Effects of the spatial distribution of trees, conspecific epiphytes and geomorphology on the distribution of epiphytic bromeliads in a secondary montane forest (Cordillera Central, Colombia)

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ABSTRACT. The spatial organization of epiphytes has come under increasing attention. This kind of information is necessary for the general understanding of their ecology and for the design of sustainable harvesting methods. In this study, the small-scale (local) distribution of epiphytic bromeliads was studied using correlograms and permutational regression on distance matrices. Fieldwork was carried out in a young secondary forest stand in the central cordillera of Colombia at 3150 m asl. A complete census of the bromeliads in this plot was made, using a lattice with 400 quadrats. Six species of bromeliad were found (1008 individuals). All of these except one showed an aggregated spatial pattern. This pattern was independent of the position of the trees in the sampled plot. The distribution of the bromeliads was determined by the availability of substrate (branch surface area per quadrat), the proximity of conspecifics and the geomorphology of the terrain. The structure of the forest surrounding an epiphyte had an influence on the position of the epiphyte in the tree (height measured as distance from the canopy). The use of two-dimensional, lattice-based sampling strategies is discussed as a possible method for comprehensive surveys of epiphyte populations in natural forests.

KEY WORDS: Bromeliaceae, conservation ecology, GIS, permutational regression, spatial ecology

INTRODUCTION

The spatial organization of vascular epiphytes in forests has come under increasing scrutiny by canopy scientists over the last few years. The three-dimensional mapping of a 1-ha plot by Nieder *et al.* (2000) is one of the most

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elaborate results. However, epiphytes inhabit a discontinuous three-dimensional landscape (Bennett 1987), and most standard methods in field ecology assume that measurements are made in a continuous landscape. Few of these standard methods are directly applicable to epiphyte studies.

In epiphyte ecology, the sampling unit is often defined as one host tree (or part thereof), but unit area and unit forest-volume have also been used. Previous studies of the distribution patterns of vascular epiphytes have been carried out on single trees (Johansson 1974, Yeaton & Gladstone 1982), in transects (Tremblay 1997) and tree stands (Hietz-Seifert *et al.* 1996, Madison 1979). These studies used different methods and their results are not easy to compare. None of these studies simultaneously accounted for both the spatial distribution of the epiphytes and the spatial distribution of the trees in the sampled plots. An added problem is that a lack of prior knowledge about the scale of a phenomenon increases the risk of pseudoreplication in field studies (Hurlbert 1984), and detailed information about the spatial scale of epiphyte distributions is scanty. In general mensurative experiments (*sensu* Hurlbert 1984) on epiphytes are difficult to design because of the complex interaction between epiphytes, hosts, forest structure and climate, and different process-scales of the components of this system. As a consequence, most epiphyte studies to date have been tree-centred, taking the host tree as a sampling unit, and as a starting point for defining the habitat of epiphyte species. From this viewpoint, the habitat characteristics, age and size of the host tree are the determining factors for epiphyte presence. As a sampling unit, however, the host tree is only suitable for a small number of ecological experiments. Furthermore, spatial autocorrelation is common in ecological data sets (Koenig 1999, Legendre 1993). Only when unit area is used in epiphyte studies, standard geostatistical tools can be used to describe the autocorrelation present in the data set since these methods assume a continuous spatial context (Cressie 1993, Rossi *et al.* 1992).

Previous studies have shown that epiphytes tend to separate vertically through the canopy (Serna Isaza 1994). This vertical stratification can be specific for groups of species, identified as guilds by Kernan & Fowler (1995). Recruitment limitation can cause species to have a distribution outside of their optimal niche (if such an optimum exists) so that it is difficult to infer the ecological requirements of species from their realized niche (Hurtt & Pacala 1995). The concept of an 'optimal niche' probably has little value when studying epiphytes in secondary forests, since the canopy in these forests is highly dynamic (Hartshorn 1980), and the micro-climate of tree patches is unlikely to remain stable over extended periods of time. Some authors suggest incorporating these dynamics by combining an architectural analysis of trees with three-dimensional mapping of epiphytes (Gradstein *et al.* 1996), but for the present study, a more quantitative approach was sought.

Many epiphytes can propagate vegetatively (non-vascular epiphytes, but also

vascular epiphytes like the bromeliads in this study) and the specific location which they occupy may reflect the time of arrival of propagules, a process largely determined by chance (Benzing 1981, Ingram & Nadkarni 1993, Schuster 1957, Wolf 1993). Another factor likely to determine the occurrence of epiphytes within a forest stand is the amount of substrate available for colonization (Bennett 1986), although tree size also affects the diversity on available microsites (Hietz & Hietz-Seifert 1995). Bennett (1986) suggested that a mass effect (*sensu* Shmida & Wilson 1985) would determine the neighbourhood relationships of vascular epiphytes, whereby seed availability would predominate over the environmental conditions of sites in determining the distribution of species.

Bromeliads (Bromeliaceae) are best known for their most prominent member – the pineapple – but other species from this family have a wide variety of uses, including those as ornamental, medicinal and ritual plants (Bennett 2000). Many of the species with ornamental and ritual uses grow as epiphytes. The local and international trade of these plants may be threatening some species with extinction, even though a considerable proportion of the traded plants are cultivated (Dimmit 2000). Methods to harvest bromeliads in forests sustainably are currently being developed (Wolf & Konings in press) but these efforts require statistical tools which can distinguish between the effects of the spatial distribution of trees, the environmental conditions at each inhabited patch and the distance to possible seed sources on the spatial distribution of epiphytes.

The purpose of this study was to test the following two hypotheses. First, we expected the spatial distribution of the epiphytic bromeliads to show a pattern which is independent of the spatial pattern of their substrate. Second, we expected to find a clear effect of the propagule supply on the structure and composition of epiphytic bromeliad communities in forest stands. During the analysis of the data, permutational regression on distance matrices (Borcard *et al.* 1992) proved to be a good method to separate the spatial and environmental components of the variation. Host specificity was not considered important in this particular forest since all tree species in the plot had been seen with epiphytes elsewhere (pers. obs.). The present paper addresses the need for more knowledge on the spatial organization of epiphytic communities, and methods to collect and analyse this type of data (Nadkarni & Parker 1994).

MATERIALS AND METHODS

Field work

Field work was carried out in the Central Cordillera of the Colombian Andes, near Santa Rosa de Cabal, Department of Risaralda (4°50′17″ N, 75°30′14″) from February to May 1999. In this area, rainfall has a bimodal distribution with two wet seasons (around April and around May, temperatures vary between 5 and 10 °C, air humidity is high and rain is common in the afternoon

(Witte 1995, Wolf 1993). The studied forest was situated on the western slope of the volcanic mountain area in Los Nevados National Park. Inside this forest, a secondary forest stand was chosen at 3150 m asl which was cut down around 1963 (*c.* 35 y old at the time of sampling). The most important criterion for this choice was the overall structure of the stand, which was 10–15 m tall and geometrically relatively simple. According to the owner, the original stand had been cleared for charcoal production but was not subsequently used for farming or pasture (J. Morales pers. comm.). The stand had an area of approximately 3 ha and was surrounded by highly disturbed secondary vegetation on the northern edge. The other edges were surrounded with older secondary forests. The understorey was relatively bare, and predominantly covered by *Psychotria longipedunculata* Dwyer (Rubiaceae), *Chusquea* sp. (Gramineae) and some Marchantiaceae (liverworts) species. The predominant tree species were *Brunellia* sp. (Brunelliaceae), *Weinmannia pubescens* Kunth and *Weinmannia rollotii* Killip (Cunoniaceae), *Saurauia* cf. *ursina* Tr. & Pl. (Actinidiaceae) and *Miconia lehmannii* Cogn. (Melastomataceae).

To determine the necessary size of the plot and quadrats, and the main sources of variation, a pilot study was carried out (Hanke 1999). On the basis of this pilot study, I placed a 50-m × 50-m plot in the centre of the forest stand. This plot was subsequently divided into 400 2.5-m × 2.5-m contiguous quadrats. These quadrats were small enough to detect pattern in bromeliad distributions but large enough to be laid out in the forest and restrict the number of quadrats to be sampled to a feasible amount (Hanke & VanDunné unpublished data). The quadrats were demarcated with coloured rope, and in each quadrat all bromeliad ramets (>5 cm) were counted using binoculars. This was made possible by the low stature and generally open structure of the forest plot. Species were reliably identified vegetatively in all size classes after a year of working in the area, including time spent on other field work and the aforementioned pilot study. For each bromeliad genet the height in the tree, host-tree number and life stage (small juvenile, juvenile, vegetative adult, adult with ramets, flowering, fruiting, decaying flower or senescing plant) were recorded. The size classes used are shown in Table 1.

The difference in ground height between quadrats, was measured from the centre of each quadrat using a water level. Tree heights, the height along the stem at which the crown starts, and the height of epiphyte positions were recorded using a clinometer (Suunto PM-5/1520P and PM-5/66).

Table 1. The limits of individual height (expressed in cm) delimiting the size classes used in the field to distinguish between small juveniles (SJU), juveniles (JUV) and adults (ADU). Shown are the values for *Racinea penlandii* (RP), *R. tetrantha* (RT), *Tillandsia biflora* (TB), *T. compacta* (TC) and *T. orbicularis* (TO).

	RP	RT	TB	TC	TO
SJU	>5–10	>5–10	>5–10	>5–10	>5–10
JUV	>10–15	>10–15	>10–20	>10–20	>10–20
ADU	>15–20	>15–20	>20	>20	>20

For each tree, the dbh, number of branch nodes >5 cm diameter, tree height and crown projection surface were recorded. The length of tree branches was estimated for each of four branch-diameter classes (>5–10 cm, >10–15 cm, >15–20 cm, >20 cm), including trunks.

For each quadrat, the branch length in each diameter class and the openness of the canopy above each of the quadrats were assessed. Additionally the number of branch nodes overhanging the quadrat were counted. Canopy openness was assessed by estimating the percentage of the projected area above each quadrat that was covered by vegetation. Epiphytes occurring on lianas were not given a host tree number. The estimates of the branch length in each quadrat were checked against the estimates of the total branch length of the trees. An overview of the recorded variables is shown in Table 2.

Vouchers of terrestrial and epiphytic species have been deposited at the Herbarium of the University of Antioquia (HUA) in Medellín and the National Institute of Sciences (COL) in Bogotá.

Statistical analysis

The bromeliad census data and the environmental variables were entered into a lattice-based Geographical Information System (GIS) (PCRaster version 2, Utrecht University) and a database program (Filemaker Pro version 4.0, Filemaker Inc.). The GIS was used for visual inspection of the data and data manipulation, database management, and calculation of data summaries. In the sampling design and data storage, height is treated as a variable, but not as a position, i.e. all mapping techniques used in this study are based on a (x, y) coordinate system.

As a measure for the environmental conditions in the quadrats, a window average of the variables was made using the GIS. A window average is the average value of a variable in all surrounding cells, and is attributed to the centre cell (the centre cell can be included or excluded from the average). The size of these windows was based on the results of the correlograms. In this way, the models can test whether the abundance of a species, or the juveniles of a species, depends on the abundance of bromeliads and forest structure in the surrounding quadrats. These windows had an area of 156.25 m^2 (25 quadrats), except in the case of the conspecific species, where a window of 24 quadrats had to be used, excluding the centre cell, to avoid using the data already included in the independent variable of the regression.

The age classes were collapsed into juveniles (JU), vegetative adults (VA) and other adults (OA). The latter group included all genets which had reproduced, and included plants with one or more ramets. I use the terms 'genets' for genetic individuals that are the products of a single germination event and 'ramets' as a unit of clonal plant growth as defined by Menges (2000). Total abundance in each quadrat was recoded into five classes for the data from one quadrat (0 = 0, 1 = 1, 2 = 2–3, 3 = 4–6, 4 = more than 6 individuals). The total abundance of each window was recoded into seven classes (0 = 0, 1 = 1–5, 2 =

Table 2. A list of the measured and calculated variables used in this study. Note that some attributes are not directly attributed to the cells. For example, tree height is an attribute to each tree, but after calculating the canopy height, this average is assigned to each cell.

Cell attributes
    Estimated or measured in the field
        Spatial position
            (x, y) coordinates
        Quadrat structure
            Canopy openness
            Canopy height above quadrat
            Number and order of ramifications
            Branch length in diameter classes of overhanging trees
        Topography
            Cell elevation
        Epiphytes
            Count of individuals
        Trees
            Height
            Diameter at breast height (1.3 m)
            Status (dead/alive)
            Number and order of ramifications
            Branch length in diameter classes
    Calculated variables
        Quadrat structure
            Basal area of living trees
            Basal area of dead trees
        Window averages
            Average canopy openness
            Average canopy height
            Basal area living trees
            Sum of ramifications

Epiphyte attributes
    Estimated or measured in the field
        Spatial position
            Distance to the ground
        Characteristics
            Species
            Size class
    Calculated values
        Spatial position
            Distance to the canopy
            Distance to topographical zero

6–10, 3 = 11–20, 4 = 21–40, 5 = 41–80, 6 = more than 80) (cf. Leduc *et al.* 1992, Svenning & Balslev 1999). The recoded data were later used in the regression analysis to compute the distance matrices of the species data (see below).

The variable 'canopy height' is a weighted average of the tree heights, weighted by the cover fraction of the trees in each quadrat. In this way, a tree which has a large cover of a quadrat contributes proportionally more to the canopy height of that quadrat than a tree with a smaller cover.

The total amount of tree surface was estimated by calculating the total area on the branches (tba) for each tree, and for each quadrat based on the length and average dbh of each class. Both values are expressed in m^2. Trunks were included in the tba and measured in the same classes as branches. For those

trunks found in the >20 cm diameter class (this class has no centre value) an average was made for each tree separately between 20 cm and its dbh (maximum dbh was 29.9 cm). Taper was not taken into account, even though this makes the estimate less accurate, but estimating taper from photographs proved to be difficult. However, in this young stand tapering off of branches did not seem pronounced.

Moran's *I* correlograms were calculated using the Autocorrelation module of R Package (Université de Montréal, version 3.03), and the (two-dimensional) euclidean distances between the quadrats were divided into 27 classes. A distance interval (lag) of 2.49 m was used for the correlograms.

Morisita's (Morisita 1964) index was used as suggested by Hurlbert (1990), which expresses the chance of drawing r individuals from the same quadrat as a ratio of the same chance under a random distribution. Full curves (i.e. across all crowding levels) were not calculated, because quadrat crowding varied widely among species classes, from 2 to 16 (*R. tetrantha*) genets per quadrat.

Three regression models were performed using permutational regression on distance matrices with significance testing by permutation using Permute! (version 3.4a9) (Legendre *et al.* 1994, Legendre & Legendre 1998). The first with the species abundances in each quadrat, to test for each species whether its abundance depends on the presence of other bromeliads, either of the same species or of a different species. Second a similar model is tested for the juveniles of each species. The third model tests for an effect of topography, structure (as before) and euclidean distance on two measures of position on the z axis: the distance to the ground and distance from the canopy.

The distance matrices of most variables in the regression analysis were based on a binary-state (i.e. including one variable for each object) or a multi-state (i.e. including more than one variable for each object) difference matrix. For the binary-state matrices of the species, a difference matrix where $D_1 = |y_{1j} - y_{2j}|$ was computed. For the multi-state matrices the average distance was used (Legendre & Legendre 1998, p. 278).

A multi-state matrix of the forest structure variables created using Gower's coefficient of similarity (Legendre & Legendre 1998, p. 278, Svenning & Balslev 1999) and was then converted to distances by subtracting it from 1. This latter matrix included the variables cell cover, number of ramifications, canopy height, basal area of living trees and basal area of dead trees.

The geographic distances were used to create a euclidean-distance matrix of the centre coordinate of each quadrat. A binary-state matrix was made of the digital elevation model of the plot (the elevation values of each grid cell stored in the GIS) data using Gower's coefficient of similarity, converted to a distance by subtracting it from 1 (cf. Svenning & Balslev 1999).

RESULTS

In the 0.25-ha plot, 831 living trees and 512 dead trees and stumps with a dbh > 1 cm were sampled yielding a total branch area (tba) of 2265 m^2. A

total of 1008 bromeliads of six species were recorded. The species were: *Racinea penlandii* (Ruiz & Pav.) M.A. Spencer & L.B. Sm., *Racinea tetrantha* (Ruiz & Pav.) M.A. Spencer & L.B. Sm., *Tillandsia biflora* Ruiz & Pav., *Tillandsia compacta* Griseb., *Tillandsia orbicularis* L.B. Sm. and *Guzmania* sp. Only two genets of *Guzmania* sp. were found in the plot and these were excluded from the analysis. The living trees encountered in the plot had an average height of 11.5 ± 3.8 m (the results show averages followed by standard deviations, unless otherwise stated), with a maximum of 22.0 m. The dead trees and stumps had an average height of 4.1 ± 2.9 m.

Compared to the overall average, *T. orbicularis* and *T. biflora* had the highest proportion of juveniles of the sampled species (Figure 1) while *Racinea tetrantha* had a high occurrence in the plot which influenced the overall average. *Racinea tetrantha* and *T. compacta* showed the largest amount of vegetative propagation, and there were very few decaying plants and plants with decaying inflorescences observed (Figure 1).

Visual inspection of the data suggested that the distribution for all species and age classes is aggregated (Figure 2). The spatial pattern of the juveniles and vegetative adults seem to follow the pattern of the other adults in the plot, on visual inspection. The Morisita index for the 6.25-m^2 cells decreased for most species from older plants to younger plants suggesting that the older plants were more aggregated than the juveniles (Table 3).

Both the variables of forest structure and the bromeliad abundance were autocorrelated (Figure 3). The correlograms of the bromeliads decline monotonically (Figure 3), which may indicate that quadrats which are close together
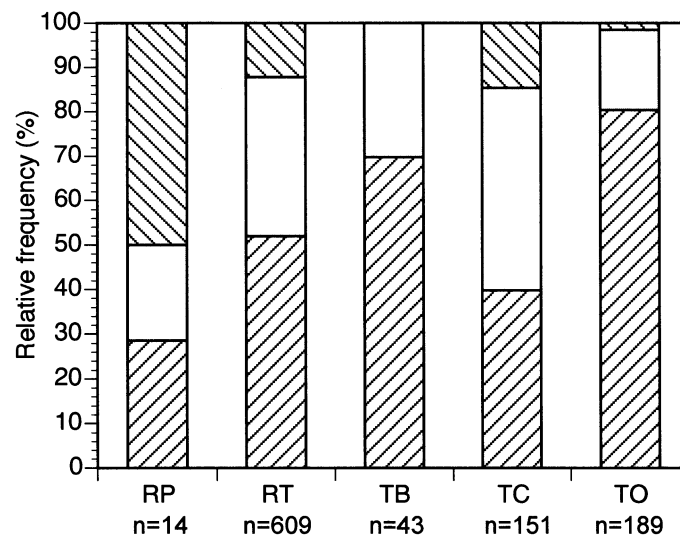

Figure 1. Relative frequencies of the size classes of bromeliad species in the censused plot. Shown are the values for *Racinea penlandii* (RP), *R. tetrantha* (RT), *Tillandsia biflora* (TB), *T. compacta* (TC) and *T. orbicularis* (TO) expressed as percentages of the total amount of genets in the plot. The number of genets is shown below the x-axis. The bars show the percentages of juveniles (lower, hatched), vegetative adults (middle, unshaded) and older adults (upper, hatched).
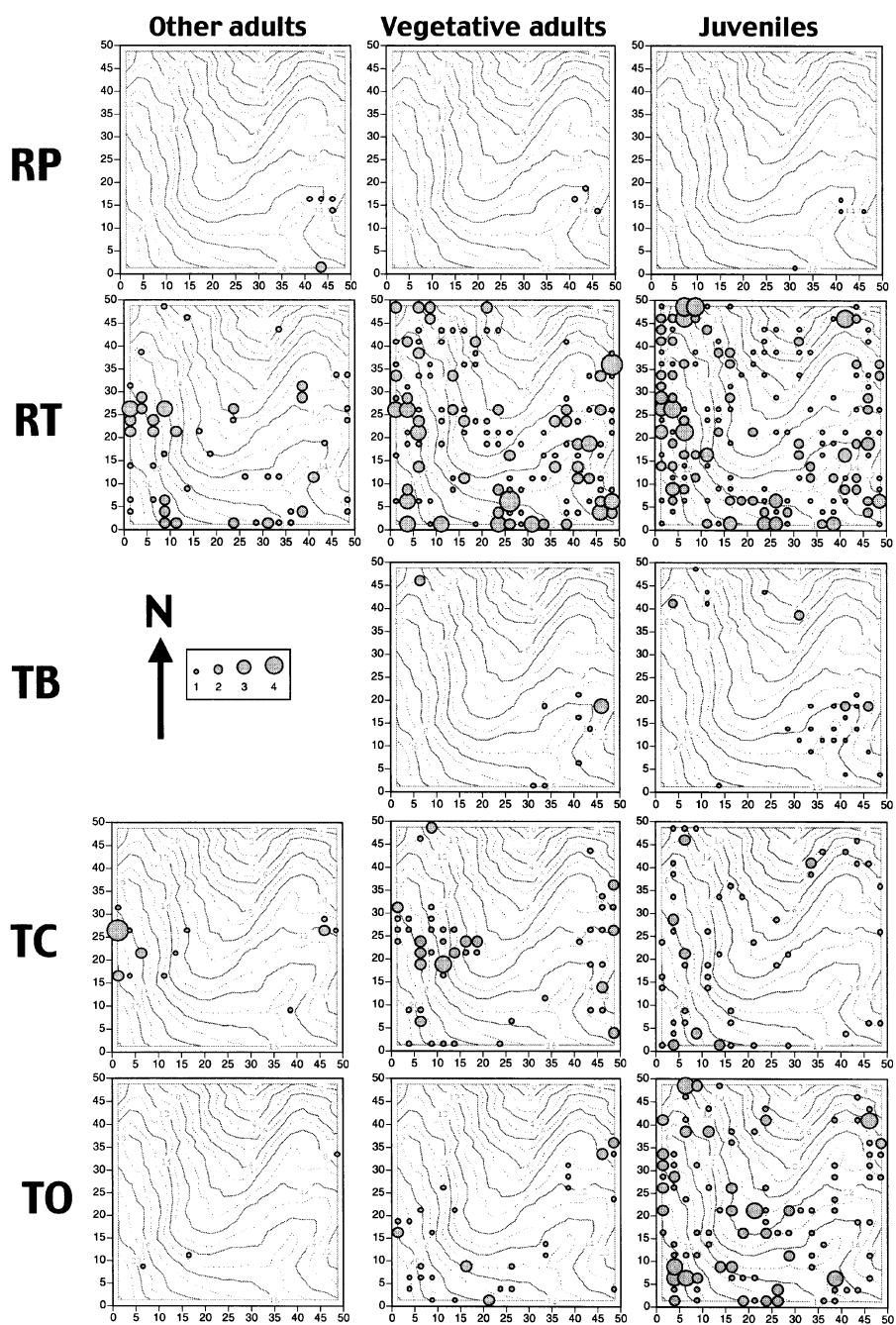
Figure 2.   Spatial distribution of species in the 50-m × 50-m plot. The three age classes of each species are shown, independently against the topography of the plot. The isoclines are shown for every metre difference in topographical height, referenced to the lowest point in the area (see zero mark on northern edge). Other adults are genets which have flowered and genets with more than one ramet. The abbreviations of the plant names are as follows: *Racinea penlandii* (RP), *R. tetrantha* (RT), *Tillandsia biflora* (TB), *T. compacta* (TC) and *T. orbicularis* (TO). The dot size indicates the frequency of the species in each quadrat. The arrow next to the legend shows the compass direction.

Table 3. Morisita index at three different values of r (the number of individuals sharing a cell). This index is a measure for the divergence of the species occurrences in the cells from a random distribution of the individuals over the sampled area. Higher values of r could only have been calculated for some of the species, and are not shown, because it was uncommon for more than four individuals of a given species and age class to occur in one cell. The species abreviations follow Table 1. In the columns the values for the juveniles (JU), vegetative adults (VEG) and other adults (OA). The last column shows Morisita's index for all individuals of a given species, regardless of their size class. Cases for which I could not be calculated are marked with n.a.

		JU	VEG	OA	All
RP	r = 2	0	0	57.1	39.6
	r = 3	0	0	11.4	3.3
	r = 4	0	n.a.	0	0
RT	r = 2	3.37	3.17	4.74	2.84
	r = 3	0.06	0.04	0.06	0.035
	r = 4	0	0	0.001	
TB	r = 2	3.68	35.9	n.a.	9.74
	r = 3	0	5.59	n.a.	0.648
	r = 4	0	0.56	n.a.	0.049
TC	r = 2	2.49	4.26	41.6	4.56
	r = 3	0.02	0.05	9.09	0.091
	r = 4	0	0	1.91	0.002
TO	r = 2	3.24	3.57	0	3.17
	r = 3	0.04	0	0	0.035
	r = 4	0	0	n.a.	0

are similar in species abundance while quadrats further apart are not, or less, similar. There are some irregularities in this monotonic decline but the peaks are not strong enough to suggest any clear grouped structure of the data set. The 0.25-ha plot was probably too small to show these.

The aggregated pattern of the species is also suggested by the values for Morisita's index in Table 3. In comparison to a random distribution of individuals, it was between three to forty times more likely to draw a quadrat at random with a pair of any species from the observed data. The co-occurrence of three individuals in a quadrat was likely for individuals of *R. penlandii* and *T. biflora*, but diverged only slightly from a random distribution in the case of the other species. Higher order aggregations were not marked in the data as this was uncommon in the sampled plot (Table 3).

Most values for Moran's I are low, but significance survived Bonferroni correction well and, as discussed in the Methods section, these correlograms were used to decide on the size of the windows used for averaging. For this, I looked at the distance at which the last positive and significant Moran's I was calculated. For the data on forest structure, the last positive value of Moran's I lay between lag 2 (dead basal area) and lag 7 (canopy height). The bromeliads have slightly higher lags at which the last positive Moran's I is calculated, namely 3 (*R. penlandii*) and 9 (*T. orbicularis*). On the basis of these values, a window of 25 adjacent quadrats (5 × 5) was chosen for the calculation of window averages to be included as variables in the permutational regression.

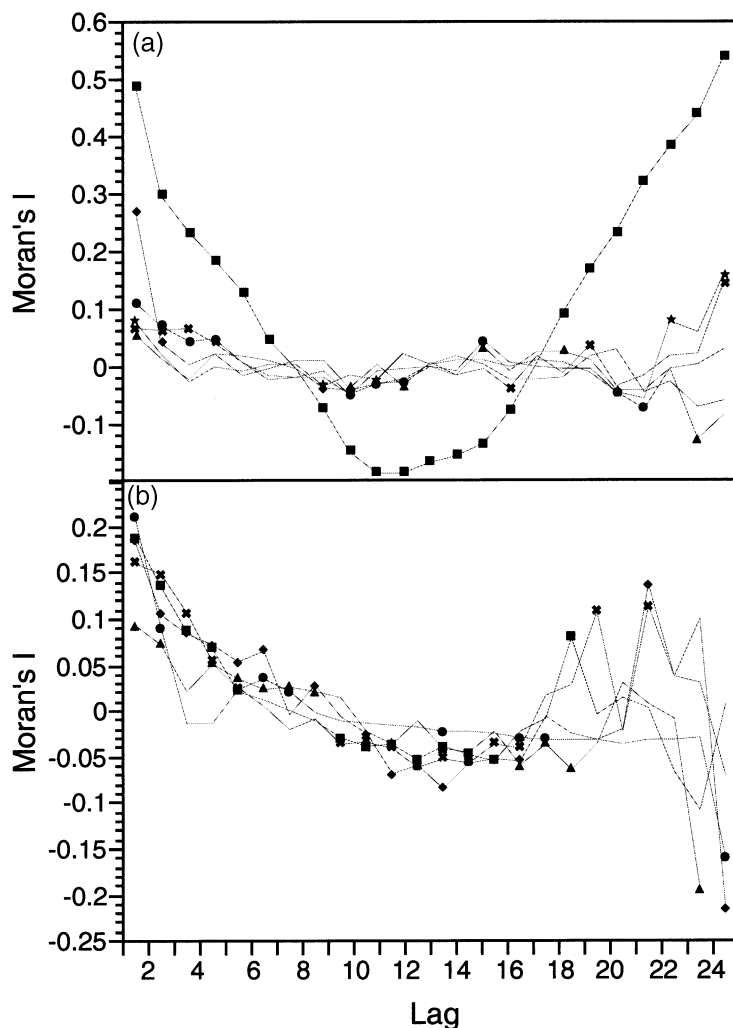The bromeliads showed different responses to the variables substrate,

Figure 3. Correlograms of the variables of forest structure (a) and species abundances (b) in the sampled plot based on Moran's *I*. Only the points which showed a significant autocorrelation are shown (P < 0.05, progressive Bonferroni correction). In (a) the following variables are shown: total branch surface (circles), cell cover (diamonds), canopy height (squares), number of ramifications (crosses), basal area of living trees (triangles) and basal area of dead trees (stars). In (b): *Racinea penlandii* (circles), *R. tetrantha* (diamonds), *Tillandsia biflora* (crosses), *T. compacta* (squares) and *T. orbicularis* (triangles). Each lag is 2.49 m wide, lags 26 and 27 are not shown because there were not enough comparisons possible at those distances.

structure and space, and the spatial position of conspecifics in the regression model of bromeliad abundances per quadrat (Table 4). *Racinea penlandii* showed a marked response to the surrounding conspecific individuals in the model. A similar effect was observed for *T. biflora* in the partial regression, but not in the full model where *T. biflora* abundance was best predicted by the values for branch area, the structure of the surrounding forest and the topography of the area. For the remaining species, *R. tetrantha*, *T. compacta* and *T. orbicularis*, the variables branch area, structure and space had significant contributions to both

Table 4. Results of the permutation regression on the species. On the first line, the R² values of the full model are shown, followed by the models with only species data and environmental data. Significance of the beta coefficient is displayed as follows: * = 0.05 < P < 0.01, ** 0.01 ≤ P < 0.001. Non-significant coefficients are not shown. Species abbreviations follow Table 1. After the variable names the size of the window used for the window-average is shown (w24, w25). Those variables where a window-average was not used are marked (cell).

Model	Variable	RP	RT	TB	TC	TO
Full	Branch area (cell)		0.176 **	−0.053 *	0.243 **	0.155 **
	Other species (w25)		0.044 *			
	Conspecifics (w24)	0.393 **				
	Structure (w25)			0.23 **	0.185 **	
	Topography (cell)			−0.075 *		
	Space (cell)		0.093 **	0.067 **	0.063 **	0.075 **
	R²	0.154 **	0.044 **		0.104 **	0.031 **
Species	Other species (w25)		0.065 **			
	Conspecifics (w24)	0.388 **		0.247 **	0.202 **	
	R²	0.153 **	0.005 **	0.061 **	0.04 **	
Structure and Space	Structure (w25)					
	Branch area (cell)		0.176 **	−0.065 **	0.25 **	0.155 **
	Topography (cell)			−0.114 **		
	Space (cell)		0.1 **	0.083 **	0.061 *	0.072 **
	R²		0.043 **	0.015 *	0.071 **	0.029 **

the full model and in the partial models. A very similar pattern is apparent for the juvenile individuals which all show an effect of the abundance of conspecifics in the neighbouring quadrats, except *R. tetrantha* (Table 4). The abundance of older individuals of *R. tetrantha* in surrounding quadrats did not have an effect on the abundance of juvenile *R. tetrantha* individuals either (Table 5) while the juveniles of the other species again showed an effect of conspecific abundances. However, there is a difference between the models shown in Tables 4 and 5. In comparison to the contribution of variables to the species model in Table 4, the model of the juvenile individuals in Table 5 showed a similar, or sometimes higher, contribution of the species data (Table 6). On the other hand the substrate–structure–space variables had a lower contribution to the model in Table 5 than they had in the model in Table 4, with the exception of *T. compacta* (Table 6).

The effect of total branch area was also tested by calculating Spearman's non-parametric regression coefficient between tree surface and the number of epiphytes on the tree for each tree that had one or more epiphytes ($r_s = 0.27$, $P < 0.0001$, n = 349). Only 895 epiphytes are included in the correlation, since some of them grew on lianas (no host tree recorded), or on trees overhanging the plot but standing outside it (no measurements of tree size taken).

Position within the canopy

Because of the large differences in the number of observations of each bromeliad species, the averages of the distance to the ground and to the canopy could not be compared. The regression of the height values on the structure, (x, y) coordinates and topography did not give consistent results for each one of the species (Table 7). For some species the distance to the ground increased with a change in topography (*R. tetrantha*, *T. compacta*), structure (*T. compacta*, *T. orbicularis*) or location in the plot (*T. orbicularis*). For the other species the distance to the ground decreased with a change in location in the plot (*R. tetrantha*, *T. compacta*).

The distance to the canopy increased with a change in the structure of the surrounding quadrats (*R. tetrantha*, *T. compacta*), topography (*R. tetrantha*, *T. biflora*, *T. orbicularis*) and location in the plot (*T. orbicularis*). In one case it decreased with a change in spatial position (*T. biflora*).

Epiphytes on trees that stood in local depressions within the plot were found further from the ground ($r_s = -0.208$, $P < 0.0001$, n = all 1006 observations) and closer to the canopy ($r_s = 0.129$, $P < 0.0001$, n = all 1006 observations). The correlation coefficients of the individual species show a similar (significant) trend.

DISCUSSION

This study shows that there is an aggregated spatial pattern of bromeliads in the secondary forest studied. This pattern can best be explained by the position

Table 5. Results of the permutation regressions on the juveniles of each species. On the first line, the R² values of the full model are shown, followed by the models with only species data and environmental data. Significance of the beta coefficients is displayed as follows: * = 0.05 < P < 0.01, ** 0.01 ≤ P < 0.001. Non-significant coefficients are not shown. Species abbreviations follow Table 1. Behind the variable names the size of the window used for the window-average is shown (w24, w25). Those variables where a window-average was not used are marked (cell).

Model	Variable	RP	RT	TB	TC	TO
Full	Branch area (cell)		0.143 **		0.094 **	0.149 **
	Older other species (w25)		0.124 **			
	Older conspecifics (w25)	0.239 **				
	Structure (w25)			0.32 **	0.075 *	0.109 **
	Topography (cell)		0.099 **		0.068 *	0.062 **
	Space (cell)					
	R²	0.059 **	0.05 **	0.105 **	0.025 **	0.037 **
Species	Older other species (w25)					
	Older conspecifics (w25)	0.234 **	0.146 **	0.318 **	0.08 *	0.114 **
	R²	0.057 **	0.022 **	0.101 **	0.009 *	0.013 **
Structure and Space	Branch area (cell)		0.147 **	−0.062 **	0.098 *	0.15 **
	Structure (w25)			−0.089 **	0.067 **	0.067 **
	Topography (cell)					
	Space (cell)		0.117 **	0.062 *		
	R²	0.003 n.s.	0.035 **	0.011 *	0.02 **	0.026 **

Table 6. A comparison between the fit of the partial models and the full model in Table 4 and Table 5 (expressed as a percentage of R^2). See Table 1 for full names of species.

Species	Species model		Juvenile model	
	Species (%)	Space structure (%)	Species (%)	Space structure (%)
RP	99.4	–	95.8	–
RT	10.7	96.2	44.9	69.8
TB	90.2	22.7	96	10.2
TC	38.2	68.7	37.5	79.7
TO	2.6	93.8	33.8	71

of conspecific bromeliads and it is independent of the placement of trees. The structure of the forest surrounding an epiphyte has an influence on the position of the epiphyte in the tree. This latter result suggests that while at least some environmental conditions at a specific location will have changed over the years, some echo of the earlier conditions can still be measured. Whether the requirements for seedlings or for adult plants are similar, and whether one set of conditions is more important than the other for the spatial pattern observed, cannot be answered from this data set and will require future work. Below, each of these points will be discussed in detail.

Spatial aggregation

Wind-dispersed seeds are likely to remain close to the parent plant (Malanson & Armstrong 1996), and more likely to do so when seeds are larger (Augspurger 1986). In this study, juvenile genets of all species show a significant effect on the abundance of older individuals in the surrounding cells, except for *R. tetrantha* (Table 5). This exception was probably due to the high quadrat occupancy of *R. tetrantha*, which might have made a pattern less discernible (Figure 2). The effect of the proximity of older conspecifics on the presence of juveniles suggests that these bromeliads are dispersal limited. In other words, successful establishment of these epiphytes is more likely in close vicinity to the parent plants.

The Morisita Index (I_m) shown in Table 3 has the advantage over other measures of spatial aggregation that it is independent of density and is unchanged by random mortality (Hurlbert 1990). The availability of tree surface for colonization did contribute to the overall model in the case of the most abundant species (*R. tetrantha*, *T. compacta*, *T. orbicularis*). It is likely that this reflects the high occurrence of these epiphytes. The more frequent a species is, and the more trees it occupies, the more closely its spatial distribution will follow that of the trees. The abundance of the two most infrequent species (*R. penlandii* and *T. biflora*) can be better predicted by the number of conspecifics in surrounding cells, than by the amount of available substrate or the structure of the surrounding forest (Table 4 and 5). Apparently, the distribution of these species is limited by dispersal and few seeds from the surrounding forest have successfully established in the sampled plot.

Madison (1979) showed clumped, gregarious and random distributions on trees in a rubber plantation and suggested that the distribution pattern of epiphytes is determined by the seed-dispersal mechanisms of each individual species. However, his conclusions were based on the variance-to-mean ratio of species occurrences, which has since been shown to be an erroneous measure of deviation from a random pattern (Hurlbert 1990). Spatial aggregation of epiphytes has also been shown in transects (Tremblay 1997), but this author did not take into account the shifts in tree density along the transect either.

Influence of substrate availability

Bennett (1986) found a relationship between the number of epiphytes on trees and the number of vertical stems that these trees had, but not with the dbh of the trees. He concluded that although available space was important for epiphyte settlement, other factors play a larger role. My results support the idea that even within a relatively small forest area, variations in epiphyte occurrence can be explained in part by substrate availability. This was found for all species except *R. penlandii*. As mentioned above, there are few individuals of *R. penlandii* present and substrate does not limit its distribution in the plot. Probably, when its abundance increases this clear-cut pattern will become more diffuse, as in the case of *R. tetrantha*. This is one of the reasons why finding patterns in older epiphyte populations (in more mature forests) is challenging. Another reason is that the tallying of available tree-surface area will be more difficult and time consuming in a structurally more complex forest.

Micro-habitat

The 'structure' variable in the regression models reflects the differences in tree density and canopy height of the quadrats surrounding the quadrat where the number of epiphytes are counted. For neither all size classes (the species model) nor the juveniles is there a significant effect of this variable, suggesting that the differences in micro-climate caused by the structure of the surrounding forest does not influence the number of epiphytes present. On the other hand, given the highly dynamic nature of the forest, the distribution of epiphytes in the present is likely to reflect climatic conditions in the past, not in the present. It might be much more worthwhile to describe the ecological preferences of epiphytic species in terms of forest architecture, and to describe their population ecology using terms from tree architecture and identify the hosts of the past, hosts of the present and hosts of the future (Gradstein *et al.* 1996, Oldeman 1983, Vester 1997).

Topography did have an effect on the abundance of *R. penlandii* and *T. biflora* and the abundance of *T. biflora* juveniles, caused by a depression in the landscape (see contour lines in Figure 2). The sampled plot is too small to correlate bromeliad abundance with elevation, but Sugden (1981) has shown a relationship between topology and bromeliad density, which varied for different species. Trees standing on ridges have a higher incidence of wind, and consequently seeds will be deposited there more often. Trees standing on the

ridges also have a higher incidence of light. The combination of higher seed input and more favourable environmental conditions is a likely cause of higher local abundance.

Location in the canopy

The response in the regression model of the bromeliad position (height in tree) to topography and forest structure suggests that there is a relationship between forest characteristic and the height of epiphytes. Especially the response to topography – epiphytes on the ridges of the plot are closer to the ground – was surprising because the ground level differences are small, with a maximum difference of 22 m. In Sugden's (1981) study, the maximum difference in elevation was much higher (close to 300 m). Gullies in the canopy, like those shown by Herwitz & Slye (1992), were not apparent in the digital elevation model of the canopy heights in the studied plot. However, the scale of my study was likely to be too small to incorporate large-scale irregularities of the canopy, and the forest stand may have been too young to show them.

It was not possible to test the differences between the average heights of the six bromeliad species studied because of the large differences in the number of observations. The significance of the (x, y)-component in the regression results in Table 7, suggest that there is an effect of space so that individuals close together differ less in their height than individuals far apart (except in the

Table 7. Results of the permutation regression of the height values of the species, measured as distance from the ground and distance from the canopy. The probabilities are based on 999 permutations. Significance of the beta coefficients is displayed as follows: $* = 0.05 < P < 0.01$, $** 0.01 \leq P < 0.001$. Non-significant coefficients are not shown. The species names follow the abbreviations of Table 1.

Species	Variable	Distance to ground Beta coefficient	Distance to canopy Beta coefficient
RP	Structure		
	Topography		
	XY distance		
	R^2		
RT	Structure		0.209 **
	Topography	0.164 **	0.042 *
	XY distance	−0.07 **	
	R^2	0.023 **	0.046 **
TB	Structure		
	Topography		0.263 **
	XY distance		−0.181 **
	R^2		0.077 *
TC	Structure	0.134 **	0.293 **
	Topography	0.115 **	
	XY distance	−0.133 **	
	R^2	0.035 **	0.09 **
TO	Structure	0.072 *	
	Topography		0.132 **
	XY distance	0.093 *	0.155 **
	R^2	0.013 **	0.039 **

case of *T. compacta*). This is a further argument in favour of the idea that most individuals stem from the local (within-stand) propagule supply. Unfortunately it was not possible to assess the proportion of individuals which resulted from germination of seeds from parents outside the plot. A better understanding of bromeliad dispersal distances would facilitate the generation and testing of hypotheses about bromeliad population biology, and ultimately it would facilitate strategic conservation management.

Assessment of the methodology

Instead of attempting to replicate this study, the emphasis was put on sampling as large an area as possible within the time limits of the field work. Also, according to Dutileul (1998) none of the procedures for random spatial sampling can guarantee a spatially independent set of sample values. Large-scale studies of epiphytes of the kind Condit *et al.* (2000) have reported for trees would be fascinating, but in the mean time, there is much to be gained from studies on a smaller scale. However, to make the studies comparable across different vegetation types, some consensus on the methodologies employed must be reached among epiphyte ecologists.

Legendre & Legendre (1998) have several recommendations for estimating the scale of a sampling design aimed at answering an ecological question incorporating spatial patterns. Following these recommendations, and taking into account the results from this study, when sampling wind-dispersed epiphytic bromeliads the following suggestions can be made for future work.

The sampling grain should be larger than 1 m^2 (the size of the largest plant), and smaller than 156 m^2 (from correlograms, Figure 3). The sampling extent of 0.25-ha, used in this study, was not large enough to estimate the distance of dispersal, because only one, or at most two clusters of parent plants with their possible offspring are included in the 0.25-ha plot. An area at least four times as large would be necessary to do so in this secondary forest, and a larger area will be required in a more mature forest.

The optimal sampling interval cannot be readily determined from the present data. Sampling efficiency, however, could be increased by using the same number of samples (400) and spreading these out over a larger area, for example in a chequerboard array. Combining this method with genetic information about the sampled plants, so that inferences about the population structure can be based on the combination of genetic and spatial nearness, will be an important step in understanding the structure of epiphyte populations and the underlying ecological processes.

The chosen grain of the study (6.25 m^2) involved a substantial amount of work, but did give a good resolution. An error of approximately 20 cm was made while laying out the quadrats and no corrections were made for the slope in the plot. Also, the assignment of branch area and epiphytes to quadrats was sometimes difficult because the borders had to be projected upward. However, the assignment to quadrats was unique (no one epiphyte assigned to two

quadrats). All in all, total error may well have been close to the length of one quadrat (2.5 m), so that all borders are fuzzy.

Few natural forests are structurally as simple as the one sampled for this study. The approach used here for the determination of the total branch area in each quadrat will be difficult to use in cases where single trees have to be divided over many quadrats. In such cases a possible solution may be to use a larger grain, possibly the size of the average or maximum tree crown projection area. The amount of available tree surface must be quantified as accurately as possible, although not all forests will require the same detail. In forest where there is a strong correlation between tree size and epiphyte abundance, less complex measures of tree size can be considered.

There are a number of alternatives to the permutational regression I have used here. Of these, partial canonical analysis (Borcard *et al.* 1992) is the most compelling. However, this method has two main disadvantages for its application to this particular data set (results are not shown). First, the variability of species data per quadrat is low and this leads to inflated percentages of explained variance on the axes. Second, the matrix of spatial variables (containing the terms of a polynomial trend-surface model) may not be applicable to a discontinuous spatial phenomenon because the trend-surface model assumes a continuous (stationary) process (Isaaks & Srivastava 1989, p. 532). Last, it was not possible to include a third matrix in the partial canonical analysis, namely the matrix containing the tree surface data.

Concluding remarks

The bromeliads in this study showed an aggregated spatial distribution which can be explained in terms of the distance to conspecifics and structural characteristics of the forest stand (including geomorphology). Both factors are a source of autocorrelation in epiphyte data, and should be taken into account (and partialled out in some way) in ecological studies, especially when a comparison is made between two different forest plots. Three-dimensional surveys of epiphytes will probably remain difficult to carry out if the amount of available substrate needs to be incorporated (i.e. for any study which needs to be spatially explicit). A two-dimensional lattice-based sampling design which comprises a larger area, with less detail, may offer much more information about the structure of epiphyte populations in relation to forest structure.

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