-PO₄, K, Ca and SO₄ were determined. Further details on the methodology are given in Wolf (1993 a).

The epiphytic vegetation in the transect is dominated, in terms of species richness and abundance, by cryptogams (Wolf 1993 a, b). In addition to 74 taxa of phanerogams, 34 fern, 187 liverwort, 108 moss, 140 macrolichen and 38 crustose lichen taxa were recognized. Plants which could not be reliably classified to species level were grouped into taxa of higher taxonomic rank. Since such taxa typically comprised several species, a downweighing of these taxa was applied in CCA. Approximately 90% of the bryophytes and macrolichens encountered could be classified to species (Wolf, in press). The classification of sterile vascular plants and crustose lichens was more problematical. A phytosociological analysis of all taxa, using TWINSpan (Hill 1979 b), yielded 22 communities (Wolf 1993 a, b).

A canonical correspondence analysis has been performed with the computer program CANOCO, version 3.10 (ter Braak 1987, 1990). Excluded from the analysis were relevés taken in the structurally distinct forests at 1000 m and 4130 m a.s.l., leaving only relevés in forests which may be classified as Montane Rain forests, sensu Grubb *et al.* (1963). In addition, relevés domi-

nated by plants which could not be identified to species level and relevés which were outliers on the first few axes in a DECORANA (Hill 1979 a) analysis, usually dominated by rare taxa, were omitted. The final analysis comprised 454 relevés which contained 521 taxa of vascular and non-vascular epiphytes.

Species cover values were lognormal transformed, as recommended when abundance value distributions are skewed (Jongman *et al.* 1987). Sample scores on the ordination axes are weighted mean species scores.

The environmental variables entered in the analysis are summarized in Table 1. Species of host tree are regarded as variables.

The occurrence of host specificity was tested in a Monte Carlo permutation procedure (Jongman *et al.* 1987). Host tree species were entered as variables and remaining variables as co-variables.

In addition to the position of the species on the constrained axes as generated by CCA the standard deviations of these scores are analyzed. The standard deviation may be seen as a measure of niche-width or tolerance (ter Braak 1987, 1990).

In a first analysis variables concerning the chemical composition of suspended soil were omitted. The species response to suspended soil quality was investigated in a separate analysis of those relevés, 110 in total, which yielded sufficient suspended soil to determine nutrient concentrations. Only relevés from altitudes over 2550 m were taken into account, thus avoiding collinearity of soil characteristics with altitude.

Results

CCA of all relevés

The dataset is rather awkward in containing a great number of zero values, 96.1 percent.

CANOCO detected a high correlation between explanatory variables. The diffuse site factor, diameter, inclination and tree base (tree zone I) were all highly ($r \geq 0.40$) correlated with relative height of the relevé in the host tree (Table 2). The presence of suspended soil in a layer of over

Table 1. Environmental variables entered in the canonical correspondence analysis; * denote quantitative variables.

*Altitude (m a.s.l.)	Dendropanax cf. macrocarpum Cuatr.
*Height in the tree (%)	Diplostegium violaceum Cuatr.
Tree zone (I–V, following Johansson, 1974)	Escallonia myrtilloides L.f. var. myrtilloides
*Inclination (= – [deviation from vertical – 90°])	Ficus cf. velutina Willd.
*Diameter substrate (cm)	Gordonia cf. pubescens Pl. & Lindbl. ex Tr. et Pl.
*Diffuse site factor (%; 2log transformed)	Hyeronima scabrida (Tull.) Müll. Arg.
*Thickness of suspended soil (cm)	Indet
Presence of a layer of suspended soil of > 0.5 cm	Lauraceae sp. 1
Chemistry of suspended soils:	Lauraceae sp. 2
*Residue on ignition (%)	Lauraceae sp. 3
*EGV	Lauraceae sp. 4
*pH	Machaerium capote Triana ex Dugand
*N mg/g	Matisia sp.
*P–PO ₄ mg/g	Nectandra cf. globosa (Aublet.) Mez.
*K mg/g	Ocotea cf. guianensis Aubl.
*Ca mg/g	Polylepis sericea Wedd.
*SO ₄ mg/g	Rosaceae (cf.) indet
Host trees	Senna pistaciifolia (H.B.K.) Irwin & Barneby
Aegiphyla bogotensis (Spreng.) Mold.	Solanum inopinum Ewan
Axinaea sp. (Melastomataceae)	Talauma sp. (Magnoliaceae)
Brunellia cf. goudotii Tul.	Tetrorchidium boyacanum Croiz.
Brunellia occidentalis Cuatr.	Weinmannia mariquitae Szyszyl.
Chrysophyllum cf. auratum Miq.	Weinmannia rollotii Killip var. rollottii
Cinchona sp. (Rubiaceae)	Weinmannia pubescens H.B.K.
Clusia aff. multiflora H.B.K.	Weinmannia sp.

0.5 cm and the host tree *Weinmannia mariquitae* showed a positive correlation with altitude.

Rejecting these variables, a multicollinearity problem may be avoided (Jongman *et al.* 1987). Doing this, the eigenvalues of the canonical axes and species-environment correlations barely decreased and the variable inflation factors (VIF's) dropped to less than 6.0, allowing for an inter-

pretation of the canonical coefficients (ter Braak 1987, 1990).

The first three constrained axes extracted are long, showing a gradient-length of 6.65, 4.95 and 3.46 sd respectively using Hill's scaling (Hill 1979 a). Both the eigenvalues and the correlations with environmental variables of these axes are high (Tables 3, 4) allowing for an ecological interpretation (Jongman *et al.* 1987). The sample scores on the first axis are strongly correlated with altitude (and associated variables) and those on the second axis with the relative height in the host tree. The third axis is best correlated with a species of host tree, *Brunellia occidentalis*, a fast growing pioneer tree.

However, no clear relation between these environmental variables and the species composition at sites may be expected since only 4.3% of the variance in the species data can be explained by the first three constrained axes (Table 3). All environmental variables together merely explained 16.2% of the total inertia. In spite of the

Table 2. Weighted correlation between the two environmental variables altitude and relative height in the host tree and those variables which showed a correlation of $r \geq 0.40$ with at least one of the two.

	Relative height (%)	Altitude (m a.s.l.)
Diameter	– 0.82	– 0.04
Zone I (= tree base)	– 0.80	0.07
Inclination	– 0.54	0.12
Diffuse site factor	0.52	0.32
<i>Weinmannia mariquitae</i>	– 0.02	0.59
> 0.5 cm of soil accumulated	– 0.16	0.40

Table 3. Eigenvalues of the first four constrained axes as generated by a canonical correspondence analysis of all relevés and the amount of variance explained of the species data and of the species-environment relation by these axes.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.788	0.580	0.497	0.360	43.142
Cumulative percentage of variance explained					
1) of species data	1.8	3.2	4.3	5.2	
2) of species-environment relation	11.2	19.5	26.6	31.7	

small amount of variability explained, the relevés pertaining to a particular community-type, as defined on phytosociological criteria, are clustered remarkably well in an ordination diagram of the samples scores on the first two constrained axes as generated by CCA (Fig. 1).

The position of the species on the first and second constrained axes are given in Figures 2 and 3, as are the standard deviations of the species scores on the axes. Species with low standard deviation values on the two axes may be regarded as specialists with respect to altitude and height in the host tree, respectively. Species in the diagrams are boxed in arbitrarily.

In the procedure used to test for host specificity the variables *Weinmannia mariquitae*, strongly correlated with altitude, and *Brunellia occidenta-*

lis, already shown to be correlated with the sample scores on a constrained axis in the previous analysis, were omitted. The analysis revealed that the mean abundance of epiphytes differs significantly among host species ($p = 0.01$). Host specificity was not preponderant on a single species of tree (Table 5).

CCA of relevés on organic soils

Next, a CCA analysis of those relevés (110) in the Upper Montane Rain forest in which suspended soil could be gathered, was performed. This time the variables concerning the chemical composition of the soil were included.

The species scores on the first two constrained

Table 4. Canonical coefficients and inter-set correlations between the site scores on the first four constrained axes and environmental variables as generated by canonical correspondence analysis of all relevés. Only variables with a correlation higher than 0.20 with one of the axes are given.

Variables	Inter-set correlations				Canonical coefficients			
	axis 1	axis 2	axis 3	axis 4	axis 1	axis 2	axis 3	axis 4
Altitude (m)	-0.96	-0.07	0.02	-0.08	-0.82	0.00	-0.06	0.05
Relative height (%)	0.02	-0.82	-0.14	0.08	0.03	-0.39	-0.10	0.05
<i>Brunellia occidentalis</i>	0.07	-0.12	0.50	-0.01	0.02	-0.10	0.48	0.08
<i>Weinmannia rollottii</i>	-0.05	-0.01	0.29	0.38	0.03	-0.01	0.30	0.30
<i>Matisia</i> sp.	0.25	0.04	-0.23	0.31	-0.02	0.05	-0.10	0.25
<i>Hyeronima scabrida</i>	0.18	0.02	0.06	-0.28	0.05	0.02	0.12	-0.13
Rosaceae sp.	0.28	0.01	-0.02	-0.20	0.05	0.03	0.09	-0.05
Lauraceae sp. nr. 3	0.16	0.04	-0.16	0.23	-0.01	0.02	-0.09	0.19
<i>Gordonia</i> cf. <i>pubescens</i>	-0.12	0.16	0.20	0.21	-0.07	0.09	0.24	0.18
Lauraceae sp. nr. 2	0.18	0.05	-0.17	0.21	-0.02	0.06	-0.08	0.18
Phorophyte indet	0.21	0.06	-0.19	0.21	-0.02	0.09	-0.09	0.19
<i>Ficus</i> cf. <i>velutina</i>	0.21	0.14	-0.16	0.10	0.04	0.06	-0.07	0.11
<i>Nectandra globulosa</i>	0.11	-0.02	0.03	-0.21	0.00	-0.03	0.09	-0.09

axes again were best correlated with altitude and relative height in the tree (Tables 6, 7). No significant differences between the presence and abundance of species on suspended soils of different

chemistry could be demonstrated in a Monte Carlo procedure, when other variables were entered as co-variables; $p = 0.11$ ($p = 0.22$, when rare species are downweighted).

Table 5. Correlation (weighted by the total abundance of species in the relevé) between species of host tree and the species scores on the first constrained canonical axis. Variables other than species of host tree were entered as co-variables.

Host tree	Correlation
Weinmannia rollottii	- 0.35
Matisia sp.	0.30
Solanum inopinum	- 0.30
Gordonia cf. pubescens	- 0.25
Weinmannia sp.	- 0.24
Lauraceae sp. 3	0.23
Phorophyte indet	0.22
Lauraceae sp. 2	0.21
Ficus cf. velutina	0.20

Discussion

Ecological factors

The complex environmental variable 'altitude above sea level' explains more of the variation in

the species data than 'height in the host tree' (Table 4). This is at least partly due to the great length of the altitudinal gradient, comprising 2420 meters. Topography has a strong influence on the local climate through associated wind patterns. Consequently, temperature, hours of sunshine, relative humidity and rainfall may all be related to altitude (van der Weert *et al.* 1986; Witte, in press).

Eco-physiological studies on corticolous cryptogams show that moisture availability and radiation intensities may determine the vertical distribution of species within the tree (Hosakawa *et al.* 1964; Tobiessen *et al.* 1977). The importance of the factor light may also be deduced from the strong correlation between the height in the tree and the diffuse site factor (Table 2) and from the ordination diagram (Fig. 1): the outer ends of the second axis are formed by an extreme shade community of hollows within trunks and by a photophilous lichen community.

Fig. 1. Ordination diagram of the sample scores on the first two constrained axes, highly correlated with altitude and relative height in the host tree respectively, as generated by canonical correspondence analysis. Sample scores are weighted mean species scores. Squares are relevés pertaining to communities of the Lower Montane Rain forest (1250–ca. 2460 m) and circles pertain to communities of the Upper Montane Rain forest (ca. 2550–3670 m). Open symbols are relevés of canopy communities and closed symbols of tree base and lower trunk communities. For a description of the communities, see Wolf (1993 a, b). Environmental variables shown by a broken arrow are passive variables of which the position in the diagram was calculated afterwards. This also applies to the two nominal environmental variables *Weinmannia mariquitae* and > 0.5 cm of organic soil accumulated of which the centroids are indicated by *.

Fig. 2. Species scores on the first constrained canonical axis, highly correlated with altitude, as generated by canonical correspondence analysis and their standard deviation. The standard deviation may be seen as a measure of niche-width. Rare species, i.e. with an abundance weighted occurrence (N2) of less than 2, are omitted.

Species in box A are the crustose lichen *Leprocaulon albicans*, the foliose lichen *Hypotrachyna gigas*, the mosses *Catagonium brevicaudatum*, *Porotrichodendron superbum*, *Pyrrhobryum mnioides*, *Zygodon squarrosus*, the liverworts *Blepharostoma trichophyllum*, *Herbertus subdentatus*, *Lophocolea quadridentata*, *Plagiochila fuscolutea*, *Plagiochila* sp. B, *Riccardia ciliolata*, the ferns *Elaphoglossum* aff. *lindigii*, *E. sp. A*, and the angiosperms *Plutarchia monantha* (Ericaceae) and *Relbunium hypocarpium* subsp. *nitidum* (Rubiaceae).

Species in box B are the macrolichens *Canoparmelia carneopruinata*, *Heterodermia speciosa*, *Leptogium marginellum*, *Parmelinopsis spumosa*, *Parmotrema haitiense*, *Parmotrema tinctorum*, *Parmotremopsis antillensis*, *Physcia erumpens*, *Pyxine caesiopruinosa*, *Rimelia commensurata*, the mosses *Bryum* sp. B, *Leucodontopsis geniculata*, *Orthostichopsis tetragona*, the liverworts *Brachiolejeunea phyllorhiza*, *Bryopteris diffusa*, *Frullania ecuadorensis*, *Frullania ericoides*, *Frullanoides liebmänniana*, *Lopholejeunea subfusca*, *Plagiochila jamesonii*, *Porella brasiliensis*, *P. crispata*, *Radula caldani*, *Schiffneriolejeunea polycarpa* and the fern *Dicranoglossum furcatum*.

Species in box C are the crustose lichens *Buellia modesta*, *Phyllospora parvifolia*, the macrolichens *Dictyonema glabratum* (= *Cora pavonia*), *Hypotrachyna costaricensis*, *Hypotrachyna imbricatula*, *Hypotrachyna laevigata*-group, *Normandina pulchella*, *Sticta* cf. *laciniata* and the liverworts *Frullania brasiliensis* and *Lepidolejeunea involuta*.

Species in box D are the moss *Prionodon densus* var. *luteo-virens*, the liverworts *Anastrophyllum piligerum*, *Lejeunea* aff. *ambigua*, *Leptoscyphus amphibolius*, *Metzgeria leptoneura*, *Plagiochila adiantoides*, *P. dominicensis*, *P. sylvicultrix*, *Prionolejeunea* sp. A, *Taxilejeunea lancifolia*, the fern *Polypodium glaucophyllum* and the angiosperms *Fernandezia sanguinea* (Orchidaceae) and *Themistoclesia recondita* (Ericaceae).

Table 6. Eigenvalues of the first four constrained axes as generated by a canonical correspondence analysis of only those relevés (110) in the forests above 2550 m for which a chemical analysis of the suspended soils was performed. The amount of variance explained of the species data and of the species-environment relation by these axes are also shown.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.606	0.569	0.436	0.356	15.594
Percentage of variance explained					
1) of species data	3.9	3.6	2.8	2.3	
2) of species environment correlation	11.0	10.4	7.9	6.5	

Specialists and generalists

In Figure 2 the species in box A are characteristic for the forests near the forest line. Box B contains many species such as *Leptogium marginellum*, *Leucodontopsis geniculata*, *Lopholejeunea subfusca*, *Orthostichopsis tetragona* and *Radula caldana*, which are also known as epiphytes in lowland rain forest (Cornelissen & ter Steege 1989). Species with a score near the centre of the axis range from generalists that have a high tolerance in respect of altitude (box C), to specialists, confined to a mid-elevational belt (box D). Box C contains many lichen-generalists with a wide-tropical (e.g. *Hypotrachyna costaricensis*) or temperate distribution (*Normandina pulchella*) and the common wide-spread neotropical liverwort *Frullania brasiliensis*.

In Figure 3, box A contains typical outer canopy species, mostly lichens. In addition, various species of tiny liverworts growing closely appressed to the bark substrate with large leaflobules (*Diplasiolejeunea*) or water-sacs (*Colura*, *Frullania*) fall in this category. Such leaf modifications seem to be related to water retention

(Thiers 1988). Box C contains species that are characteristic for the understory of the forest, all bryophytes (and a species of filmy fern). Box B contains inner- and middle canopy species. Many vascular plants fall in this category. The species of the three boxes show a different tolerance towards height in the tree. Understory species display wider vertical ranges than outer canopy species. This pattern probably reflects the occasional occurrence of tree base species in shaded habitats in the inner-canopy. In contrast, the locations where canopy species are likely to be encountered such as near the forest floor in gaps or on the edge of the forest were not sampled for epiphytes in this study. Interestingly, the tolerances of middle height species are low, even lower than for tree base and twig specialists. Thus, species with a score near the centre of the axis are adapted to the apparently exclusive conditions prevalent in the inner- and middle canopy. The age of the substrate, its inclination, the amount of organic soil accumulation, and the climate, including light conditions are some of the variables that may contribute to the uniqueness of the inner canopy habitat.

Table 7. Canonical coefficients and inter-set correlations between the site scores on the first four constrained axes and environmental variables as generated by canonical correspondence analysis of those relevés (110) in the forests above 2550 m for which a chemical analysis of the suspended soils was performed. Only variables concerning characteristics of the suspended soil and variables with a correlation higher than 0.50 with one of the axes are shown.

Variables	Inter-set correlations				Canonical coefficients			
	axis 1	axis 2	axis 3	axis 4	axis 1	axis 2	axis 3	axis 4
Altitude (m)	-0.87	0.16	-0.13	-0.16	-0.78	0.03	0.06	-0.27
Relative height (%)	-0.01	-0.80	0.21	0.07	-0.16	-0.46	0.08	-0.25
Weinmannia rollottii	0.16	0.25	0.66	-0.19	-0.03	0.18	0.52	-0.16
Diffuse site factor (scale 1-6)	-0.13	-0.53	0.15	-0.18	-0.03	-0.19	0.14	-0.10
Presence of soil of >0.5 cm	0.14	0.30	-0.03	-0.16	0.00	-0.06	-0.03	-0.12
Thickness of the soil (cm)	0.03	0.34	-0.28	-0.20	0.00	0.13	-0.11	-0.18
Residue on ignition (%)	0.20	0.18	-0.15	-0.26	-0.10	0.09	-0.15	-0.10
EGV	0.00	-0.09	0.04	0.09	0.04	0.00	0.00	0.00
pH	0.34	-0.30	0.16	-0.37	-0.04	-0.10	-0.12	-0.52
N content (mg/g)	0.52	0.25	-0.17	-0.28	0.18	-0.09	0.01	0.00
P content (mg/g)	0.34	-0.01	-0.22	-0.32	0.04	-0.04	-0.23	-0.16
K content (mg/g)	0.02	-0.30	0.19	0.13	0.01	-0.04	0.04	0.33
Ca content (mg/g)	0.32	-0.15	0.20	-0.32	0.07	0.08	0.29	0.20
SO ₄ content (mg/g)	-0.13	-0.17	0.21	-0.22	-0.02	-0.08	-0.01	0.02

Fig. 3. Species scores on the second constrained canonical axis, highly correlated with the relative height in the host tree, as generated by canonical correspondence analysis and their standard deviation. The standard deviation may be seen as a measure of niche-width. Rare species, i.e. with an abundance weighted occurrence (N2) of less than 2, are omitted.

Species in box A are the crustose lichens *Caloplaca brebissonii*, *Lecidea piperis*, *Lopezaria versicolor*, *Megalospora admixta*, *Ochrolechia pallescens*, the macrolichen *Erioderma verruculosum*, *Everniastrum catawbiense*, *Hypotrachyna reducens*, *H. rhabdiformis*, *H. sinuosa*, *Menegazzia* sp. A, *Parmelinopsis spumosa* and the liverworts *Colura naumannii*, *C. tenuicornis*, *Diplasiolejeunea pauckertii* and *Frullania tetraptera*.

Species in box B are the macrolichen *Heterodermia isidiophora* and the mosses *Bryum* sp. B, *Campylopus* sp. A, *Pterobryon densum*, the liverworts *Anastrophyllum piligerum*, *Ceratolejeunea* sp. A, *Cyrtolejeunea* sp. A, *Leptolejeunea elliptica*, *Leptoscyphus physocalyx*, *Metzgeria leptoneura*, *Plagiochila adiantoides*, *P. sylvicultrix*, the ferns *Elaphoglossum* aff. *cuspidatum*, *E.* sp. A, *Polypodium glaucophyllum*, *P. remotum* and the angiosperms *Elleanthus auriantiacus* (Orchidaceae), *Peperomia angularis*, *P.* cf. *enantiostrachya* (Piperaceae), *Scaphosepalum* sp. A (Orchidaceae) and *Themistoclesia recondita* (Ericaceae).

Species in box C are the mosses *Dicranodontium meridionale*, *Leskeodon cubensis*, *Leucomium compressum*, *Neckeropsis undulata*, *Porothamnium* aff. *comosum*, *Pyrrhobryum mnioides*, *Rhizogonium lindigii*, *Thuidium antillarum*, *T. delicatulum* var. *peruvianum*, the liverworts *Blepharostoma trichophyllum*, *Calypogeia cyclostipa*, *C. peruviana*, *Cephalozia crassifolia*, *Lopholejeunea subfusca*, *Plagiochila rutilans*, *Porella brasiliensis*, *Radula caldana*, *Riccardia aberrans*, *R. ciliolata*, *Scapania portoricensis* and the filmy fern *Hymenophyllum* sp. B.

Host specificity

The Monte Carlo procedure shows that epiphytic species assemblages differ among host trees, independently from the other variables regarded in this study.

In temperate areas a relationship between phorophytes and epiphyte vegetation is often observed when comparing broad-leaved trees and gymnosperms (Barkman 1958; Nimis 1985; Oksanen 1988; Palmer 1986; Slack 1976). Bark characteristics, the structure of which was held relatively constant in this study, are usually held largely responsible and the clearest cases of host

specificity and host tree shunning are attributed to bark properties (Beever 1984; Benzing 1990; Cornelissen & ter Steege 1989; Johansson 1974; Slack 1976). Slack (1976) observed that in the Northeast of America tree species which did not show a great change in their bark properties with age, e.g. *Acer pensylvanicum*, showed no great change in epiphytes with age.

Host specificity is clearest for *Brunellia occidentalis*. On this fast growing pioneer tree not only time for colonization and growth of epiphytes is less, but also the substrate is of a different quality. Branches of *Brunellia occidentalis* carried no or tiny amounts of suspended soil in contrast with

primary forest trees at these altitudes, such as in the genus *Weinmannia*, that typically carry several centimetres of soil on their branches. Here, bark epiphytes are being replaced in time by humus epiphytes.

Host specificity is misleading in the sense that it is not the identity of the host tree that is responsible for specific tree-epiphyte relationships, but the ecological conditions prevailing on its branches and trunk. The conditions on a host tree species are bound to be less unique when more tree species are investigated. In the end, host specificity may well be limited to a few clear cut cases. For example, tree ferns that have unique 'bark' characteristics, may support a specific epiphytic flora (Beever 1984; Pócs, 1982).

Suspended soil chemistry and the distribution of epiphytes

In the Upper Montane Rain forest, no correlation could be detected between species presence and abundance of epiphytes and the EGV, pH, Ca-, N-, P-, K-, or mineral content of the organic soil on which they were growing. For the ectohydric non-vascular plants this is not unexpected since these are often thought to be dependent from atmospheric inputs for the bulk of their nutrients and water requirements (e.g. Anderson & Bourdeau 1955; Brown & Bates 1990). However, substrate dependency may not entirely be ruled out (Brown & Bates 1990). For example, the moss *Hypopterygium tamariscinum*, which appears an obligate limestone dweller in Florida (Breen 1953), attained high abundance on soil with a pH value of 7.1 (Wolf 1993 a). Moreover, suspended soil in the canopy may influence the growth of understory bryophytes by changing throughfall chemistry (During & Verschuren 1988; Tamm 1950).

Sample heterogeneity

A phytosociological analysis revealed that the recognized community-types have a characteristic

distribution with respect to altitude and position within the host tree (Wolf 1993 a, b). The defined high and low altitude communities are also clearly separated in the ordination diagram of the sample scores on the first two constrained axes, as are tree base and canopy communities (Fig. 1). The good separation of these community-types in the ordination diagram is surprising since both axes only explain 3.2% of the total variation in the species data (Table 3). The low percentage of variance accounted for is no reliable indicator whether the results may be interpreted (cf. Gauch 1982), but requires discussion.

High variability may be due to the occurrence of many low frequency-high abundance species, or when in general species abundance distribution is skewed. A downweighing of rare species and the log transformation of the species abundance values decreased the sum of all eigenvalues in a correspondence analysis from 63.97 to 41.99 and 43.14 respectively, values which are still substantial.

Assuming that the underlying model of an unimodal species response along gradients is correct, possibly the remaining variation may be attributed to unmeasured ecological factors. However, candidate variables would have to be independent from altitude or position in the host tree to provide additional explanatory power. This greatly reduces options and suggests that the variation in the species data is mostly not in response to an environmental gradient.

Noise, *i.e.* random variation of the observed response around the expected response, may be considerable in species data (ter Braak 1987, 1990). In addition, part of the high heterogeneity in this study may be attributed to the relatively small sample area. Individual trunk or branch segments sampled carried generally less than 30% of species pertaining to a community-type (Wolf 1993 a).

A high within-habitat variability is often reported for non-vascular epiphytic vegetation (Oksanen 1988; Russell & Miller 1977; Schuster 1957; Steere 1951). Epiphytic communities appear to be composed of ecologically (near)-equivalent species (Schofield 1972; Schuster

1957; Slack 1977). Thus, it has been suggested that chance, *i.e.* the arrival of propagules, is the major factor determining the species quality of epiphytic communities and accountable for the high variability between sites at identical habitats (Benzing 1981; Schuster 1957). Stochastic processes may also account for differences in abundance value. Schuster (1957) and Barkman (1958, p. 220) postulate that first arriving cryptogams (priority) are able to form pure patches through growth and vegetative reproduction, excluding new arrivals. Vascular epiphyte communities are likewise believed to be mostly organized by the relative abundances of propagules of each species (Yeaton & Gladstone 1982).

Species with overlapping Gaussian responses may coexist in dynamic environments where communities may be far from competitive equilibrium (e.g. Huston 1979). The epiphytic habitat is likely to be dynamic due to small-scale disturbances as by animals (Nadkarni & Matelson 1989; Perry 1978), branch/tree falls and expansion of the tree crown. For tropical montane epiphytes no data are available on competitive replacement rates. In temperate areas indications are that habitually competitive equilibrium is not reached, at least for (terrestrial) bryophytes (During & ter Horst 1987; During & van Tooren 1988; Slack 1977; Watson 1980).

In conclusion, epiphytic vegetation on branch or trunk segments is characterized by a high variability between samples that appears not to be related to properties of the habitat. The randomness in the supply of propagules seems the major factor responsible for the composition of the presumably non-equilibrium communities. The value of the constrained correspondence analysis for such highly variable species data is demonstrated by the good interpretability of the ordination diagram. Colonization and competitive replacement experiments are highly recommended for future research.

Acknowledgements

The assistance with identification is gratefully acknowledged of Drs. B. H. Allen, A. Aptroot,

S. P. Churchill, J.-P. Frahm, D. Griffin III, R. Grolle, R. Moberg, J. Vaa, D. H. Vitt, K. Yamada and R. H. Zander. As to vascular plants the aid of Drs J. T. Atwood, R. Callejas, K. U. Kramer, H. E. Luther, M. T. Murillo and J. O. Rangel is appreciated. Special thanks for the identification of numerous collections is forwarded to Dr. H. Sipman (lichens), Drs. G. B. A. van Reenen (mosses), Dr. S. R. Gradstein (liverworts) and the late Dr. H. Inoue (*Plagiochila*). I thank Dr. C. J. F. ter Braak, Dr. A. M. Cleef, Dr. S. R. Gradstein, Dr. M. J. A. Werger and an anonymous reviewer for their comments on the manuscript. Finally, this study would not have been possible without the tireless field assistance of J. Klomp. The study was supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO, grant W84-236).

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