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Vertical Distribution of Vascular Epiphytes in Four Forest Types of the Serranía de Chiribiquete, Colombian Guayana

Rafael Arévalo*

Laboratorio de Botánica y Sistemática, Universidad de los Andes, Apartado 4976, Bogotá, Colombia. Email: rafarev@gmail.com

Julio Betancur

Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá, Colombia. Email: jcbetancurb@unal.edu.co

Abstract. The spatial distribution of vascular epiphytes was studied in four forest types in the southeast region of the Chiribiquete National Park, Colombian Guayana. The authors identified the forest types as seasonally flooded forest or várzea (SF), nonflooded forest or tierra firme (TF), varillar forest (V), and transition forest (T). In each forest type, 500 m^2 were sampled, including all vascular epiphytes on phorophytes with dbh (diameter at breast height) $\geq$ 2.5 cm. A total of 2016 epiphytes were recorded, corresponding to 182 species, 71 genera, and 27 families. The results show that the spatial distribution of epiphytes was different in each forest type, mainly as the result of structural differences among the phorophytes, but humidity and light conditions also were factors. In all four forests, a positive correlation was found between the number of epiphytes hosted by the phorophytes and their dbh. Also a positive correlation existed between the number of epiphytes and the total height of the phorophytes in SF, TF, and T. Most of the phorophytes had few epiphytes; only in SF did 20% of phorophytes host more than ten epiphytes. The higher humidity of SF, caused by its proximity to the river and periodical flooding, may explain the abundance and complexity of the epiphyte community. In all forest types, the vertical distribution of epiphytes was clumped for the community in general, as well as for most families and species. Epiphyte type, either autotroph (holoepiphytes and hemiepiphytes) or heterotroph (hemiparasites), appeared to be a determining factor in the spatial location of the species and in the stratification that some families showed.

Key words: Chiribiquete, Colombia, Colombian Guayana, phorophyte structure, spatial distribution, vascular epiphytes

Resumen. Se estudio la distribución espacial de las epífitas vasculares en cuatro tipos de bosques del sureste de la Serranía de Chiribiquete, Guayana colombiana. Los bosques estudiados se denominaron como: bosque inundable de rebalse (SF), bosque de tierra firme (TF), bosque de varillar (V), y bosque de transición (T). En cada tipo de bosque se muestreó 500 m^2, en los cuales se censaron todas las epífitas vasculares presentes en forofitos con DAP $\geq$ 2.5 cm. Se encontraron 2016 individuos epífitos en total, correspondientes a 182 especies, 71 géneros, y 27 familias. La distribución espacial de las epífitas fue diferente en cada bosque, debido principalmente a las diferencias estructurales de los forofitos y a la humedad e intensidad lumínica que se presenta en cada bosque. En todos los bosques se presentaron correlaciones positivas entre el número de epífitas hospedadas y el DAP de los forofitos, así como con la altura total de los forofitos en SF, TF, y T. La mayoría de los forofitos presentaron muy pocas epifitas y solamente en SF el 20% de los forofitos presentó más de diez epifitas. La alta humedad en SF, dada por la proximidad al río y las inundaciones periódicas a las que está sometido el bosque, parecen explicar la mayor abundancia y complejidad de la comunidad de epífitas. En todos los tipos de bosques se encontró una distribución vertical agregada de las epífitas para la comunidad en general y para la mayor parte de las familias y especies. El tipo de epifita, autótrofas (holoepífitas y hemiepífitas) o heterótrofas (hemiparásitas), fue determinante en la ubicación espacial de las especies y en la estratificación mostrada por algunas familias.

Palabras clave: Chiribiquete, Colombia, distribución espacial, epifitas vasculares, estructura de forofitos, Guayana colombiana

Introduction

Vascular epiphytes are significant components of tropical forests, not just because of the number of species they represent, but also because of the biomass they accumulate (Nadkarni 1994, Gentry & Dodson 1987, Benzing 1990, Isaza et al. 2004). A major part of the diversity registered in neotropical forests is provided by vascular epiphytes, representing up to 25% of vascular plant species and half the total number of individuals (Wolf 1994, Galeano et al. 1998, Nieder et al. 2001).

Epiphyte distribution varies according to ver-

* Corresponding author.

tical and horizontal ecological gradients (Nieder et al. 2001). Horizontally, they can vary between forest types and host species (phorophytes); while vertically, they vary within the same tree (ter Steege & Cornelissen 1989, Kernan & Fowler 1995, Freiberg 1996). Distribution patterns of vascular epiphytes are influenced by factors such as the following: phorophyte structure (Freiberg 1996, Hietz 1997, Barthlott et al. 2001, Zotz & Vollrath 2003); substrate availability (Bøgh 1992, Kernan & Fowler 1995, VanDunné 2002); and dispersal syndromes (Kelly 1985, Todzia 1986, Gentry & Dodson 1987, Fischer & Araujo 1995). Microclimatic variables, also distribution factors, include humidity (Fischer & Araujo 1995, Annaselvam & Parthasarathy 2001, Leimbeck & Balslev 2001, Callaway et al. 2002) and light intensity (ter Steege & Cornelissen 1989, Richards 1996).

Vertical distribution of epiphytes is mostly determined by light and water availability (ter Steege & Cornelissen 1989). Richards (1996), however, considers that the availability of light, more than the humidity, better explains the differences in the vertical distribution of epiphytes. Phorophyte characteristics, such as tree size, age, and crown architecture, contribute to habitat heterogeneity and create vertical stratification, which promotes epiphyte diversity (Bennet 1986, Sillet & Bailey 2003). Consequently, bigger trees offering a larger area and more microhabitats are expected to have larger numbers of epiphytes (Annaselvam & Parthasarathy 2001, Flores-Palacios & García-Franco 2006). Branch diameter, inclination and position, occurrence of crotches and knotholes, as well as bark rugosity, affect the ability of an epiphyte to adhere to the substrate (Kernan & Fowler 1995, Freiberg 1996, Hietz 1997, Callaway et al. 2002). Thus the availability of suitable substrates also influences the establishment and growth of epiphytes and determines their vertical distribution (Bøgh 1992, Nieder et al. 2000). Although horizontal distribution is related to phorophyte structure and substrate availability, it also is influenced greatly by characteristics of the forest structure, which include species distribution, stand height, phorophyte density, and disturbances such as tree falls (Nieder et al. 1999, Barthlott et al. 2001, VanDunné 2002).

Epiphyte diversity may vary locally and on a large scale (Barthlott et al. 2001, Leimbeck & Balslev 2001, Küper et al. 2004, Arévalo & Betancur 2004, Kreft et al. 2004, Benavides et al. 2005). Spatial distribution of epiphytes, which depends to a great extent on forest structure, also should vary in relation to forest type (Catling & Lefkovitch 1989, Flores-Palacios & García-Franco 2006). Arévalo and Betancur (2004) documented the diversity of vascular epiphytes in four forest formations located in the southeast region of the Chiribiquete National Park and found differences in floristic composition among them. In the present study, we continue exploring the spatial distribution of vascular epiphytes of these forests in an attempt to identify structural differences among the epiphyte communities.

Materials and Methods

Study Site

The study was carried out in the Biological Research Station Puerto Abeja (0°04′16″N, 72°26′48″W). The area, located in the southeast region of the Serranía de Chiribiquete National Park (Caquetá province), is part of the Guianan Shield. In phytogeographical terms, it is included in the western Guianan Province (Berry et al. 1995). The research station covers an area of ca. 300 ha, from the black-water Mesay river, to a low sandstone table mountain, reaching an altitude of 250–350 m. Data collected at the station in 1998–2002 show annual precipitation at 3000–3876 mm and average monthly air temperature at 25–28°C. Relative humidity is fairly constant at 86–87% (Peñuela & von Hildebrand 1999).

In the study area, four vegetation types were considered (Arévalo & Betancur 2004): (1) a seasonally flooded or várzea forest, along the banks of the Mesay River (SF); (2) a nonflooded or tierra firme forest (TF), located on a tertiary sedimentary plain; (3) a low sclerophyllous forest, locally known as varillar (V), found on top of the sandstone mountains; and (4) a transition forest (T), corresponding to a transition area between TF and V. A synopsis of vegetation structure and composition of the area can be found in Arévalo and Betancur (2004).

Data Collection

Fieldwork was carried out from January to June 2002. In each of the four forest types, 500-m^2 plots were laid out. The number and size of the plots varied according to the area of each forest. In SF and TF, two 50 × 5 m plots could be set out; but in T and V, two plots were 20 × 5 m in size, and another two plots measured 30 × 5 m. In each plot, all trees with a diameter at breast height (dbh = ca. 1.3 m from the ground) of 2.5 cm or more were sampled. All trees were marked, and total height and distance from the ground to the first branch were recorded.

Vascular epiphytes were sampled using tree-climbing equipment to gain access to the cano-

TABLE 1. Richness and abundance of epiphytes and phorophytes in four forest types in the Serranía de Chiribiquete in Colombia.

	Forest types			
	Seasonally flooded (SF)	Tierra firme (TF)	Transition (T)	Varillar (V)
Epiphyte species (no.)	100	94	55	30
Epiphyte plants (no.)	879	514	405	217
Forest trees with dbh ≥ 2.5 cm (no.)	209	207	241	453
Phorophytes with dbh ≥ 2.5 cm (no.)	103	95	90	118
Proportion of phorophytes (%)	49.3	45.9	37.3	26
Average dbh per phorophyte (cm)	11.2 ± 10.5	10.8 ± 14.5	10.8 ± 8.7	5.2 ± 3
Average total height per phorophyte (m)	11.8 ± 5.2	12.6 ± 7.6	11.1 ± 4.9	4.6 ± 1.4
Average height to first branch (m)	7.1 ± 4.3	7.9 ± 5.0	6.6 ± 3.9	2.1 ± 1.3
Epiphyte plants per phorophyte (no.)	8.5 ± 13.4	5.4 ± 11.7	4.5 ± 6.9	1.8 ± 1.8
Epiphyte species per phorophyte (no.)	5.1 ± 5.5	3.0 ± 4.2	2.5 ± 2.3	1.3 ± 0.7

py. Following a classification based on relationships to the host tree (sensu Benzing 1990), we considered vascular epiphytes as all vascular plants that grow on other plants including autotrophs (as holoepiphytes and hemiepiphytes) and heterotrophs (as hemiparasites). Individual epiphytes on trunks and branches were counted and collected when necessary, using pruning-shears. Species occurring in dense stands, such as most of the ferns, some orchids, and aroids were counted as one stand (sensu Barthlott et al. 2001), denoting one ‘‘individual.’’ Plants were identified, and height above ground and horizontal distance to the principal axis of the phorophyte was measured using a Leica DISTO™ hand-held laser meter. For plants with hemiepiphytic or epiphytic-scandent growth habits, height was measured at the highest point reached by the whole plant. Voucher specimens were deposited at the Herbario Nacional Colombiano (COL), with duplicates at the Herbario Amazónico Colombiano (COAH).

Data Analysis

Non-parametric statistics were applied. Statistical analyses were conducted using SPSS for Windows, Version 10.0. A Kruskal-Wallis test was carried out to establish differences in the structural variables measured for the phorophytes (dbh, total height, and height to the first branch) and the number of epiphytic individuals and species they hosted. Multiple comparison tests were applied when significant differences were found (Zar 1999). The Spearman's coefficient of rank correlation (Zar 1999) was calculated to evaluate the relationship between number of epiphytes and phorophyte height and dbh.

Vertical distribution of epiphytes in each forest was analyzed using Morisita's index of dispersion (Krebs 1998). This distribution was analyzed independently for the whole epiphyte community as well as for the most important families and for species with more than eight individuals.

The most important families in each forest type are those used by Arévalo and Betancur (2004) and established by means of the Family Importance Value (FIV, modified from Mori & Boom 1983), taking into account diversity and relative abundance. To examine differences in the vertical distribution of the most important families in each forest type, Kruskal-Wallis and multiple comparison tests also were used (Zar 1999).

RESULTS

Phorophytes

In the four forest types sampled, 1110 trees with dbh ≥ 2.5 cm were found, of which only 406 were phorophytes. Forest type V (varillar) had more trees with dbh ≥ 2.5 cm than did the other forest types. The number of phorophytes, however, did not vary significantly among them. Consequently, the proportion of phorophytes was greater in SF and TF and much less in V (TABLE 1).

The structural variables measured for the phorophytes were significantly different among the forest types (Kruskal-Wallis test, $N = 406$, $\chi^2 = 45.6$, $P < 0.001$ for dbh; $\chi^2 = 194.9$, $P < 0.001$ for total height; and $\chi^2 = 161.6$, $P < 0.001$ for height of first branch). The average value of these variables was much less in V than in SF, TF, and T forests (TABLE 1).

Average values for epiphyte individuals and species per phorophyte were also significantly different among the forest types (Kruskal-Wallis test, $N = 406$, $\chi^2 = 64.7$, $P < 0.001$, and $\chi^2 = 88.5$, $P < 0.001$, respectively). The SF forest

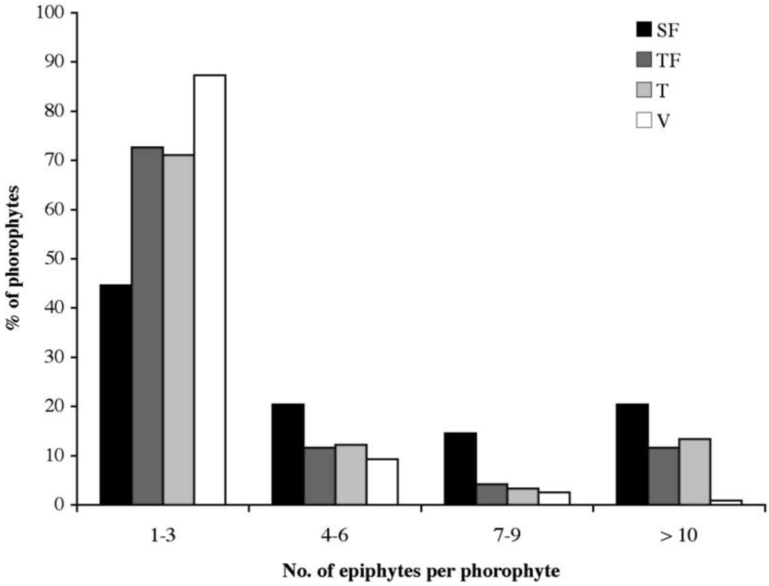

FIGURE 1. Number of vascular epiphytes per phorophyte in four forest types of the Serranía de Chiribiquete (Colombia). SF = seasonally flooded; TF = tierra firme; T = transition; V = varillar.

showed the highest average values, while V had the lowest (TABLE 1). Throughout the four forest types studied, the majority of phorophytes had very few epiphytes, especially TF, V, and T, where more than 70% of the phorophytes only had one to three epiphytes. The SF forest had the greatest number of phorophytes with more than ten epiphytes (20%); whereas in V, only one phorophyte had more than ten (FIGURE 1). The phorophyte with the most epiphytes was a species of *Eschweilera* (Lecythidaceae) with 93 individuals, corresponding to 10.6% of the total for SF.

A positive correlation was found between the number of epiphytes and phorophyte dbh for all forest types. The correlation, however, was much weaker in V (SF: $r_s = 0.50$, $P < 0.0001$; TF: $r_s = 0.47$, $P < 0.0001$; T: $r_s = 0.59$, $P < 0.001$; and V: $r_s = 0.22$, $P = 0.018$). To the contrary, only SF, TF, and T showed a positive correlation between the number of epiphytes and phorophyte height (SF: $r_s = 0.46$, $P < 0.001$; TF: $r_s = 0.49$, $P < 0.001$; and T: $r_s = 0.51$, $P < 0.01$). V did not show any correlation ($r_s = -0.0014$, $P = 0.9883$).

Vertical Distribution

Morisita's index of dispersion showed that vascular epiphyte communities in all four forest types had clumped distribution patterns (TABLE 2). Epiphytes in T and V forests were noticeably clumped around a height of 2 m, after which, a progressive decrease resembled a reverse J-shaped curve (FIGURE 2).

In TF forest, a large concentration of epiphytes occurred around a height of 2 m, decreasing after this height and increasing again after 8 m, after which slight oscillations in vertical distribution were shown. In the SF forest, very few epiphytes were found in the lowest strata, with a pronounced increase at 4–6 m, after which, the number of epiphytes decreased and remained relatively similar but always above the levels of the other forest types until 18.1–20 m (FIGURE 2).

By Species

Morisita's standardized index of dispersion (I_p) for species with more than eight individuals in each forest shows that more than half of them have clumped vertical distribution patterns. Species with higher indices of clumped dispersion were found in V and correspond to the orchids *Scaphyglottis amethystina, Epidendrum nocturnum,* and *Maxillaria tarumaensis.* The majority of species with uniform distribution were found in SF and TF forests, mainly hemiepiphytes of the families Araceae and Clusiaceae (TABLE 3).

By Families

In all forests, the five families with the highest Family Importance Value (FIV) showed clumped distribution patterns, except Clusiaceae in TF and Loranthaceae in V, which showed random distribution patterns (TABLE 2). The Krus-

TABLE 2. Morisita's standardized index of dispersion (I_p) for the vertical distribution of the vascular epiphyte community (total no. of epiphytes) and of families with the greatest Family Importance Value (FIV) in four forest types in the Serranía de Chiribiquete (Colombia).

Forest type	Communities and families	Morisita's standardized index of dispersion (I_p)	Distribution pattern
Seasonally flooded (SF)	Community	0.51	Clumped
	Araceae	0.51	Clumped
	Bromeliaceae	0.54	Clumped
	Clusiaceae	0.50	Clumped
	Dryopteridaceae	0.51	Clumped
	Orchidaceae	0.51	Clumped
Tierra firme (TF)	Community	0.51	Clumped
	Araceae	0.54	Clumped
	Clusiaceae	−0.08	Random
	Dryopteridaceae	0.50	Clumped
	Orchidaceae	0.51	Clumped
	Polypodiaceae	0.51	Clumped
Transition (T)	Community	0.57	Clumped
	Araceae	0.52	Clumped
	Clusiaceae	0.50	Clumped
	Dryopteridaceae	0.62	Clumped
	Hymenophyllaceae	0.94	Clumped
	Orchidaceae	0.52	Clumped
Varillar (V)	Community	0.70	Clumped
	Bromeliaceae	0.62	Clumped
	Dryopteridaceae	0.72	Clumped
	Grammitidaceae	1.00	Clumped
	Loranthaceae	−0.05	Random
	Orchidaceae	0.78	Clumped

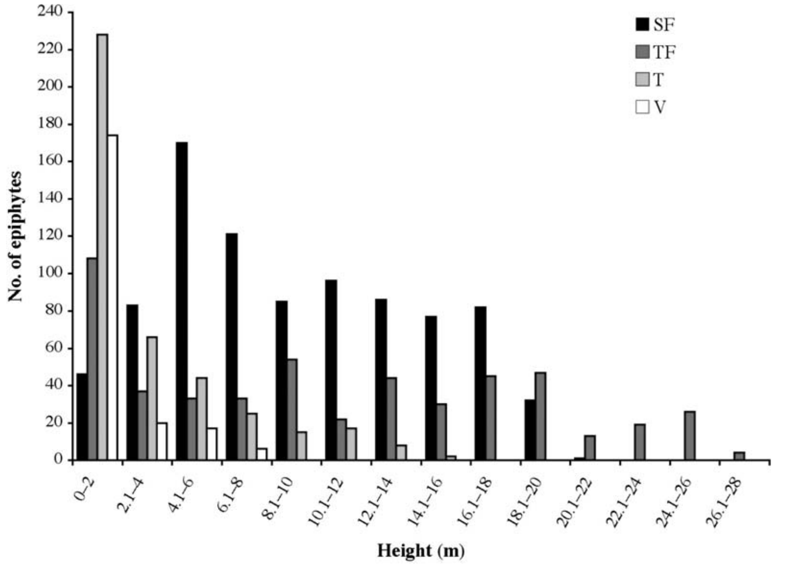

FIGURE 2. Vertical distribution of vascular epiphytes in four forest types of the Serranía de Chiribiquete (Colombia).

TABLE 3. Vertical distribution patterns (%) according to Morisita's standardized index of dispersion (I_p) for vascular epiphyte species with more than eight individuals in four forest types in the Serranía de Chiribiquete (Colombia).

Forest type	Epiphyte species (no.)	Epiphyte species with >8 individuals (no.)	Distribution pattern (%)		
			Uniform	Random	Clumped
Seasonally flooded (SF)	100	35	8.57	34.29	57.14
Tierra firme (TF)	94	18	0.00	27.78	72.22
Transition (T)	55	5	6.67	26.67	66.67
Varillar (V)	29	6	0.00	16.67	83.33

kal-Wallis test showed that in all forest types, the five families with the highest FIV had significantly different vertical distributions (SF: $N = 710$, $\chi^2 = 103.5$, $P < 0.001$; TF: $N = 458$, $\chi^2 = 213.9$, $P < 0.001$; T: $N = 364$, $\chi^2 = 29.5$, $P < 0.001$; and V: $N = 209$, $\chi^2 = 47.8$, $P < 0.001$).

In the SF forest, families with the highest FIV made up two groups. The first (Orchidaceae and Clusiaceae), were found in the highest strata of the forest, whereas the second (Araceae, Bromeliaceae, and Dryopteridaceae) preferred the lower parts of the forest. In TF, families with the highest FIV formed three groups. The first only included the family Araceae, concentrated in the lowest strata of the forest; the second group (Dryopteridaceae and Clusiaceae) was found at intermediate heights, and the third group (Clusiaceae, Orchidaceae, and Polypodiaceae) showed a tendency for the higher strata of the forest. This trend was strongest in Orchidaceae and Polypodiaceae (FIGURE 3).

In the T forest, families with the highest FIV also formed three groups. The first only included the family Hymenophyllaceae, distributed exclusively among the lowest parts of the forest. The second group was made up of Araceae, Clusiaceae, and Dryopteridaceae, and the third group by Araceae, Clusiaceae, and Orchidaceae (FIGURE 3). Lastly, families with the highest FIV in the V forest formed two groups. The first was made up of Bromeliaceae, Dryopteridaceae, Grammitidaceae, and Orchidaceae, distributed in the lowest strata of the forest. In contrast, the second group, made up of only Loranthaceae, exclusively preferred the highest strata of the forest (FIGURE 3).

Horizontal Distribution

By Individuals

Horizontal distribution of epiphytes with respect to the distance from the phorophyte trunk was similar in all four forest types. The great majority of epiphytes (78–94%) were found on the central trunk or at a distance of less than 1 m from the trunk. Epiphytes at greatest distance from the trunk were found in SF (FIGURE 4).

By Species

More than the half the vascular epiphyte species found in each forest were located on the main trunk of the phorophyte or at a distance of less than 1 m. In TF, 30% of species (28) had individuals at a distance of more than 1 m from the main trunk of the phorophyte. Only nine of these were found at a distance of more than 2 m. In the T forest, seven species of epiphyte (12%) were found at a distance of more than 1 m from the main trunk and only two orchids (*Encyclia aspera* and *Octomeria amazonica*) presented individuals at more than 2 m. In V, individuals of only three species were found at a distance of more than 1 m from the main trunk of the phorophyte (*Tillandsia paraensis, Phthirusa stelis,* and *Encyclia aspera*).

Lastly, in the SF forest, almost half of the species (47) showed individuals at more than 1 m from the main trunk, and 39 of these had at least one individual at a distance of more than 2 m. More than half of these species (20), however, were found on only one phorophyte: the same *Eschweilera* sp. (Lecythidaceae) that had the greatest number of individual epiphytes.

DISCUSSION

The structure of each forest type was reflected in the number of phorophytes and epiphytes found (TABLE 1). The most structurally complex forest types (SF, TF, and T) had a higher proportion of phorophytes and epiphytes (Arévalo & Betancur 2004), very possibly the result of their greater size, area, variety in branch diameters, as well as availability of crotches and knotholes for epiphyte colonization (Annaselvam & Parthasarathy 2001, Flores-Palacios & García-Franco 2006). These forests showed pos-

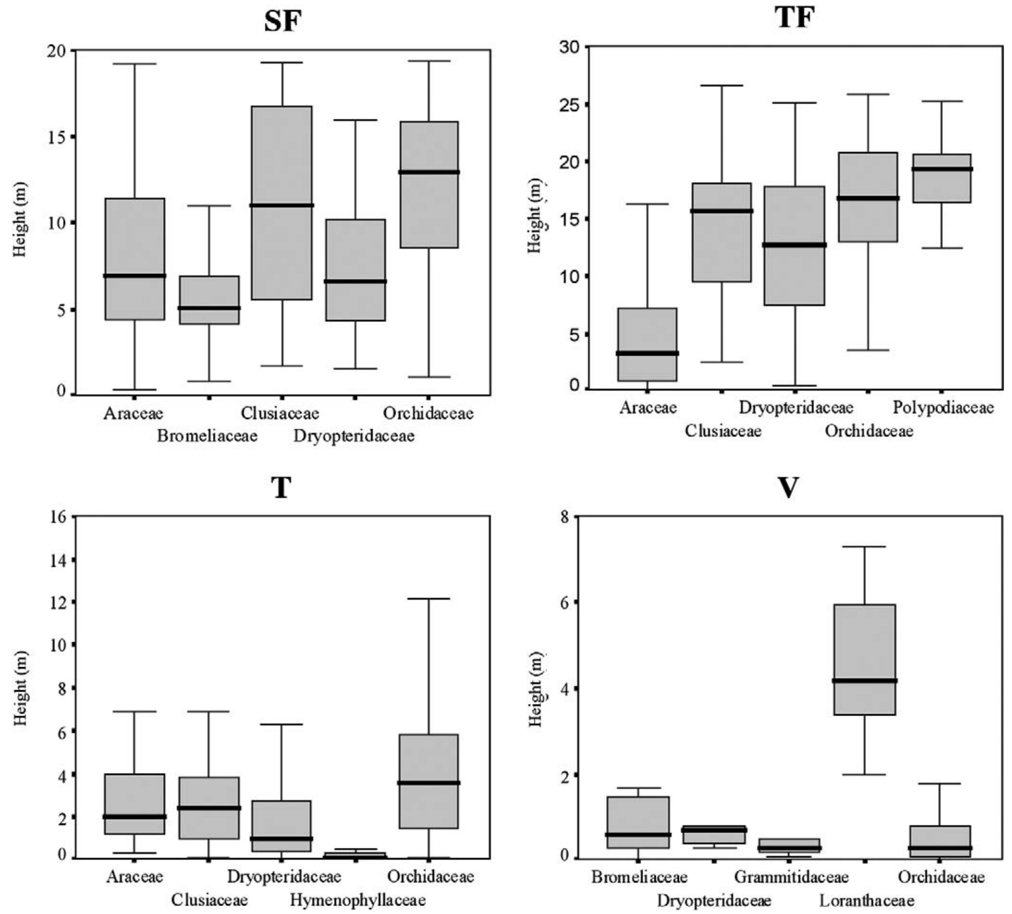

FIGURE 3. Vertical distribution of families with greatest Family Importance Value in four forest types in the Serranía de Chiribiquete (Colombia).

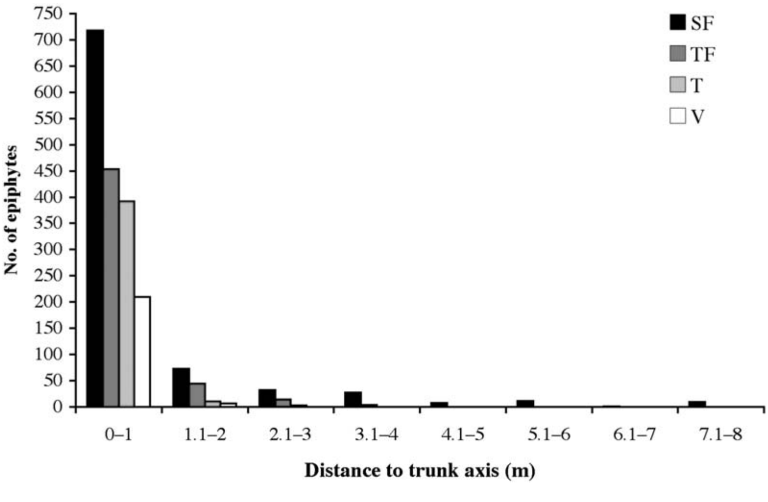

FIGURE 4. Horizontal distribution of vascular epiphytes in four forests of the Serranía de Chiribiquete (Colombia), with respect to the distance from the phorophyte trunk axis.

itive correlations between the number of epiphytes and some of the structural variables measured, such as dbh and phorophyte height. The smallest number of epiphytes was found in the lowest (in terms of height) and least stratified forest V with the lowest proportion of phorophytes (TABLE 1).

Although epiphyte communities showed clumped vertical distribution patterns, clumping range was not the same in the four forest types (TABLE 2, FIGURES 2, 3). This contrasted with what Benavides et al. (2005) found in different Amazonian landscape units, where the greater concentration of epiphytes was found on stem bases. Although in TF and T, almost half of the epiphytes occurred at a height of 0–4 m, the SF forest had a much smaller proportion within this height range (FIGURE 2). This may be a direct consequence of the periodic flooding experienced during the rainy season, given that the river level can rise several meters above the forest floor and inhibit the establishment of epiphytes in the lower strata of the forest. In TF, some phorophytes had buttress roots, providing more surface area and substrate for the establishment and development of epiphytes in the lowest strata of the forest (FIGURE 5). The simpler structure (thin and small trees) and microclimatic characteristics (high light penetration that generates high temperatures and low humidity) of V, seem to restrict the growth of the majority of epiphytes to the lower strata of the forest. This explains why the V forest showed the most clumped distribution pattern (TABLE 2).

Some families show trends with respect to vertical stratification, especially Orchidaceae, Clusiaceae, Araceae, Hymenophyllaceae, and Loranthaceae. This stratification could correspond to different epiphyte growth forms as well as to the morphological characteristics of the species. For example, members of Orchidaceae in SF, TF, and T showed a preference for higher strata (FIGURE 3), and individuals were distributed from the main trunk of the phorophyte to the extremes of the branches. All species of Orchidaceae found were small, holoepiphytic herbs (Arévalo & Betancur 2004), capable enough to colonize superior strata of the canopy, far from the main trunk. Araceae preferred lower strata (FIGURE 3), and the great majority of individuals were observed growing on or very close to the main trunk of the phorophyte. This distribution may be the result of the hemiepiphytic creeping habit of the majority of species. The Hymenophyllaceae, small ferns with membranous leaves and a high susceptibility to desiccation, were exclusively found in the lowest strata of the T forest (FIGURE 3). They were able to grow at this place, only because they normally are found on trunks covered with moss, which provides them the necessary humidity for their development (Iwatsuki 1990). Species of Clusiaceae, although also found in higher strata, showed a wider ranging vertical distribution, which was reflected in a random distribution pattern in TF (TABLE 2). Members of this family, both epiphytes and hemiepiphytes, also were found growing in ant gardens (Arévalo & Betancur 2004), a factor that may promote a wider ranging vertical distribution.

The distribution of species of Loranthaceae was very characteristic, given that they were found exclusively in higher strata of the V, SF, and T forests. For example, the only Loranthaceae present in V (*Phthirusa stelis*) had a random distribution pattern and was found much higher than any other epiphyte in this forest (FIGURE 3). This hemiparasitic species has ecological and physiological characteristics that allow it to colonize the highest strata. Rather than depending on water availability and environmental nutrients for its establishment and development, *Phthirusa stelis* draws on the conducting vessels of its host species. Some authors, such as Benzing (1990), classify the Loranthaceae as heterotrophic epiphytes, while others exclude them, as they are not free-living plants (Moffet 2000, Kreft et al. 2004). The results of this study also show that species of this family have a distribution different from that of other epiphytes, probably because of their hemiparasitic habit.

The greater abundance of epiphytes toward the center of the phorophyte crowns agrees with that recorded in other articles (Bøgh 1992, Freiberg 1996). A considerable number of epiphytes far from the main trunk were observed only in the SF forest (FIGURES 4, 5), which may be the result of a greater availability of light and humidity in this riverine forest (Sinclair 1990). Their proximity to a constant source of humidity as well as periodic flooding may facilitate the establishment and development of epiphytes. Furthermore, a greater horizontal distribution of these branches offers more possibilities for colonization by wind-dispersed diaspores (Fischer & Araujo 1995).

In all the forest types studied except for V, the most abundant species found at a distance of more than 1 m from the central trunk of the phorophyte were holoepiphytic orchids and pteridophytes. Species of Araceae were not found far from the main trunk, because of their hemiepiphytic creeping habit (Arévalo & Betancur 2004).

This study shows that the spatial distribution of epiphytes depends, to a great extent, on phorophyte structural variables (height, dbh, and

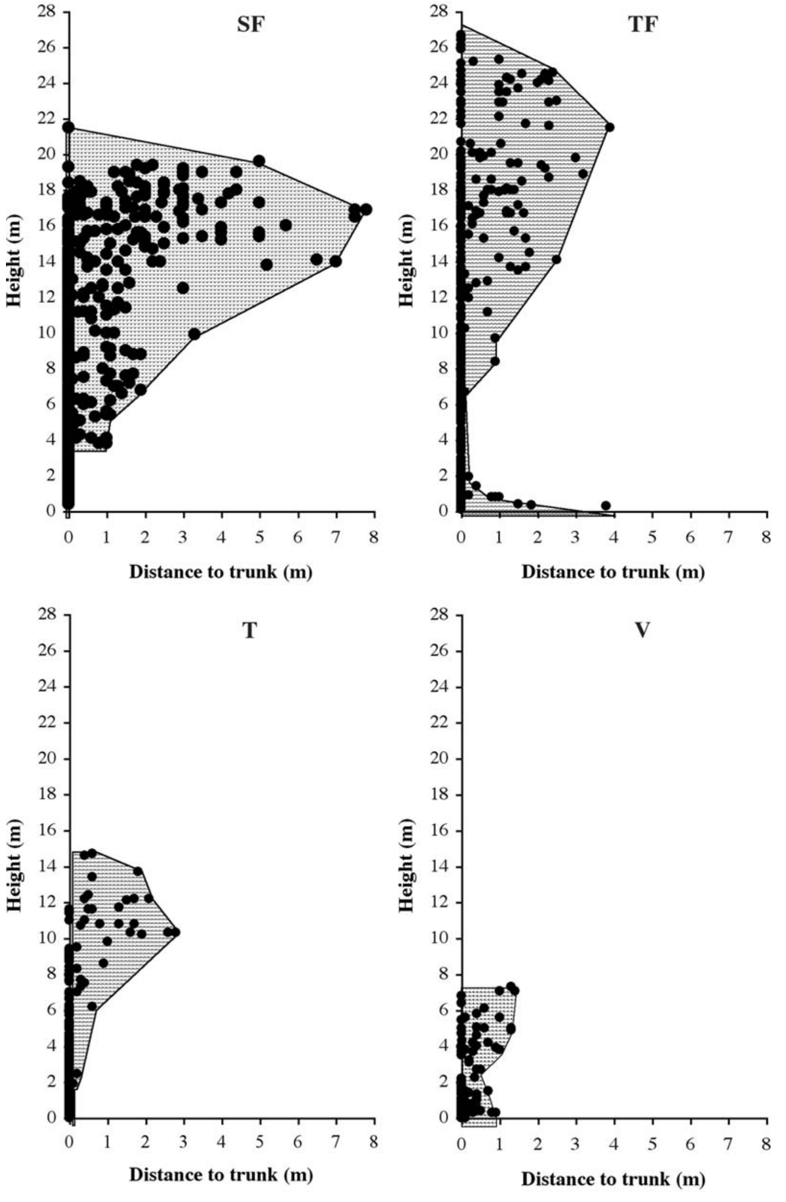

FIGURE 5. Spatial distribution of vascular epiphytes in four forest types of the Serranía de Chiribiquete (Colombia), taking into account the height at which they were found (vertical distance) and distance from the phorophyte trunk axis (horizontal distance).

availability of branches). Additionally the structural complexity of forests, as well as their vertical stratification, promotes a higher diversity of epiphyte species (Bennet 1986).

Microclimatic aspects of the forests, among them humidity and light intensity, appear to be determining factors in the vertical and horizontal distribution of epiphyte species, especially in the SF and V forests. Other influential factors are the epiphytic growth habit (holoepiphytes and hemiepiphytes vs. hemiparasites) and ecological and physiological characteristics. Thus the spatial distribution of epiphytes indirectly reflects the quantity of resources within forests and the way in which the host trees are exploited by these plants.

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