A protocol for sampling vascular epiphyte richness and abundance

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(*Accepted 6 December 2008*)

Abstract: The sampling of epiphytes is fraught with methodological difficulties. We present a protocol to sample and analyse vascular epiphyte richness and abundance in forests of different structure (SVERA). Epiphyte abundance is estimated as biomass by recording the number of plant components in a range of size cohorts. Epiphyte species biomass is estimated on 35 sample-trees, evenly distributed over six trunk diameter-size cohorts (10 trees with dbh > 30 cm). Tree height, dbh and number of forks (diameter > 5 cm) yield a dimensionless estimate of the size of the tree. Epiphyte dry weight and species richness between forests is compared with ANCOVA that controls for tree size. S_{Chao1} is used as an estimate of the total number of species at the sites. The relative dependence of the distribution of the epiphyte communities on environmental and spatial variables may be assessed using multivariate analysis and Mantel test. In a case study, we compared epiphyte vegetation of six Mexican oak forests and one Colombian oak forest at similar elevation. We found a strongly significant positive correlation between tree size and epiphyte richness or biomass at all sites. In forests with a higher diversity of host trees, more trees must be sampled. Epiphyte biomass at the Colombian site was lower than in any of the Mexican sites; without correction for tree size no significant differences in terms of epiphyte biomass could be detected. The occurrence of spatial dependence, at both the landscape level and at the tree level, shows that the inclusion of spatial descriptors in SVERA is justified.

Key Words: autocorrelation, bromeliads, Colombia, community ecology, Mexico, multivariate analysis, oak forest, species diversity

INTRODUCTION

In his classic study on the sociology of epiphytes, Went (1940) described the canopy by lying, face-up, with field glasses on a stretcher, while field-assistants transcribed his spoken observations. Plants fallen to the ground and local tree-climbers provided voucher collections. Although these techniques seem primitive compared with those used by modern canopy scientists, much of our knowledge of epiphyte distribution is still based on this type of data (Johansson 1974, Ochsner 1935, Schimper 1888, van Oye 1924).

The innovation of rope-climbing and other canopy-access techniques such as walkways, platforms, cranes and hot-air balloons to gain access to the forest canopy resulted in a burgeoning of interest in canopy research (Dial & Tobin 1994, Gottsberger & Döring 1995, Laman 1995, Mitchell *et al.* 2002, Moffett 1993, Nadkarni & Parker 1994, Parker *et al.* 1992, Perry 1978, Whiteacre 1981). In contrast, quantitative methods to sample and analyse vascular epiphyte vegetation in the canopy have received little attention, with a few exceptions (Barker & Pinard 2001, Bergstrom & Tweedie 1998, Gradstein *et al.* 1996, 2003; ter Steege & Cornelissen 1988). Comparisons among inventories and datasets are often hampered because investigators used different sample units (e.g. branch segments, branches, trees, ground surface plots) or sample sizes (e.g. number of trees, number and size of plots) (Wolf & Flamenco-S. 2003). Ideally, comparisons should be performed on trees of the same species and of the same size (Johansson 1974). Such situations, however, are difficult to find in multiple localities in species-rich tropical forests. Our objective in this paper is to develop a universal, quantitatively rigorous sample design that permits comparisons of epiphyte richness and abundance among forest stands of differing structure.

We recognize three reasons for the lack of universal sampling protocols for epiphytes. First, epiphytes grow

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in an intricately structured three-dimensional habitat within which discrete branches are patchily distributed. Even within the same tree, two branch segments differ with respect to their history, topology and microclimate. Second, epiphyte communities are very rich in species, particularly in wet tropical areas, so minimal areas (defined as the area that contains an adequate sample of species of regular occurrence; Westhoff & van der Maarel 1973) can exceed the surface area of individual branches or even whole trees (Johansson 1974, Wolf 1993a, b). Third, the distribution of epiphytes is non-random (Laube & Zotz 2006), being heterogeneous at a range of spatial and temporal scales (Bennett 1986, Nieder *et al.* 2000, Wolf 1994, 2005). Nearby trees may have more similar epiphyte vegetation than those far away (Bader *et al.* 2000, Barkman 1958, Cascante-Marín *et al.* 2006, Catling *et al.* 1986, Hietz & Hietz-Seifert 1995, Madison 1979).

For epiphytes in humid tropical forests, the combination of high richness (α-diversity) and high species turnover (β-diversity) causes the number of species and their densities to rise continuously with increasing sample area (Annaselvam & Parthasarathy 2001). In most epiphyte community studies, sample plots have been 0.1 to 1 ha, which comprise only a portion of the local epiphyte flora. For example, in a 170-ha study area in Ecuador, Gentry & Dodson (1987a, b) found 127 out of 227 vascular epiphyte species in a 0.1-ha plot. On relatively small *Annona* trees, Nieder & Zotz (1998) concluded that 30 trees must be sampled to include the 10 most abundant species with 50% certainty. If the same holds for large trees, a substantial sampling effort is needed. This problem may be handled by using a relatively scale-independent diversity measure such as parametric Fisher's alpha (Magurran 1988). However, alpha is underestimated in communities in which the spatial arrangement of individuals is strongly clustered (Schultea *et al.* 2005). Moreover, because many epiphytes are clonal, it is difficult to count discrete individuals.

These obstacles have hampered the development of a standard sampling method and diversity measure for epiphyte inventories. Gradstein *et al.* (2003) developed a useful protocol, Rapid and Representative Analysis of Epiphyte Diversity (RRED). Based on empirical evidence they suggested that sampling eight large trees – standing well apart and being representative of local variation in bark and canopy structure – and all shrubs and treelets in a 20×20-m area around each tree should represent the species richness of vascular epiphytes in 1 ha of tropical forest. Trees are subdivided in five vertical zones according to Johansson (1974); presence–absence of epiphyte species is scored in each tree zone and on the shrubs and treelets.

Here, we present a protocol to sample and analyse vascular epiphytes that addresses these issues at the community level: Sampling of Vascular Epiphyte Richness

and Abundance (SVERA). SVERA compares the richness and abundance of epiphytes in forest stands that differ in structure (as a result, for example, from disturbance). SVERA adds three critical activities to the RRED-protocol. First, SVERA estimates the true abundance of each species, in terms of species biomass. Although per cent branch cover provides a good estimate of biomass for non-vascular epiphytes (McCune 1990), it is not a good measure for vascular ones because many species extend beyond the branch surface area. Using the number of individuals is also suspect because large plants use more resources than small ones (Benavides *et al.* 2005, Zotz 2007a, b). Distinguishing true individuals (genets) in a mass of ramets is also difficult, especially in montane forests. Rare species that occur only once or twice, however, may be counted with confidence because the number of occurrences is likely the same as the number of individuals. SVERA uses the number of individuals in rare species to estimate total number of species in the inventories (S_{Chao}). In lowland forests, spatially separated stands of epiphytes have been counted (Sanford 1968) instead of individuals, but this ignores the fact that epiphytes can have hidden connections within canopy soil or on undersides of branches. Estimating biomass may overcome the problem of counting individuals but is more time-consuming. Destructive sampling can incur long-term damage (Muir *et al.* 2006). Nevertheless, dry weight from recorded plant sizes in a number of size-cohorts provides meaningful results (Benavides *et al.* 2006, Wolf 2005).

Second, SVERA incorporates tree basal area, tree density and trunk diameter frequency distributions so that epiphyte abundance data can be extrapolated to a forest area. The diameter frequency distribution can reveal the history and conservation status of the forest, and discern whether epiphyte biomass values at the plot level relate to the biomass per tree or to the density of (large) host trees. Third, SVERA samples a similar number of host trees of all sizes, which enables covariate comparison of epiphyte richness and biomass between inventories, and controls for differences in tree size. The covariate analysis assumes a strong positive relationship between epiphyte richness or biomass and tree size. This has been documented (Bartareau & Skull 1994, Burns & Dawson 2005, Dunn 2000, Flores-Palacios & Garcia-Franco 2006, Hietz 2005, Hietz-Seifert *et al.* 1996, Hsu *et al.* 2002, Werner *et al.* 2005, Wolf 2005, Wolf & Konings 2001, Zimmerman & Olmsted 1992, Zotz & Vollrath 2003, Zotz *et al.* 1999) independent of tree architecture, bark structure and microclimatic conditions. Larger trees offer more branch surface area and have been available for establishment by epiphytes over longer periods of time (Gradstein *et al.* 2003). Exceptions, however, occur, e.g. in a Costa Rican oak forest more epiphytic bryophytes occur on young, *c.* 40-y-old oak trees than on much larger, *c.* 200-y-old ones

(Holz & Gradstein 2005). Canopy closure and forest microclimate were the main factors determining epiphyte richness, not diameter or tree size. The different relationship between tree size and epiphyte species richness in this forest would be detected by SVERA. The positive correlation between vascular epiphyte abundance and tree size is smaller at more disturbed sites (Bartareau & Skull 1994, Wolf 2005), which suggests that in disturbed forests, all suitable niches are not yet occupied. Accordingly, the square of the Pearson product moment correlation coefficient (r^2) has been used to assess whether a population is near its carrying capacity.

SVERA's primary objective is to provide a protocol for sampling of epiphyte richness and abundance. Since dispersal at least partially drives epiphyte community structure and leads to spatial aggregation (Barkman 1958, Cascante-Marín 2006, Zotz & Schultz 2008), spatial components must be incorporated in epiphyte community studies. Therefore, SVERA also records geographic position of trees in the forest and of forest stands in the landscape. To assess the performance of SVERA, we applied this technique on montane epiphyte communities in oak forests in Colombia and southern Mexico. We also tested for the occurrence of spatial dependence in these epiphyte communities.

METHODS

Study area

Epiphyte vegetation was analysed on oak trees in Colombian and several Mexican oak forests (2300–2600 m). The Colombian forest was located *c.* 25 km west of the capital Bogotá D.C. and the Mexican forests are all near the municipality of San Cristóbal de Las Casas (16°42′N, 92°37′W) in the highlands of Chiapas. The Colombian forest was dominated by *Quercus humboldtii* Bonpl., whereas the Mexican forests are dominated by a cohort of several oak species, mainly *Q. crassifolia* H. & B., *Q. crispipilis* Trel., *Q. laurina* H. & B. and *Q. rugosa* Nee. With an annual rainfall of approximately 750 mm (Colombia) and 1000 mm (Mexico), associated with a pronounced dry season, the climate in all oak forests is considerably drier than in wet tropical forest. There was no evidence of anthropogenic disturbance in the Colombian forest. In the Mexican forest, we sought the least disturbed forests, but found some evidence of past disturbances such as coppiced oaks and dead stumps (Wolf 2005).

Field sampling

To analyse forest structure, we randomly selected a 30×30-m plot in the forest interior and measured all individual trees (dbh > 5 cm), which we then identified to species. Epiphyte sampling was done on a plotless basis, i.e. based on the presence of epiphytes on individual trees. We used this approach to explore the relationship between epiphyte richness or abundance and the size of the host tree, using the whole tree as sampling unit. When within-tree distribution is of interest, the host tree may be subdivided in trunk and branch segments following Ochsner (1935) or Johansson (1974). In RRED-analysis, trees varying in bark and canopy structure are deliberately included. In contrast, the SVERA protocol calls for the exclusion of epiphyte-poor trees such as ant trees or those with smooth-, hard- or sloughing barks because they mask the correlation between tree size and species richness or biomass.

Following the selection of host tree species, we randomly selected and sampled a first tree, after which we sampled its nearest neighbour, etc. Although this may slightly bias the sample (Clark & Evans 1954), it requires less time than truly random choice and is practical for mapping purposes (Cottam & Curtis 1956). We determined the geographic position of each tree by recording the distance and compass bearing to the previously sampled neighbour tree. Other measured parameters included tree height, trunk diameter (dbh) and the number of branching points (forks with a side-branch diameter > 5 cm). Field trials on climbed trees showed that those variables were estimated with little error and varied little amongst observers, as opposed to estimates for crown width, crown height and branch surface area. Tree height of the larger trees, which were climbed using rope-climbing techniques (Mitchell *et al.* 2002), was estimated with a measuring rope. We sampled a total of 35 trees: 10 large trees (dbh > 30 cm) and 25 trees equally divided over five diameter cohorts (5–10, 10.1–15, 15.1–20, 20.1–25, 25.1–30 cm). The total number of sampled trees was similar as in RRED-analysis but with SVERA we tried to attain an even distribution of tree sizes (the covariate). Thus, smaller trees are well represented as recommended by Zotz (2007a). To avoid duplicate sampling of branches we tracked branch systems with sketches.

For each tree, we non-destructively estimated the dry weight of all epiphyte species by assessing the number of leaves, fronds or rosettes, or the lengths thereof, depending on the growth form of the species. For bromeliads, the number of rosettes in three size classes (5–20, 20–50, > 50 cm) was often satisfactory. Bromeliad seedlings (< 5 cm) were not included because they are difficult to identify, have high mortality rates, and contribute little to total biomass. For ferns, orchids and species of *Peperomia*, the number of leaves provided a good quantitative measure. Cacti were best quantified by the length of their leaves; creeping ferns and aroids by the length of their rhizome or stem. For species that invest highly in their inflorescences (e.g. bromeliads) these organs were quantified separately. Dry weight was

computed from the mean weight of 10 specimens per cohort. Unattached dead organic matter was removed from the plants before weighing. Vouchers of each new species were collected, including sterile plants that were subsequently cultivated to enable identification. We also assembled a field herbarium.

Analysis

We estimated epiphyte biomass on a ground area basis in two ways. First, we multiplied mean epiphyte biomass on individual trees in the diameter cohorts by the number of trees in that cohort per hectare. Second, we extrapolated epiphyte biomass of all trees per diameter cohort. Note that this does not consider the dispersion around the fitted regression line and is only possible when the regression yields a significant relationship. When the size of the 10 trees in the largest size cohort (dbh > 30 cm) varies greatly, the second approach is preferable.

We used Chao's non-parametric diversity estimator to estimate the overall richness of the samples (Chao 1984). Her estimator (S_{Chao1}) enables a comparison between unequal-sized samples and has a relatively low sensitivity to varying species richness (Colwell & Coddington 1994). For clonal epiphytes, S_{Chao1} is particularly attractive because it does not require counts of the number of individuals in those common species that form a mass of ramets. If no singletons or doubletons are present in the inventory, a version of the estimator may be computed using EstimateS.

We evaluated and compared epiphyte richness and biomass between sites with scaled linear regressions on trees that varied in size. To visualize the regression lines, we combined dbh, tree height (Height) and the number of branching points (BP) into a single value (Tree Size). Tree Size, computed as Standardized (dbh × Height) + Standardized (BP), is a dimensionless estimate of the total bark surface area. We achieved standardization by subtracting the population mean from an individual raw score and then dividing the difference by the population standard deviation.

The regression is characterized by its slope (the regression coefficient), its elevation (the y-intercept) and an error term. When the slopes between two sites are the same, we inferred that relationships between tree size and epiphyte richness or biomass were similar. The elevation of the regression is an indicator of species richness or biomass at a site, i.e. the theoretical number of species or biomass on a tree with size 0. The advantage of this scaled approach is that elevation can be analysed statistically in an analysis of covariance (ANCOVA) that controls for Tree Size. Moreover, this analysis does not require a representative sample of the local epiphyte flora.

In ANCOVA, we compared richness or biomass values between sites pair-wise with an a priori contrast analysis (t-test). ANCOVA assumes that the slopes are equal at all sites (Sokal & Rohlf 1981). To test this homogeneity of covariate regression coefficient assumption, we determined the influence of the interaction term Tree Size × Site on a model with the predictor variables Tree Size and Site (Keppel 1991). A significant influence of the interaction term signifies that the null hypothesis of equal slopes must be rejected. Because ANCOVA remains robust when the difference in slope is not large and group sizes are equal (Keppel 1991), we used P = 0.001 as threshold. Since hemi-epiphytes may differ from holo-epiphytes in terms of dependence on tree size (Benavides *et al.* 2006, Burns & Dawson 2005), the two groups may be analysed separately. To attain homogeneity of variance and a normal distribution, it may be necessary to transform the dependent variable.

When the homogeneity assumption test shows that the slopes are not parallel, homogeneity may be achieved by elimination of sites on an individual basis. Visual inspections of the regression lines can help to select the most aberrant sites. Although omitted sites are not included in the following ANCOVA, they are of interest for ecological reasons. For example, unusually gentle regression slopes may relate to little canopy closure and the establishment of canopy species in the understorey (Holz & Gradstein 2005).

Two non-parallel regression lines will inevitably cross at some point. Differences between elevations will increase with distance from the point of intersection. As an alternative to ANCOVA, in these cases the Johnson–Neyman procedure, testing at what distance from the intersection the elevations of two regression lines are significantly different, may be applied (Aiken & West 1991, D'Alonzo 2004, Huitema 1980, Johnson & Neyman 1936). Unfortunately, this procedure is not a standard feature of any statistical software package. We used syntax from the Statistical Package for the Social Sciences (SPSS) Online Technical Support webpage (based on Aiken & West 1991).

For epiphyte spatial analysis (optional in SVERA) we assigned spatial descriptors of sampled trees and sites. Tree maps were generated based on compass readings and distances between individual trees (Reichard 2002). Site position was determined with the Global Positioning System (GPS). The x-y coordinates (trees) and GPS readings (sites) allowed for computing a Euclidean distance matrix, by applying the Macintosh R-package for multivariate and spatial analysis. We explored for spatial dependence in the data by correlating the geographic distance matrix with a species distance matrix in a Mantel test (Legendre & Legendre 1998). For the species distance matrix we used the probabilistic coefficient of Raup and Crick as the similarity index. This coefficient is

a measure of how close the arrangement of species over the samples is to a random assignment. The Mantel test yields a correlation coefficient and a probability. For the correlation, Pearson's product moment linear correlation coefficient (i.e. Mantel's r), or Spearman's r may be used. We visualized spatial dependence in a correlogram, depicting the correlation coefficient against geographical distance. To this purpose, the geographic distance matrix was transformed into a distance class matrix on the basis of Sturge's rule (number of classes = $1 + 3.3\log(n)$, where n = number of forest plots or trees).

Spatial variation may be attributed to spatially structured environmental gradients or to other factors that may have a spatial component, such as competition or dispersal. A partial Mantel test reveals whether the spatial dependence is sustained when the variation due to environmental gradients has been accounted for. For this test, we entered a Euclidean environmental distance matrix as a covariable. Canonical correspondence analysis (CANOCO, ter Braak 1986, 1988) was also applied (Borcard *et al.* 1992), which shows what proportion of the variation in the data is explained by the geographic position of the sites versus the environment. It also allows Monte Carlo significance testing of the relationship of environmental and spatial variables to community structure (Jongman *et al.* 1987). Environmental variables include altitude, climate, forest management, forest structure and geographical position. We first submitted the explanatory variables to the CANOCO procedure of forward selection of variables. We retained only those variables that contributed a significant amount ($P < 0.05$), using Monte Carlo tests based on 1000 permutations, and evaluated the statistical significance of the first canonical axes with Monte Carlo tests. Geographical coordinates may be used to derive two types of spatial descriptors of the sites (Borcard & Legendre 2002, Borcard *et al.* 1992, 2004; Legendre & Legendre 1998). Traditionally, the terms of a cubic trend-surface equation that is derived from the geographical coordinates of the sites have been used. A new method is based on the principal coordinates of neighbour matrices (PCNM, Borcard & Legendre 2002, Dray *et al.* 2006). The spatial structure is described by the eigenvectors – using positive eigenvalues only – of a principal coordinate analysis of a truncated Euclidean distance matrix or neighbour matrix. For epiphytes, cubic trend-surface analysis and PCNM analysis yield similar results (Wolf 2005).

Some ecological questions require the evaluation of the epiphyte community on the smaller spatial scale of a host tree. Environmental variables entered in the analysis depend on the research question and may include tree species, bark type, deciduousness, tree architecture, tree growth rate, animal activity, canopy soil accumulation, abundance of non-vascular epiphytes and distance to forest edge. The partitioning of the variation between environmental and spatial variables is complex because epiphyte assemblages among large trees are generally more similar than those on small trees. Since the probability that a large tree grows close to a small tree is higher than for two large trees, trees at larger distances are thus likely to be more similar in their epiphyte community. The resulting spatial pattern is not due to historical or biological processes and therefore of little interest. Hence, for autocorrelation analysis it is advisable to exclude the smaller trees. To eliminate further tree-size-related bias, the abundance of each epiphyte species on a single tree should be estimated relative to the total epiphyte biomass on that tree.

For the analysis of species richness and abundance, we used SPSS for Windows version 11.0, Microsoft Excel and EstimateS version 8.0 (R.K. Colwell, persistent URL <purl.oclc.org/estimates>). For the optional multivariate analysis of the distribution of epiphytes in relation to environmental and spatial variables we used CANOCO for Windows version 4.0 (ter Braak 1988), PACE (Reichard 2002), The R package version 4.0 d6 and Spacemaker2 (the latter two MacOS programmes are available on http://www.bio.umontreal.ca/legendre/; Windows versions are in development).

RESULTS

It took two persons approximately 20 d of fieldwork to complete an inventory. SVERA yielded results on two scales of observation: on the forest scale (Figure 1, Appendix 1) and on the host-tree scale (Table 1, Appendix 2). The raw data may be downloaded from the Canopy Databank (http://canopy.evergreen.edu/research_databank.asp?Id = 2). We encourage other researchers to also make their data available online.

Epiphyte species richness and biomass

In the Colombian oak forest, we encountered 14 epiphyte species on the 35 sampled oak trees, and 23–35 species in the Mexican oak forests sample areas (Appendix 2, Table 1). The Colombian forest shared only two epiphyte species with the Mexican ones, but at the family level the forests were similar. Bromeliads dominated in all sites where they always comprised more than *c.* 90% of total epiphytic biomass. In Colombia, epiphyte biomass on the 35 host trees (87.1 kg) fell within the range of that observed in Mexico (74.7–243.9 kg).

At all sites, there was a strong linear dependence ($P < 0.001$) of epiphyte species richness and biomass on tree size (Tree Size) of the host tree (Figures 2 and 3). Epiphyte biomass also tightly correlated with tree
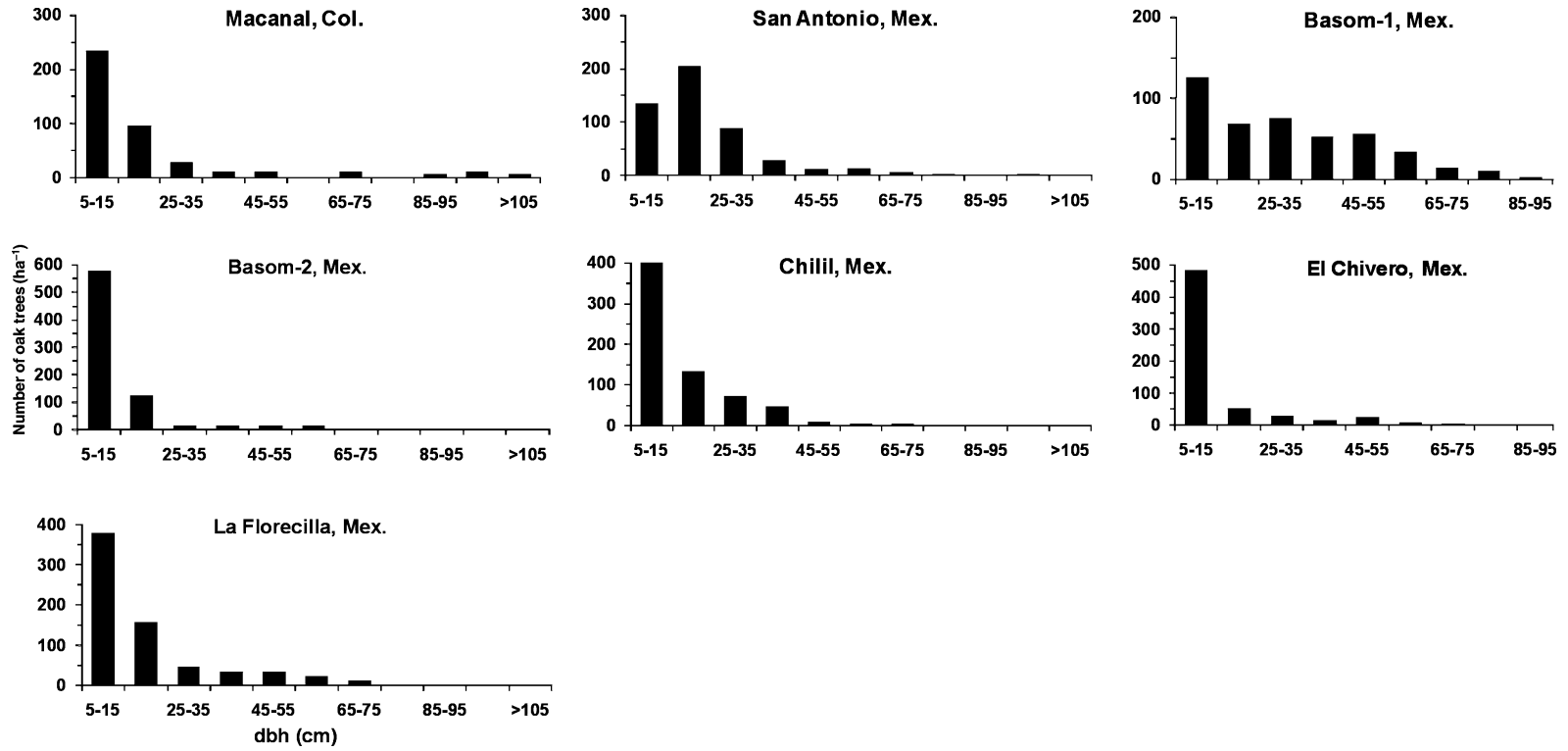
Figure 1. Number of oak trees per ha in various trunk diameter classes (dbh) at the sites, based on 900-m^2 inventories. Col. = Colombia; Mex. = Mexico.

Table 1. Epiphyte species richness and biomass (dry weight) at the study sites. The estimated total number of species in the forest (S_{Chao1}) is calculated from the number of observed species and the number of singletons and doubletons in the sample. Paired S_{Chao1} differences between sites are always significant (t-test, $P < 0.05$), except between Basom-1 and San Antonio and between Basom-1 and Chilil. Epiphyte biomass per unit stand area is calculated from the average tree load in several tree trunk diameter frequency classes. A complete species list is given in Appendix 2.

	Observed number of species (35 trees)	Estimated number of species (S_{Chao1})	Biomass (kg per 35 trees)	Biomass (kg ha^{-1})
Macanal, Colombia	14	14.5	87.1	564
San Antonio, Mexico	29	32.1	98.9	1243
Basom-1, Mexico	23	35.5	103.3	1665
Basom-2, Mexico	24	24.7	113.7	658
Chilil, Mexico	35	35.5	74.7	629
El Chivero, Mexico	34	40.1	97.6	739
La Florecilla, Mexico	27	29.0	243.9	3218

size ($P < 0.001$), using trunk diameter as the tree size variable. Therefore, the regressions at each site may be used to estimate epiphyte biomass on oaks per unit stand area. In Colombia, biomass was lower than in any of the Mexican forests (Table 1), both on the basis of single tree or diameter-size class calculations. The latter approach yielded slightly higher values per ha, but differences were not significant (paired-samples t-test, $P = 0.10$).

For species richness, visual inspection of the regression lines (Figure 2) indicated that all slopes were roughly parallel, which was corroborated by the homogeneity assumption test. In contrast, the ANCOVA showed significant differences in the elevations of the slopes (Table 2). The trees at the Colombian site supported significantly ($P < 0.05$) fewer species than in any of the Mexican sites, except at San Antonio. Species richness at La Florecilla was significantly higher than at most other sites (except at Basom-1 and El Chivero).

For biomass (Figure 3), the homogeneity assumption test showed that the regression coefficients were
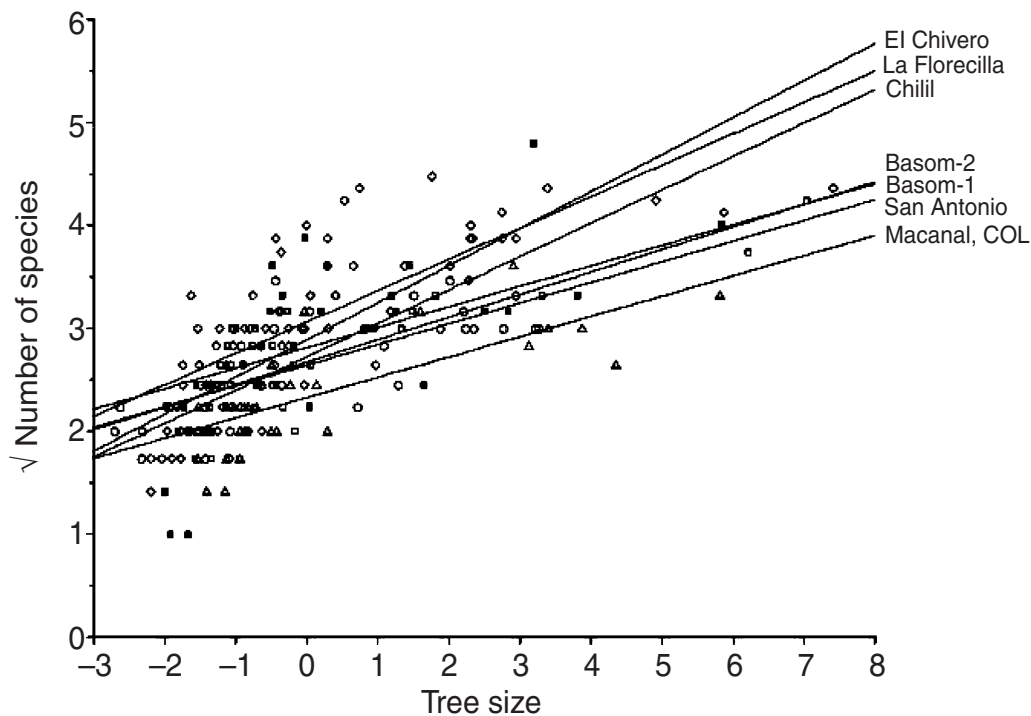

Figure 2. Scatterplot illustrating the relation between tree size and epiphyte species richness. Tree Size = Standardized(Height × dbh) + Standardized(Number of branching points). El Chivero: $\sqrt{richness} = 0.4(Tree\ Size) + 2.9$, $r^2 = 0.62$, $P < 0.001$; La Florecilla: $\sqrt{richness} = 0.3(Tree\ Size) + 3.1$, $r^2 = 0.60$, $P < 0.001$; Chilil: $\sqrt{richness} = 0.3(Tree\ Size) + 2.7$, $r^2 = 0.52$, $P < 0.001$; Basom-2: $\sqrt{richness} = 0.2(Tree\ Size) + 2.7$, $r^2 = 0.62$, $P < 0.001$; Basom-1: $\sqrt{richness} = 0.2(Tree\ Size) + 2.8$, $r^2 = 0.61$, $P < 0.001$; San Antonio: $\sqrt{richness} = 0.2(Tree\ Size) + 2.6$, $r^2 = 0.54$, $P < 0.001$; Macanal, COL: $\sqrt{richness} = 0.2(Tree\ Size) + 2.3$, $r^2 = 0.54$, $P < 0.001$. All sites in Mexico, except Macanal, COL, which is in Colombia.
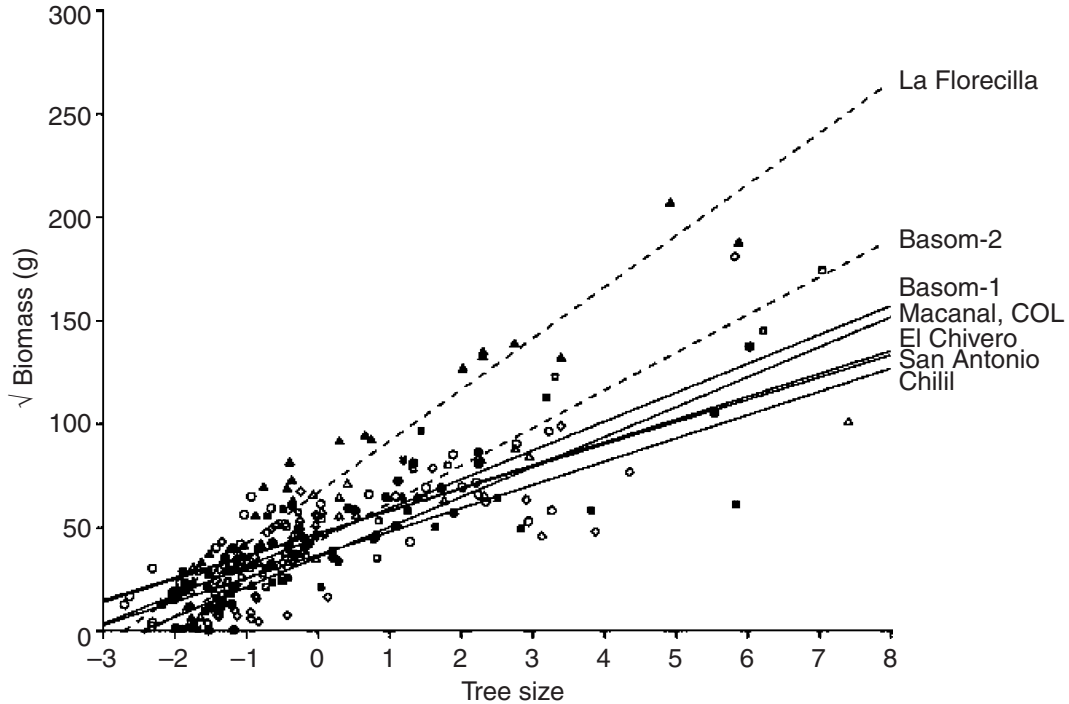
Figure 3. Scatterplot illustrating the relation between tree size and epiphyte biomass. Tree Size = Standardized(Height × dbh) + Standardized(Number of branching points). Dotted lines have a significantly different slope from the solid lines (ANCOVA, Tree Size × Site, P < 0.001). For La Florecilla, the line has a significantly higher elevation than the cohort of the homogeneous slopes (solid lines) at Tree Size > −1.30 and for Basom-2 at Tree Size > 1.08 (Johnson–Neyman procedure at P = 0.05). La Florecilla: $\sqrt{}$g biomass = 24.9(Tree Size) + 66.8, r^2 = 0.93, P < 0.001; Basom-2: $\sqrt{}$g biomass = 18.3(Tree Size) + 43.8, r^2 = 0.95, P < 0.001; Basom-1: $\sqrt{}$g biomass = 14.0(Tree Size) + 45.6, r^2 = 0.86, P < 0.001; Macanal, COL : $\sqrt{}$g biomass = 14.5(Tree Size) + 36.0, r^2 = 0.65, P < 0.001; El Chivero: $\sqrt{}$g biomass = 11.1(Tree Size) + 47.4, r^2 = 0.81, P < 0.001; San Antonio: $\sqrt{}$g biomass = 10.8(Tree Size) + 47.5, r^2 = 0.68, P < 0.001; Chilil: $\sqrt{}$g biomass = 11.3(Tree Size) + 37.1, r^2 = 0.58, P < 0.001. All sites in Mexico, except Macanal, COL, which is in Colombia.

heterogeneous (ANCOVA, Tree Size × Site $F_{6,231}$ = 15.7, P < 0.001). Exclusion of the two sites with the most aberrant slopes (La Florecilla and Basom-2) generated a remaining cohort of five parallel slopes (ANCOVA, Tree Size × Site, $F_{4,165}$ = 1.63, P > 0.05). Contrast analysis in the subsequent ANCOVA showed that the elevation of the regression line at the Colombian site was significantly (P < 0.05) lower than at San Antonio and El Chivero in Mexico (Table 2).

Visual inspection of the aberrant slopes at La Florecilla and Basom-2 suggested that the biomass at these sites was considerably higher than in any of the other sites (Figure 3). The Johnson–Neyman procedure confirmed that the elevation at La Florecilla was significantly higher than the averaged elevations of the sites in the cohort with the homogeneous slopes for most trees (Tree Size > −1.30, P = 0.05). The elevation at La Florecilla was also higher than at Basom-2 for most trees (Tree Size

Table 2. Pairwise comparisons between the study sites of epiphyte species richness and epiphyte biomass, based on ANCOVA (Bonferroni-adjusted) that controlled for Tree Size. Cell values are the differences in the adjusted means. Richness differences are shown in the upper triangle (row subtracted from column) and biomass differences in the lower triangle (column subtracted from row). Site effect on species richness: $F_{6,237}$ = 8.80, P < 0.001, and on epiphyte biomass: $F_{4,169}$ = 4.62, P < 0.01. Species richness and biomass (kg dry weight) were square root-transformed. Note that the biomass values of La Florecilla and Basom-2 were not compared (excl.) with the other sites because both sites showed deviating regression coefficients. Significant differences in bold: *0.05 < P < 0.01, **0.01 < P < 0.001, ***P < 0.001.

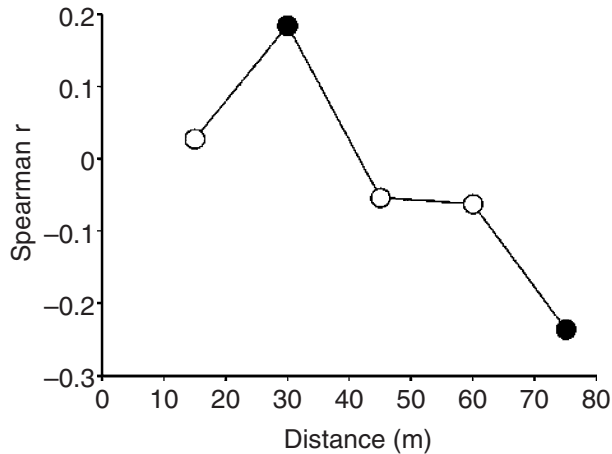|	Macanal	S. Antonio	Basom-1	Basom-2	Chilil	El Chivero	La Florec
Macanal, Colombia	—	0.31	**0.49*****	**0.34***	**0.40****	**0.56*****	**0.73*****
San Antonio, Mexico	11.47*	—	0.17	−0.03	−0.08	0.24	**0.42****
Basom-1, Mexico	9.54	−1.93	—	−0.14	−0.09	0.07	0.25
Basom-2, Mexico	excl.	excl.	excl.	—	0.05	0.22	**0.39****
Chilil, Mexico	1.01	−10.46	8.53		—	0.16	**0.34***
El Chivero, Mexico	11.32*	−1.14	1.79		10.31	—	0.17
La Florecilla, Mexico	excl.	excl.	excl.	excl.	excl.	excl.	—

Figure 4. Mantel correlogram of epiphyte vegetation on large trees at the El Chivero (Spearman r = 0.27, P < 0.05). The species similarity is based on the Raup and Crick probabilistic coefficient, using the biomass of each species relative to the total epiphyte biomass on that tree. Filled symbols indicate a significant value of Spearman r (P < 0.05).

Figure 5. Variation partitioning for the distribution of epiphytes over large trees at El Chivero between environmental and spatial variables, following Borcard *et al.* (1992). For the spatial descriptors of the trees, the terms of a cubic trend-surface equation that is derived from the x-y coordinates of the trees were used. The environmental and spatial explanatory variables were first submitted to the CANOCO procedure of forward selection of variables in two separate runs. Only the variables (2) that contributed a significant amount (Monte Carlo test, P < 0.05) were retained (i.e. the term of y^2 and trunk dbh). The first canonical axes were all significant (Monte Carlo test, P < 0.05).

> −1.90). Basom-2 showed no significantly different elevation from the slopes in the cohort for [−1.46 < Tree Size < 1.08].

Epiphyte spatial dependence

A Mantel test for spatial dependence on the 20 largest sampled host trees in each forest site revealed that only at El Chivero was there a significant linear correlation between the distance between trees and the composition of the epiphyte community (Spearman r = 0.24, P < 0.05). The correlation remained significant after controlling for environmental variables in a partial Mantel test. Environmental variables entered were tree dbh, height, number of branching points and species of host tree. Correlation between tree distance and epiphyte similarity switched from positive in nearby trees to significantly negative at the largest distance (Figure 4). Spatial descriptors explained more variation (26%) than the above-mentioned environmental variables (16%). Approximately 12% of this variation was shared by environmental and spatial variables, leaving 14% being explained by space alone (Figure 5).

DISCUSSION

Sampling

With approximately 20 d of fieldwork to complete an inventory in montane oak forest, SVERA takes about twice as long as RRED analysis. However, in addition to species richness assessed by RRED, SVERA provides data on forest structure, position and size of trees, and
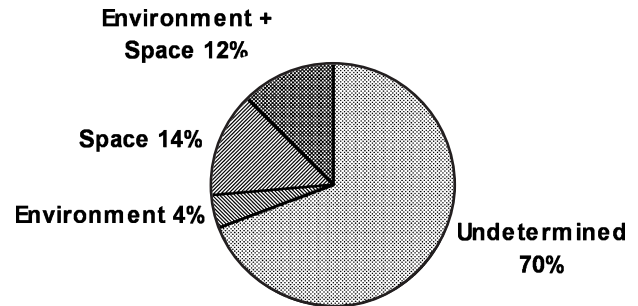
abundance of each epiphyte species. In structurally more complex large-tree lowland rain forests more time will be required. Larger trees signify that a representative sample to assess forest structure must be larger than the 30 × 30-m plot we used. Similarly, more large trees must be sampled for epiphytes, e.g. by adding more diameter size-cohorts at the upper end, to avoid the presence of outlier trees on the independent axis of the regression. Visual inspection of the regression lines will guide the number of trees that must be sampled. In forests with a higher diversity of host trees, more trees than the 35 used in this study will probably have to be sampled. On the basis of previous studies we are confident that in most cases a positive correlation may be found, even in structurally complex lowland rain forest (Zotz & Schultz 2008).

Forest structure

Tree height and diameter data may be used in two different ways. First, the diameter frequency distributions allow for estimation of total epiphyte biomass in a forest stand. Second, these data allow for comparisons of the structure of the forest between sites. For example, our data showed that the Colombian oak forest fell within the range of the Mexican stands in terms of height and total basal area. In all forests, oaks dominated (except at Basom-2 where pines contributed most to total basal area, which may have reflected selective logging and other anthropogenic disturbances, González-Espinosa *et al.* 1991).

Epiphyte biomass and richness

In epiphyte studies, biomass is most often calculated either on a per tree or per unit stand area basis (reviewed

in Wolf & Flamenco-S. 2003). SVERA provides both types of information. Per unit stand area, however, SVERA only yields a minimum value for epiphyte biomass since epiphyte-poor host tree species are not sampled. Accidental individuals on 'hostile' trees (e.g. pines in Mexico) contribute little to epiphyte richness and biomass in the forest and they may well correspond to a sink population that for its survival depends on a continuous supply of seeds from 'epiphyte-friendly' trees. Nevertheless, especially in areas where the density of epiphyte-poor trees is high, SVERA will underestimate total biomass on an areal basis.

Biomass values per unit stand area calculated on the basis of diameter-size class were slightly higher compared with those based on single tree occupancy. We attribute the higher values to larger sample trees having less influence on the regression slope than on the calculated mean biomass in the large-diameter-size cohort.

In the case study, epiphyte biomass per unit stand area in the Colombian site was smaller than in most of the Mexican sites. This is unexpected since the epiphyte biomass on the 35 sampled trees (87.1 kg) is comparable to that in Mexico, whereas the number of oak trees ha^{-1}, especially of large oaks, is higher at the Colombian site. The apparent discrepancy may be because larger trees were sampled in Colombia (despite an effort to sample trees of identical sizes). Epiphyte biomass per unit stand area results from the biomass per tree, which in turn depends on tree size, and number of trees therein. This indicates that epiphyte biomass data on a per tree basis are more informative than per unit stand area.

To factor out a tree size effect, SVERA-analyses rely on the presence of a linear dependence of biomass or richness on tree size. To eliminate spurious correlations due to outliers, SVERA distributes trees evenly on the independent size axis. At all sites, strong positive correlations were found between the square root of biomass and richness with relative tree size.

ANCOVAs of epiphyte biomass revealed that the regression coefficients of the covariate Tree Size were uniform at five of the seven sites. In five sites, the same linear relationship existed between tree size and epiphyte biomass. In the two other sites (La Florecilla, Basom-2), slopes were steeper and large trees supported significantly more biomass than smaller ones. At La Florecilla the unusually steep slope may have been due to dominance of the clonal *Tillandsia vicentina*, which has dense rosette packing.

ANCOVA also revealed that epiphyte biomass at the Colombian site, after controlling for tree size, was significantly lower than at the Mexican sites. Thus, trees of the same size supported less biomass in Colombia than in Mexico. In contrast, if we would have considered the biomass on the 35 trees alone, i.e. without controlling for tree size, we would have concluded that biomass

between sites was similar. The covariate approach thus gave valuable new insights.

Similarly, the covariate approach showed that species richness was significantly higher at the least-disturbed site (La Florecilla) than at San Antonio, Basom-2 and Chilil. This result contradicted simple species counts, which showed 27 species at La Florecilla and 29, 24 and 35 species at the other sites, respectively. ANCOVA also showed that the number of epiphyte species in the Colombian forest was significantly smaller than in any of the other sites, except at San Antonio. We might have deduced this from epiphyte species lists, but in the latter case, the conclusion could have been challenged due to the likelihood of unequal sample sizes and the lack of statistical analysis. A final advantage of the covariate approach was that differences between sites could be attributed to the number of species in the background (i.e. slope elevation) instead of tree size-richness relationship (i.e. regression coefficients).

Epiphyte spatial dependence

SVERA can test for autocorrelation, using data on the geographical position and the epiphyte floristic composition of forest stands in the landscape and of host trees in the forest (Wolf 2005). In the latter study, a Mantel test showed a strong spatial dependence of epiphyte inventories (16) within an approximately 100-km^2 area. Spatial variables explained more variance than environmental variables of the forests that were distributed over a gradient of anthropogenic disturbance. We used SVERA-analysis to test for spatial autocorrelation at the tree level, which was significant at El Chivero. The correlation remained significant after controlling for environmental tree variables in a partial Mantel test. Moreover, space alone explained more variation than the tree variables, justifying SVERA's inclusion of the geographic position of the trees as an exploratory variable.

CONCLUSIONS

Our case study showed that in comparison with conventional methods, SVERA is a useful protocol for community ecologists. The forest structure data helped to evaluate the logging history of the forest, permitted the calculation of a minimum estimate of epiphyte biomass per unit stand area, and quantitatively described the factors affecting distribution of epiphytes in the landscape. The plotless epiphyte inventories on trees facilitated a statistical comparison of epiphyte biomass and species richness between sites, while controlling for differences in tree size. These comparisons yielded different results

from more conventional plot-based sampling. To evaluate the distribution of epiphytes in the landscape and in the forest, optional in SVERA, the explicit inclusion of spatial descriptors was useful. The variation partitioning was based on CANOCO. It is best viewed as an exploratory type of data analysis that generates hypotheses that may be tested experimentally (Jongman *et al.* 1987).

This study took place in relatively simply-structured montane oak forests, and forests that are structurally complex and diverse need testing with this technique. A study in Panama indicated the potential value of SVERA, because epiphyte assemblages were significantly influenced by tree size, tree species and space (Zotz & Schultz 2008). We encourage other epiphyte community ecology researchers to use this protocol to ease comparisons of data that are difficult to collect.

LITERATURE CITED

AIKEN, L. S. & WEST, S. G. 1991. *Multiple regression: testing and interpreting interactions*. SAGE Publications, Newbury Park. 211 pp.

ANNASELVAM, J. & PARTHASARATHY, N. 2001. Diversity and distribution of herbaceous vascular epiphytes in a tropical evergreen forest at Varagalaiar, Western Ghats, India. *Biodiversity and Conservation* 10:317–329.

BADER, M., VAN DUNNÉ, H. J. F. & STUIVER, H. J. 2000. Epiphyte distribution in a secondary cloud forest vegetation; a case study of the application of GIS in epiphyte ecology. *Ecotropica* 6:181–195.

BARKER, M. G. & PINARD, M. A. 2001. Forest canopy research: sampling problems, and some solutions. *Plant Ecology* 153: 23–28.

BARKMAN, J. J. 1958. *On the ecology of cryptogamic epiphytes – with special reference to The Netherlands*. Van Gorcum & Comp. N.V., Assen. 628 pp.

BARTAREAU, T. & SKULL, S. 1994. The effects of past fire regimes on the structural characteristics of coastal plain *Melaleuca viridiflora* Sol. ex Gaert. woodlands and the distribution patterns of epiphytes (*Dendrobium canaliculatum* R. Br., *Dischidia nummularia* R. Br.) in Northeastern Queensland. *Biotropica* 26:118–123.

BENAVIDES, A. M., DUQUE, A. J., DUIVENVOORDEN, J. F., VASCO, G. A. & CALLEJAS, R. 2005. A first quantitative census of vascular epiphytes in rain forests of Colombian Amazonia. *Biodiversity and Conservation* 14:739–758.

BENAVIDES, A. M., WOLF, J. H. D. & DUIVENVOORDEN, J. F. 2006. Recovery and succession of epiphytes in upper Amazonian fallows. *Journal of Tropical Ecology* 22:705–717.

BENNETT, B. C. 1986. Patchiness, diversity, and abundance relationships of vascular epiphytes. *Selbyana* 9:70–75.

BERGSTROM, D. M. & TWEEDIE, C. E. 1998. A conceptual model for integrative studies of epiphytes: nitrogen utilisation, a case study. *Australian Journal of Botany* 46:273–280.

BORCARD, D. & LEGENDRE, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* 153:51–68.

BORCARD, D., LEGENDRE, P. & DRAPEAU, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055.

BORCARD, D., LEGENDRE, P., AVOIS-JACQUET, C. & TUOMISTO, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85:1826–1832.

BURNS, K. C. & DAWSON, J. 2005. Patterns in the diversity and distribution of epiphytes and vines in a New Zealand forest. *Austral Ecology* 30:891–899.

CASCANTE-MARÍN, A. 2006. *Establishment, reproduction and genetics of epiphytic bromeliad communities in successional premontane forests, Costa Rica*. Ph.D. dissertation, University of Amsterdam, Amsterdam.

CASCANTE-MARÍN, A., WOLF, J. H. D., OOSTERMEIJER, J. G. B., DEN NIJS, J. C. M., SANAHUJA, O. & DURÁN-APUY, A. 2006. Epiphytic bromeliad communities in secondary and mature forest in a tropical premontane area. *Basic and Applied Ecology* 7:520–532.

CATLING, P. M., BROWNELL, V. R. & LEFKOVITCH, L. P. 1986. Epiphytic orchids in a Belizean grapefruit orchard: distribution, colonization and association. *Lindleyana* 1:194–202.

CHAO, A. 1984. Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11:265–270.

CLARK, P. J. & EVANS, F. C. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453.

COLWELL, R. K. & CODDINGTON, J. K. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society (Series B)* 345:101–118.

COTTAM, G. & CURTIS, J. T. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451–460.

D'ALONZO, K. T. 2004. The Johnson–Neyman procedure as an alternative to ANCOVA. *Western Journal of Nursing Research* 26:804–812.

DIAL, R. & TOBIN, S. C. 1994. Description of arborist methods for forest canopy access and movement. *Selbyana* 15:24–37.

DRAY, S., LEGENDRE, P. & PERES-NETO, P. R. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196:483–493.

DUNN, R. R. 2000. Bromeliad communities in isolated trees and three successional stages of an Andean cloud forest in Ecuador. *Selbyana* 21:137–143.

FLORES-PALACIOS, A. & GARCIA-FRANCO, J. G. 2006. The relationship between tree size and epiphyte species richness: testing four different hypotheses. *Journal of Biogeography* 33:323–330.

GENTRY, A. H. & DODSON, C. H. 1987a. Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* 19:149–156.

GENTRY, A. H. & DODSON, C. H. 1987b. Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden* 74:205–233.

GONZÁLEZ-ESPINOSA, M., QUINTANA-ASCENCIO, P. F., RAMÍREZ-MARCIAL, N. & GAYATÁN-GUZMÁN, P. 1991. Secondary succession in disturbed *Pinus-Quercus* forests in the highlands of Chiapas, Mexico. *Journal of Vegetation Science* 2:351–360.

GOTTSBERGER, G. & DÖRING, J. 1995. 'COPAS'. An innovative technology for long-term studies of tropical rain forest canopies. *Phyton (Horn, Austria)* 35:165–173.

GRADSTEIN, S. R., HIETZ, P., LÜCKING, R., LÜCKING, A., SIPMAN, H. J. M., VESTER, H. F. M., WOLF, J. H. D. & GARDETTE, E. 1996. How to sample the epiphytic diversity of tropical rain forests. *Ecotropica* 2:59–72.

GRADSTEIN, S. R., NADKARNI, N. M., KRÖMER, T., HOLZ, I. & NÖSKE, N. 2003. A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. *Selbyana* 24:105–111.

HIETZ, P. 2005. Conservation of vascular epiphyte diversity in Mexican coffee plantations. *Conservation Biology* 19:391–399.

HIETZ, P. & HIETZ-SEIFERT, U. 1995. Structure and ecology of epiphyte communities of a cloud forest in central Veracruz, Mexico. *Journal of Vegetation Science* 6:719–728.

HIETZ-SEIFERT, U., HIETZ, P. & GUEVARA, S. 1996. Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz, Mexico. *Biological Conservation* 75:103–111.

HOLZ, I. & GRADSTEIN, S. R. 2005. Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica – species richness, community composition and ecology. *Plant Ecology* 178:89–109.

HSU, C. C., HORNG, F. W. & KUO, C. M. 2002. Epiphyte biomass and nutrient capital of a moist subtropical forest in north-eastern Taiwan. *Journal of Tropical Ecology* 18:659–670.

HUITEMA, B. E. 1980. *The analysis of covariance and alternatives*. Wiley, New York. 460 pp.

JOHANSSON, D. 1974. Ecology of vascular epiphytes in west African rain forest. *Acta Phytogeographica Suecica* 59:1–123.

JOHNSON, P. O. & NEYMAN, J. 1936. Tests of certain linear hypotheses and their application to some educational problems. *Statistical Research Memoirs* 1:57–93.

JONGMAN, R. H. G., TER BRAAK, C. J. F. & VAN TONGEREN, O. F. R. 1987. *Data analysis in community and landscape ecology*. Pudoc, Wageningen. 299 pp.

KEPPEL, G. 1991. *Design and analysis: a researcher's handbook*. Prentice Hall, Englewood Cliffs. 672 pp.

LAMAN, T. G. 1995. Safety recommendations for climbing rain forest trees with single rope technique. *Biotropica* 27:406–409.

LAUBE, S. & ZOTZ, G. 2006. Neither host-specific nor random: vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany* 97:1103–1114.

LEGENDRE, P. & LEGENDRE, L. 1998. *Numerical ecology*. Elsevier Science B.V., Amsterdam. 853 pp.

MADISON, M. 1979. Distribution of epiphytes in a rubber plantation in Sarawak. *Selbyana* 5:107–115.

MAGURRAN, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton. 179 pp.

MCCUNE, B. 1990. Rapid estimation of abundance of epiphytes on branches. *The Bryologist* 93:39–43.

MITCHELL, A. W., SECOY, K. & JACKSON, T. 2002. *The Global Canopy handbook. Techniques of access and study in the forest roof*. Global Canopy Programme, Oxford. 248 pp.

MOFFETT, M. W. 1993. *The high frontier: exploring the tropical rain forest canopy*. Harvard University Press, Cambridge. 192 pp.

MUIR, P. S., NORMAN, K. N. & SIKES, K. G. 2006. Quantity and value of commercial moss harvest from forests of the Pacific Northwest and Appalachian regions of the U.S. *Bryologist* 109:197–214.

NADKARNI, N. M. & PARKER, G. G. 1994. A profile of forest canopy science and scientists – who we are, what we want to know, and obstacles we face: results of an international survey. *Selbyana* 15:38–50.

NIEDER, J. & ZOTZ, G. 1998. Methods of analyzing the structure and dynamics of vascular epiphyte communities. *Ecotropica* 4:33–39.

NIEDER, J., ENGWALD, S., KLAWUN, M. & BARTHLOTT, W. 2000. Spatial distribution of vascular epiphytes (including hemiepiphytes) in a lowland Amazonian rain forest (Surumoni crane plot) of southern Venezuela. *Biotropica* 32:385–396.

OCHSNER, F. 1935. Oekologische Untersuchungen an Epiphytenstandorten. *Bericht über das Geobotanische Forschungsinstitut Rübel in Zürich* 60:69–80.

PARKER, G. G., SMITH, A. P. & HOGAN, K. P. 1992. Access to the upper forest canopy with a large tower crane: sampling the treetops in three dimensions. *BioScience* 42:664–671.

PERRY, D. R. 1978. A method of access into the crowns of emergent and canopy trees. *Biotropica* 10:155–157.

REICHARD, J. S. 2002. A computer program for use with pace and compass exercises. *Journal of Geoscience Education* 50:544–548.

SANFORD, W. W. 1968. Distribution of epiphytic orchids in semi-deciduous tropical forest in southern Nigeria. *Journal of Ecology* 56:697–705.

SCHIMPER, A. F. W. 1888. *Die epiphytische Vegetation Amerikas. Botanische Mittheilungen aus den Tropen, Heft 2*. Gustav Fischer, Jena. 162 pp.

SCHULTEA, R. P. O., EGBERT, A., LANTING, A. B. & HAWKINS, M. J. 2005. A new family of Fisher-curves estimates Fisher's alpha more accurately. *Journal of Theoretical Biology* 232:305–313.

SOKAL, R. R. & ROHLF, F. J. 1981. *Biometry*. W.H. Freeman and Company, London.

TER BRAAK, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179.

TER BRAAK, C. J. F. 1988. CANOCO – an extension of DECORANA to analyze species-environment relationships. *Vegetatio* 75:159–160.

TER STEEGE, H. & CORNELISSEN, J. H. C. 1988. Collecting and studying bryophytes in the canopy of standing rain forest trees. Pp. 285–290 in Glime, J. M. (ed.). *Methods in bryology.* Hattori Botanical Laboratory, Nichinan.

VAN OYE, P. 1924. Sur l'écologie des épiphytes de la surface des troncs d'arbres à Java. *Revue Générale Botanique* 36:12–30, 68–83.

WENT, F. W. 1940. Soziologie der Epiphyten eines tropischen Urwaldes. *Annales du Jardin Botanique de Buitenzorg* 50:1–98.

WERNER, F. A., HOMEIER, J. & GRADSTEIN, S. R. 2005. Diversity of vascular epiphytes on isolated remnant trees in the montane forest belt of southern Ecuador. *Ecotropica* 11:21–40.

WESTHOFF, V. & Van Der MAAREL, E. 1973. The Braun–Blanquet approach. *Handbook of Vegetation Science* 5:617–726.

WHITEACRE, D. F. 1981. Additional techniques and safety hints for climbing tall trees, and some equipment and information sources. *Biotropica* 13:286–291.

WOLF, J. H. D. 1993a. Epiphyte communities of tropical montane rain forests in the northern Andes. I. Lower montane communities. *Phytocoenologia* 22:1–52.

WOLF, J. H. D. 1993b. Epiphyte communities of tropical montane rain forests in the northern Andes. II. Upper montane communities. *Phytocoenologia* 22:53–103.

WOLF, J. H. D. 1994. Factors controlling the distribution of vascular and nonvascular epiphytes in the northern Andes. *Vegetatio* 112:15–28.

WOLF, J. H. D. 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. *Forest Ecology and Management* 212:376–393.

WOLF, J. H. D. & FLAMENCO-S., A. 2003. Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography* 30:1689–1707.

WOLF, J. H. D. & KONINGS, C. J. F. 2001. Toward the sustainable harvesting of epiphytic bromeliads: a pilot study from the highlands of Chiapas, Mexico. *Biological Conservation* 101:23–31.

ZIMMERMAN, J. K. & OLMSTED, I. C. 1992. Host tree utilization by vascular epiphytes in a seasonally inundated forest (Tintal) in Mexico. *Biotropica* 24:402–407.

ZOTZ, G. 2007a. Johansson revisited: the spatial structure of epiphyte assemblages. *Journal of Vegetation Science* 18:123–130.

ZOTZ, G. 2007b. The population structure of the vascular epiphytes in a lowland forest in Panama correlates with species abundance. *Journal of Tropical Ecology* 23:337–342.

ZOTZ, G. & SCHULTZ, S. 2008. The vascular epiphytes of a lowland forest in Panama – species composition and spatial structure. *Plant Ecology* 195:131–141.

ZOTZ, G. & VOLLRATH, B. 2003. The epiphyte vegetation of the palm *Socratea exorrhiza* – correlations with tree size, tree age and bryophyte cover. *Journal of Tropical Ecology* 19:81–90.

ZOTZ, G., BERMEJO, P. & DIETZ, H. 1999. The epiphyte vegetation of *Annona glabra* on Barro Colorado Island, Panama. *Journal of Biogeography* 26:761–776.

Appendix 1. Characteristics of the study sites. Forest height is the average of the five tallest trees in the inventory. Tree density corresponds to individuals with trunk dbh > 5 cm. NP means not present. Large oaks refer to oaks with dbh > 45 cm. Rainfall in Mexico is the average amount (1978–1995) at San Cristóbal de Las Casas (Wolf 2005).

Locality	Macanal Colombia	S. Antonio Mexico	Basom-1 Mexico	Basom-2 Mexico	Chilil Mexico	El Chivero Mexico	La Florecilla Mexico
Altitude (m asl)	2570	2370	2490	2450	2300	2360	2350
Latitude (N)	04° 39′ 28″	16° 43′ 24″	16° 44′ 28″	16° 44′ 33″	16° 40′ 33″	16° 40′ 10″	16° 42′ 38″
Longitude (W)	74° 19′ 56″	92° 31′ 58″	92° 29′ 17″	92° 29′ 22″	92° 29′ 18″	92° 31′ 34″	92° 35′ 52″
Rainfall y^{-1} (mm)	738	1042	1042	1042	1042	1042	1042
driest month (mm)	32	3.9	3.9	3.9	3.9	3.9	3.9
wettest month (mm)	85	208	208	208	208	208	208
Forest height (m)	24.4	21.8	29.2	28.6	23.2	22.2	22.6
Basal area (BA) oaks (m^2 ha^{-1})	33.2	25.9	45.3	14.6	20.3	17.7	31.6
BA other broad-leaved (m^2 ha^{-1})	4.1	12.5	10.2	1.1	2.6	3.3	0.2
BA pines (m^2 ha^{-1})	NP	8.2	4.3	56.8	7.0	15.2	6.5
BA tree ferns (m^2 ha^{-1})	1.3	NP	NP	NP	NP	NP	NP
BA total (m^2 ha^{-1})	38.6	46.6	59.8	72.4	29.9	36.2	38.3
Density (D) oaks (indiv. ha^{-1})	411	486	433	744	664	608	678
D other broad-leaved (indiv. ha^{-1})	477	602	1090	244	432	17	33
D pines (indiv. ha^{-1})	NP	247	13	622	299	348	111
D tree ferns (indiv. ha^{-1})	167	NP	NP	NP	NP	NP	NP
D total (indiv. ha^{-1})	1055	1336	1537	1611	1395	973	822
BA large oaks (m^2 ha^{-1})	25.5	9.9	32.6	4.9	3.2	9.3	17.5
Coppiced oaks (%)	0	31.4	14.3	31.4	11.4	11.4	8.6

Appendix 2. List of epiphyte species recorded on 35 host trees at the study sites.

Species	Family	Macanal Colombia	San Antonio Mexico	Basom-1 Mexico	Basom-2 Mexico	Chilil Mexico	El Chivero Mexico	La Florecilla Mexico
Begonia sp.	Begoniaceae			+				
Catopsis sp.	Bromeliaceae				+	+		
Tillandsia biflora Ruiz & Pav.	—		+					
Tillandsia butzii Mez	—			+				+
Tillandsia carlsoniae L.B. Smith	—							+
Tillandsia complanata Benth.	—		+					
Tillandsia denudata André	—		+					
Tillandsia eizii L.B. Smith	—		+		+	+	+	+
Tillandsia fendleri Griseb.	—		+					
Tillandsia guatemalensis L.B. Smith	—		+	+	+	+	+	+
Tillandsia lautneri Ehlers	—			+	+			
Tillandsia pastensis André	—		+					
Tillandsia ponderosa L.B. Smith	—		+	+	+	+	+	+
Tillandsia restrepoana André	—		+					
Tillandsia tovarensis Mez	—		+					
Tillandsia vicentina Standley	—		+	+	+	+	+	+
Vriesea fragrans (André) L.B.Smith	—		+					
Vriesea tequendamae (André) L.B.Smith	—		+					
Disocactus aff. *ackermannii* (Haworth) Barthlott	Cactaceae		+					
Epiphyllum crenatum (Lindley) G. Don	—					+	+	+
Nopalxochia mcdougalli (Alexander) Marshall	—					+	+	
Neomirandea sp.	Compositae							+
Echeveria chiapensis Rose	Crassulaceae		+				+	+
Arphophyllum sp.	Orchidaceae					+	+	
Coelia guatemalensis Rchb. f.	—						+	+
Encyclia ochracea (Lindley) Dressler	—					+	+	+
Encyclia varicosa (Lindley) Schltr.	—			+			+	+
Encyclia vitellina (Lindley) Dressler	—		+	+	+	+		
Epidendrum eximium L.O. Williams	—			+	+		+	+
Epidendrum propinquum A. Rich. & Galeotti	—		+				+	
Homalopetalum pumilio (Rchb. f.) Schltr.	—							
Isochilus aurantiacus Hamer & Garay	—					+	+	+
Liparis arnoglossophylla Rchb. f. ex Hemsley	—			+				
Pleurothallis tubata (Lodd.) Steud.	—					+	+	
Ponera sp.	—		+			+	+	
Rhynchostele stellata Soto Arenas & Salazar	—		+	+	+	+	+	+
Osmoglossum pulchillum Schltr.	—							+
Peperomia alpina Miquel	Piperaceae		+	+	+	+	+	+
Peperomia arboricola C. DC.	—		+					
Peperomia galioides HBK	—		+	+	+	+	+	+
Peperomia hartwegiana Miq.	—		+					
Peperomia quadrifolia (L.) HBK	—			+		+		
Peperomia sp.	—					+		
Solanum americanum P. Mill.	Solanaceae							+
Asplenium monanthes L.	Aspleniaceae		+		+		+	
Asplenium praemorsum Sw.	—		+			+	+	+
Asplenium resiliens Kunze	—					+		
Asplenium sp.	—					+		
Cystopteris fragilis (L.) Bernh.	Dryopteridaceae					+		
Dryopteris munchii A.R. Smith	—							+
Elaphoglossum cf. *latifolium* (Sw.) J. Smith	Lomariopsidaceae		+	+	+	+		
Lycopodium reflexum Lam.	Lycopodiaceae			+				
Lycopodium sp.	—							+

Appendix 2. Continued.

		Macanal Colombia	San Antonio Mexico	Basom-1 Mexico	Basom-2 Mexico	Chilil Mexico	El Chivero Mexico	La Florecilla Mexico
Campyloneurum angustifolium (Sw.) Fée	Polypodiaceae		+	+	+	+	+	
Campyloneuron amphostenon (Kunze ex Klotzsch) Fée		−	+	+	+	+		
Pleopeltis crassinervata (Fée) Moore		−	+	+	+	+	+	+
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.		−	+	+	+	+		
Polypodium adelphum Maxon		−	+			+	+	+
Polypodium fissidens Maxon		−	+	+	+	+	+	
Polypodium furfuraceum S. & C.		−	+			+	+	
Polypodium hartwegianum Hook.		−	+	+	+	+	+	+
Polypodium laevigatum Cav.		−	+					
Polypodium plebeium S. & C.		−	+	+	+		+	
Polypodium plesiosorum Kunze ex Mett.		−		+	+	+		
Polypodium pleurosorum Kunze ex Mett.		−			+			
Polypodium sanctae-rosae (Maxon) C. Chr.		−	+		+	+	+	+
Polypodium sessilifolium Desv.		−	+					
Polypodium sp. A		−	+			+		
Polypodium sp. B		−	+			+	+	
Polypodium sp. C		−	+			+	+	
Adiantum andicola Liebm.	Pteridaceae					+	+	+
Vittaria sp.	Vittariaceae				+			