EFFECT OF FOREST DISTURBANCE ON ABUNDANCE AND DISTRIBUTION OF EPIPHYTIC BROMELIADS AND ORCHIDS

Peter Hietz[1], Gerald Buchberger & Manuela Winkler

Institute of Botany, University of Natural Resources and Applied Life Sciences (BOKU) Vienna, Gregor-Mendel Str. 33, 1180 Vienna, Austria

Abstract. Vascular epiphytes are important and sensitive components of humid tropical forests, whose diversity has been shown to be negatively affected by forest disturbance or conversion to secondary vegetation. We compared the abundance and distribution of mature individuals of three orchid and five bromeliad species between a relatively undisturbed and an adjacent disturbed plot in a Mexican humid montane forest. Most species were attached at lower positions on the trees in the disturbed plot, and in a few cases showed differences in preferred branch diameter or inclination. The spatial aggregation of epiphytes, assessed with the Morisita dispersion index and the Nearest Neighbor Index, did not differ between the plots. Five of the eight species were less common in the disturbed plot, including the orchid *Lycaste aromatica*, which was completely absent. Because three bromeliad species were substantially more common in the disturbed plot, the total density of all investigated epiphytes was almost three times higher in the disturbed plot. As these were the most abundant species of the entire epiphyte community, this translates to generally higher individual numbers and most likely also higher epiphyte biomass in the disturbed plot. *Accepted 25 July 2006.*

Key words: Bromeliaceae, dispersion, epiphyte, forest disturbance, humid montane forest, Mexico, Orchidaceae.

INTRODUCTION

Epiphytes are important components of tropical forests, contributing directly (about 10 % of vascular plant species are epiphytes) and indirectly (providing resources for canopy-dependent fauna) to their biodiversity and playing important roles in ecosystem processes such as water and nutrient cycling (Benzing 1990). With the continuing destruction of tropical forests being the major cause of species loss (Sala *et al.* 2000), the effects of deforestation, forest disturbance and replacement of primary forests by secondary vegetation has been studied for many organisms, including some epiphytes.

Generally, vascular epiphyte diversity has been found to be higher in primary than in secondary or disturbed vegetation (Hickey 1994; Hietz 1998; Barthlott *et al.* 2001; Flores-Palacios & García-Franco 2001). The degree to which epiphytes are negatively affected depends on the severity of disturbance, the size of the remnant trees, or the age of the secondary forest. For instance, 15-year-old fallows in Bolivia had 60–70 % fewer species than nearby primary forests (Krömer & Gradstein 2003); only 13 species were

found on a plantation of some 400 *Cedrela* trees *ca.* 8 m tall in contrast to 178 species in a primary forest plot in Venezuela (Barthlott *et al.* 2001), whereas selective logging reduced epiphyte species numbers by only 24 % in an Indian lowland moist forest (Padmawathe *et al.* 2004). Others found little difference in species numbers between natural and remnant or secondary vegetation when differences in tree density or size were accounted for (Hietz-Seifert *et al.* 1996; Hietz 2005).

In addition to total species numbers, disturbance also affects species composition. For instance, tree species composition changes from species with hard to species with softer wood when the forest is repeatedly disturbed (ter Steege 2003). Similarly, epiphyte species from shady canopy strata decline in more open vegetation types compared with natural forests (Hietz-Seifert *et al.* 1996; Acebey *et al.* 2003; Hietz 2005; Holz & Gradstein 2005).

For a species to survive it must successfully complete all stages of the life cycle, each stage being susceptible to changes in microclimate or vegetation structure. For instance, the probability of reaching reproductive maturity increases with light availability in three of the species investigated in the present study, and survival rates of the orchid *Jacquiniella teretifolia*

[1] e-mail: peter.hietz@boku.ac.at

as well as juveniles of *Tillandsia* spp. increase with canopy openness (Winkler 2005). We therefore expected that disturbance affecting microclimate and forest structure would be reflected in the distribution of epiphytes within the forest.

The present study compared the densities and within-forest distribution of individuals of eight relatively abundant species of epiphytic bromeliads and orchids between two adjacent plots, one of which was disturbed by wood extraction. We generally expected densities to be lower in the disturbed forest plot, and species growing on thicker branches and in the more humid part of the canopy to be more strongly affected. Since the persistence of populations of epiphytic bromeliads and orchids studied so far relies mostly on the survival of large, flowering individuals (Zotz *et al.* 2005; Zotz & Schmidt 2006; Winkler 2005), and juveniles of several species were too numerous and difficult to identify, only reproductively mature individuals were recorded.

MATERIAL AND METHODS

Study site. The study was carried out in the Rancho Guadalupe, a small 29-ha forest reserve adjacent to the Instituto de Ecología, 2.5 km south of Xalapa, in central Veracruz, Mexico (19°31'N, 96°57'W), at *ca.* 1350 m elevation. Average temperature is 19°C, and annual precipitation is *ca.* 1500 mm, most of which falls in the June-October wet season. According to the Holdridge life-zone system (Holdridge 1967), the forest is at the transition between premontane and lower montane moist forest. The typical vegetation is classified as 'bosque mesófilo de montaña' (mesophilous montane forest; Rzedowski 1986) in Mexico and comprises trees of mainly temperate origin mixed with tropical shrubs, herbs, and epiphytes. The centre of the reserve, though not a virgin forest, is a closed forest with a canopy height of 24 m and mature trees, dominated by *Quercus* spp., *Liquidambar styraciflua*, *Carpinus caroliniana*, and *Clethra mexicana* (Williams-Linera & Tolome 1996). The forest on the periphery of the reserve is adjacent to cultivated areas and was previously unfenced. Consequently it has been disturbed by the illegal extraction of wood, resulting in a more open forest with a denser ground cover of herbs and grasses and smaller trees. Disturbance is mostly by cutting of small to medium sized (< 20 cm diameter) trees and branches.

Two plots chosen to compare the distribution and abundance of selected epiphyte species were separated by a small path, and were at some parts less than 10 m distant from each other. The relatively undisturbed plot (1) was located on the lower half of a NW-facing slope with an average inclination of 29°, the disturbed plot (2) covered mostly the middle slope, facing also mostly NW and with an inclination of 27°. The diameter, height, crown radii in the four cardinal directions, and position of all trees ≥ 10 cm diameter at breast height (dbh) were measured on both plots. In addition, on the disturbed plot, all trees < 10 cm dbh that carried any of the target epiphytes were measured.

Details on the forest structure of both plots are given in Table 1. Practically no target epiphytes were on trees < 10 cm dbh of Plot 1. Tree species covering > 10 % of total basal area were *Carpinus caroliniana*, *Quercus germana*, *Meliosma alba* (due to one very large individual), *Liquidambar styraciflua*, and *Quercus xala-*

TABLE 1. Stand characteristics of two forest plots for trees > 10 cm dbh. Canopy height was defined as the average tree height of the tallest 20 % of trees. Crown cover was calculated by dividing the sum of projected crown areas (calculated from the average of four radii per crown) by the total plot area.

	Plot 1	Plot 2
Area (m^2)	1400	1800
Trees / ha	350	278
Basal area (m^2 / ha) all trees	27.4	14.9
Basal area (m^2 / ha) Quercus spp.	9.0	10.3
dbh (cm, average ± SD)	26.0 (18.1)	21.1 (15.6)
Tree height (m, average ± SD)	14.9 (4.5)	10.6 (5.1)
Canopy height (m)	21.4	19.1
Crown cover of trees >14 m height (m^2 / m^2)	1.6	0.5

TABLE 2. Densities of mature individuals of eight epiphyte species in a natural (Plot 1) and a disturbed forest plot (Plot 2). The Chi^2-test, calculated with absolute numbers, shows if the distribution of one species differs significantly from that of all individuals.

Species	Plot 1		Plot 2		Chi^2-test significance	% reproductive plants
	density (ha^{-1})	rel. abundance (%)	density (ha^{-1})	rel. abundance (%)		
C. sessiliflora	357	8.7	211	1.8	0.000	11.0
J. leucomelana	1457	35.3	1267	11.1	0.000	17.8
J. teretifolia	207	5.0	78	0.7	0.000	6.5
L. aromatica	157	3.8	0	0.0	0.000	36.4
T. deppeana	121	2.9	17	0.1	0.000	1.4
T. juncea	414	10.0	3206	28.0	0.002	12.9
T. multicaulis	857	20.8	2700	23.6	0.614	5.4
T. punctulata	550	13.3	3983	34.8	0.003	24.8
Total	4129	100.0	11461	100.0		

pensis in Plot 1, and *Quercus leiophylla, Q. germana,* and *Q. xalapensis* in Plot 2. *Quercus* spp. accounted for 33% of basal area on Plot 1 and 66% on Plot 2. When including only trees with a dbh ≥ 10 cm, the tree species composition was nearly significantly different between the two plots (Chi^2 test, p = 0.065), but most species were present with a few individuals and the study was not designed to test for host species effects.

A complete three-dimensional sampling of epiphytes is tedious and has only once been achieved for a large plot with relatively few individuals and the help of a crane (Nieder *et al.* 2000). In the present study, trees were climbed using single rope technique and the position of all reproductively mature individuals (i.e., those with old or new inflorescences) of eight abundant species of orchids and bromeliads (Table 2) was recorded relative to a vantage-point on the tree. By measuring the position of these vantage-points relative to the stem base, and adding the position of the tree within the plot, the three-dimensional distribution of all individuals was obtained. Branch diameter and distance from the ground and from the stem were measured. In the case of epiphytes on exposed branches that could not be accessed directly, the position was assessed by measuring the length of a thread thrown onto the branch, and the vertical and horizontal direction from the vantage-point on the tree, and estimating the branch diameter. The proportion of mature plants in the populations was recorded on six

trees for the orchids, and on 175 branch sections of nine trees for the bromeliads (Winkler 2005).

The orchids *Jacquiniella teretifolia* (Sw.) Britton & P. Wilson and *J. leucomelana* (Rchb. f.) Schltr. have caespitose erect stems with distichous, almost terete leaves growing in dense clusters, those of *J. teretifolia* to a height of *ca.* 40 cm, those of *J. leucomelana* not exceeding 15 cm. *Lycaste aromatica* (Graham ex Hook.) Lindl. has thin, drought-deciduous leaves at the top of a broad pseudobulb, with clustered, stalked flowers arising from the base of the pseudobulb. *Tillandsia deppeana* Steud., *T. multicaulis* Steud., and *Catopsis sessiliflora* (Ruiz & Pavón) Mez have broad, thin leaves forming water-impounding tanks, those of *T. deppeana* with a diameter of *ca.* 70 cm and a pinnate inflorescence, up to 80 cm tall, those of *T. multicaulis* about half as large and those of *Catopsis* forming a narrow tank, 15–20 cm high. *T. punctulata* Schltdl. & Cham. is of tank-atmospheric habit, while *T. juncea* (Ruiz & Pav.) Poir. is atmospheric with filiform, fasciculate leaves that cannot store water externally, and is the only species exhibiting crassulacean acid metabolism. *T. deppeana* is largely monocarpic, i.e., produces only one rosette that dies after fruiting, the other species being polycarpic.

Data analysis. The Morisita dispersion index (I$_\delta$, Morisita 1962) has been used as a measure of spatial aggregation of individual epiphytes (Nieder *et al.* 2000; Isaza *et al.* 2004). I$_\delta$ = q [Σ(n$_i$)^2 – N]/(N^2-N), where q is the number of cells, N the number of individu-

als in the entire plot, and n_i the number of individuals in cell i. I_δ is 1 in the case of random distribution, < 1 for hyperdispersed, and > 1 for clustered populations. We tested cell sizes of 2 x 2 and 5 x 5 m. Cells can also be three-dimensional, but this has never been done for epiphytes and we therefore calculated I_δ of the epiphytes' distribution projected to the ground area to be able to compare with other published results. Alternatively, the Nearest Neighbor Index (NNI, Clark & Evans 1954) compares the mean distances to the nearest neighbors to the distance that would be expected if individuals were randomly distributed. The mean nearest neighbor distance was calculated by computing distances from the three-dimensional coordinates of all conspecific individuals per plot. The average nearest neighbor in a randomly distributed population is 0.5 $(A/N)^{1/2}$ for a two-dimensional area and 0.5 $(V/N)^{2/3}$ for a three-dimensional space, where A is the area, V the volume, and N the number of individuals. The volume theoretically available was taken as plot area times average tree height. For a

better comparison with I_δ, Table 3 shows 1/NNI so that values > 1 also indicate clustering. The NNI calculated from plots is somewhat biased because neighbors that are outside the plot are ignored and thus the nearest neighbor distance of individuals close to the border tends to be underestimated (Sinclair 1985). Using a correction that includes information about plot shape for two-dimensional distances (see Sinclair 1985) increased the random nearest neighbor distance in our plots in one case by 27% and on average by only 8%. We know of no attempt to correct for the border-bias of three-dimensional plots, which mathematically is not trivial. However, since the bias for the two-dimensional distribution is small, and no individual has a neighbor in the third dimension outside the plot as there are no epiphytes above or below the forest, we are confident that the bias in the uncorrected NNI for three-dimensional distribution (Table 3) is minor or mostly the same for all species, and certainly does not affect the general outcome. Differences in the epiphytes' abundance on plots were
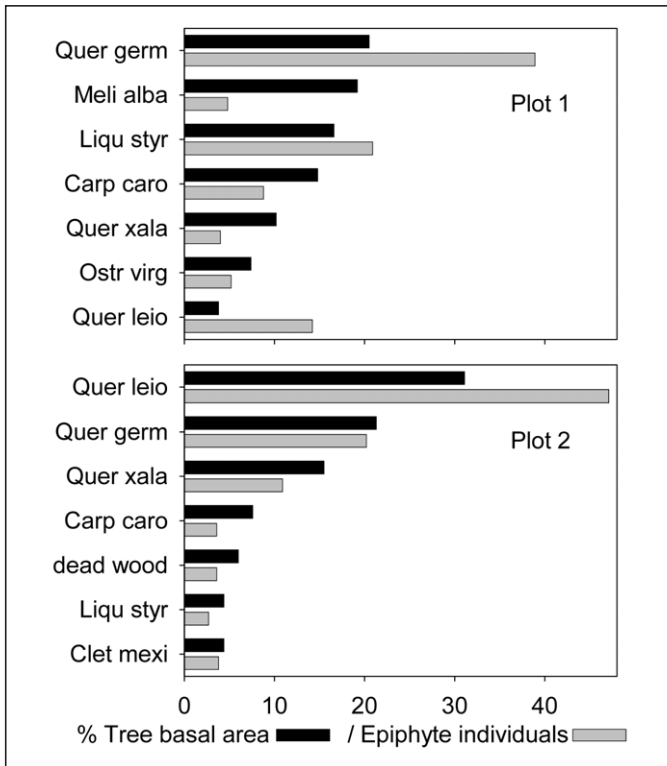

FIG. 1. Relative abundance of host species and the proportion of epiphyte individuals they carried.
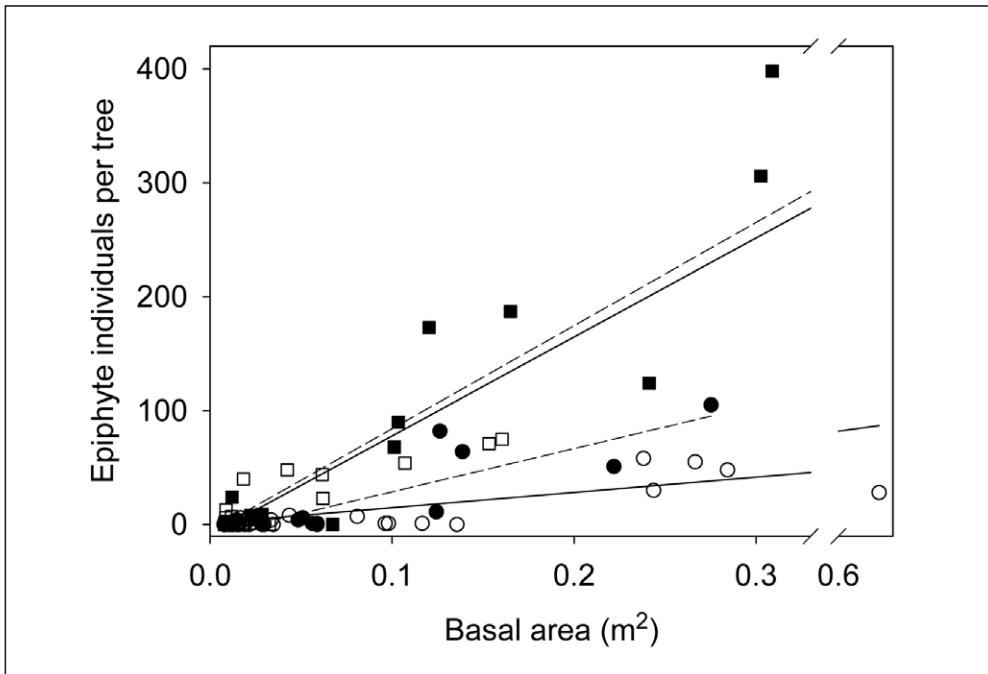
FIG. 2. Regression between tree basal area and the number of mature individuals of eight epiphyte species growing on the trees in a natural (Plot 1, circles) and a disturbed (Plot 2, squares) forest plot. Filled symbols and broken regression lines represent *Quercus* spp., empty symbols are other trees, and solid lines are regressions for all host trees.

tested with a Chi^2 test, comparing the distribution of one species between the two plots with that of all individuals.

RESULTS

The number of trees >10 cm dbh was similar on Plots 1 and 2 (49 and 50 respectively), but density was somewhat higher on the smaller Plot 1. On Plot 2 an additional 27 trees <10 cm dbh hosted mature individuals of the epiphyte species investigated. Although trees <10 cm dbh were not thoroughly searched on Plot 1, very few, if any, appeared to carry mature epiphytes. Half (25) of the trees sampled on Plot 1 did not carry any of the target epiphytes, in contrast to only 13 trees >10 cm dbh on Plot 2. Average dbh for trees >10 cm was 4.9 cm larger, trees were on average 4.3 m taller, and the undergrowth of shrubs and small trees was generally less dense on Plot 1.

The density of epiphytes was almost three times higher on Plot 2 (11 460 individuals ha^{-1}) than on Plot 1 (4130 ha^{-1}). Absolute densities and relative frequencies of all orchids and of *Catopsis sessiliflora* and *T. deppeana* was higher on Plot 1, and much higher on Plot 2 for the other three *Tillandsia* species (Table 2). *Lycaste* did not occur at all on Plot 2 and *T. deppeana* only with three individuals. Reproductive individuals comprised between 1.4 % (monocarpic *T. deppeana*) and 36.4% (*L. aromatica*) of the populations.

The proportion of basal area occupied by a tree species approximately corresponded to the number of epiphytes it carried, suggesting that, apart from size, tree species differed little in their suitability for epiphytes (Fig. 1). To test if the higher epiphyte density on Plot 2 was an effect of differences in tree size or species composition, we compared regressions between tree basal area and the number of epiphytes carried per tree for all trees on the two plots, and for *Quercus* spp. only. The slope of the regression was significantly higher on Plot 2 in both cases (t-test, p < 0.001, Fig. 2).
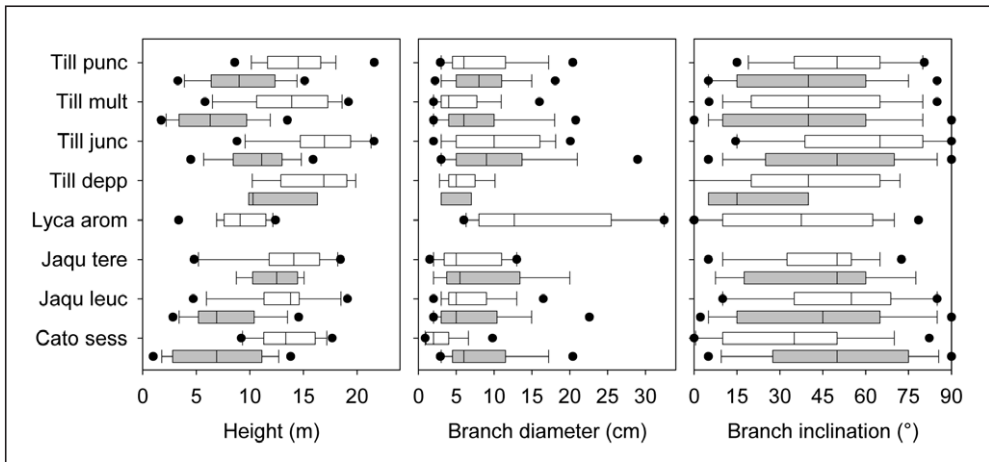
FIG. 3. Preferred height of attachment, branch diameter and branch inclination of mature individuals of eight epiphyte species in an undisturbed (Plot 1, white box) and a disturbed (Plot 2, grey box) forest plot. Boxes indicate 25, 50, and 75 %, whiskers 10 and 90 % and dots 5 and 95 % quantiles.

With the exception of *J. teretifolia* and *T. deppeana*, all species were found at significantly (Spearman p < 0.001) higher canopy positions in Plot 1 than in Plot 2, on average 4.7 m, i.e., about the difference in tree height (Fig. 3). Differences in the preferred branch thickness were significant (p < 0.001) only in *T. multicaulis*, which on average grew on thicker branches in Plot 2. Branch inclination was significantly (p < 0.05) higher in Plot 2 for *C. sessiliflora*, and higher in Plot 1 for *J. leucomelana*, *T. juncea*, and *T. punctulata*.

With the exception of *T. deppeana* in Plot 2, where the only three individuals occupied one cell each and an I_δ of 0 consequently indicated perfect hyperdispersion, I_δ was always > 3 (Table 3). I_δ varied only about two-fold among most other species, but was substantially higher for *Lycaste aromatica*. On Plot 1, orchids grew more clustered than bromeliads, while among the bromeliads *T. juncea* on most counts showed somewhat higher aggregation than the other species. I_δ was always higher for the 2 x 2 m than for the 5 x 5 m grid. The reciprocal of the Nearest Neighbor Index (1/NNI) was always > 1, also in the case of *T. deppeana* with only three individuals. Although the pattern of aggregation indicated by the NNI was similar to the I_δ, there were some notable differences. For instance on Plot 1, 1/NNI of most *Tillandsia* spp. was higher than in *J. teretifolia* and *C. sessiliflora* had the second lowest clustering in Plot 2. The Pearson cor-

relation coefficient between I_δ for the 2 x 2 and 5 x 5 m grid was 0.90, r^2 between 1/NNI and I_δ5x5 was 0.76 and between 1/NNI and I_δ2x2 0.88.

DISCUSSION

Because epiphytes depend on trees, their distribution is very unlikely to be completely randomized or even hyperdispersed. It may be difficult to devise a measure that indicates the randomness of their distribution independent of the available substrate. It is particularly difficult to distinguish if the apparent aggregation results from the restricted availability of substrate or, and to which degree, from other processes that determine community structure, such as dispersal, facilitation, or competition. One study found that the spatial pattern of six bromeliad species in a secondary forest was independent of the position of the trees (Van Dunné 2002), although the geographical information system-approach and the 2.5 x 2.5 m grid did not fully account for the three-dimensionality of the epiphytic habitat.

We can, however, compare dispersal indices between species or locations. Since Morisita's I_δ strongly depends on cell size, comparisons between studies that use different grids are problematic. For instance, a cell size of 10 x 50 m resulted in I_δs very close to 1 (random) for several bromeliads in a montane forest (Isaza *et al.* 2004), whereas five bromeliads in a secondary

forest analyzed with a cell size of 6.25 m² showed an aggregated spatial pattern with I_δ between 2.8 and 40 (Van Dunné 2002), and it remains unclear whether these differences result from differences in forest structure, species, or grid size. By comparison, the very high I_δ (4.8 to 238) reported for a Venezuelan lowland forest, in spite of a relatively large cell size of 8 x 8 m, does reflect a rather strong clustering of most species (Nieder *et al.* 2000). In some species this was explained by a strong preference for ant gardens, which were located on young trees in a large gap, and in other species by strong clustering on a few large trees.

In contrast to the Morisita's I_δ, the Nearest Neighbor Index is independent of scale and can be used whenever the exact position of individuals (instead of their presence in individual cells) is available. A previous analysis of the spatial distribution of epiphytes in the same forest, which tested the odds against having a conspecific neighbor by chance (Hietz & Hietz-Seifert 1995b), found that orchids generally showed stronger clustering than any other group. This was confirmed for *L. aromatica* and to some extent for *J. leucomelona*, but not for *J. teretifolia*. Though the latter species is regularly found in small groups, most individuals do not flower and the nearest flowering individual is often at a substantial distance. The small dust-like seeds of orchids float easily (Arditti & Ghani 2000) and should be as suitable as those of bromeliads or ferns for dispersal to new branches. It has therefore been proposed that strong aggregation results

from a low probability of finding the fungus necessary for germination on branches where no orchids are present (Hietz & Hietz-Seifert 1995b). This is supported by experimental evidence from germination studies, in combination with fungal species that have been isolated from orchid roots (Peterson *et al.* 1998). Woody ectomycorrhizal plants also show improved seedling growth and survival close to established individuals with mycorrhizae (Simard & Durall 2004).

The relatively low number of individuals of any tree species and/or the differences in average tree size hinder any meaningful statistical analysis of potential host preferences of any epiphyte species with the present data. *Meliosma alba* appears to be a poor host, but here the large basal area results from one large individual that had lost a substantial proportion of its crown. In general, *Quercus* may be more suitable than *Carpinus* owing to its rough bark and large and spreading branches, and the fact that *Quercus* spp. carry particularly high epiphytes loads has been reported previously (Hietz & Hietz-Seifert 1995a; Wolf 2005). If the tree species composition does differ between the two plots (p = 0.065), this can be due to pre-existing differences between the two plots independent of disturbance, to differences in tree recruitment that are an effect of disturbance, and certainly also to selective cutting of trees from Plot 2. As we have no information on the epiphyte abundance prior to disturbance, differences in epiphytes between the two plots could also predate and be independent of disturbance. While this cannot be ruled out, it appears

TABLE 3. Morisita index (I_δ) of aggregation for cell sizes 2 x 2 and 5 x 5 m, average distance to the nearest conspecific neighbor and the reciprocal of the Nearest Neighbor Index (1/NNI). 1/NNI is shown for better comparison with I_δ so that for both indices values > 1 indicate clustering.

	C. sessiliflora	J. leucomelana	J. teretifolia	L. aromatica	T. deppeana	T. juncea	T. multicaulis	T. punctulata
Plot 1								
Morisita I_δ 2 x 2	7.8	13.7	15.3	59.1	9.1	12.8	6.3	8.9
Morisita I_δ 5 x 5	3.7	4.1	4.9	16.3	5.2	7.4	4.1	4.7
nearest neighbor	2.72	0.46	3.42	0.86	2.94	1.54	1.82	1.25
1/NNI	10.26	23.73	11.74	56.06	19.50	16.42	8.58	16.79
Plot 2								
Morisita I_δ 2 x 2	8.3	10.1	5.9		0	9.4	4.8	4.9
Morisita I_δ 5 x 5	5.1	4.2	4.9		0	5	3.5	4.1
nearest neighbor	3.61	0.57	4.02		16.76	0.58	0.90	0.69
1/NNI	8.75	16.88	15.31		10.24	8.83	6.39	6.46

unlikely to account for the pattern found, while other results from the area are broadly in line with those reported here, as discussed below.

Epiphytes, dependent on host trees and strongly affected by microclimate, are considered sensitive indicators of environmental change resulting from forest disturbance and may be more affected than other plants. Which species are affected, and how severely, will depend on the degree and type of disturbance and also on the time period since the disturbance. Two studies of epiphytes on remnant forest trees surrounded by pasture found numbers of epiphyte species per tree that were similar to those in closed forests, though the species composition differed somewhat and the number of epiphytes per ground area was certainly much lower in the pasture than in the forest (Hietz-Seifert *et al*. 1996; Flores-Palacios & García-Franco 2001). This shows that large trees can continue to support a high number of epiphytes in severely disturbed habitats, though not all species from a closed forest, which was also found on coffee shade trees (Hietz 2005). In contrast, the species diversity in young, regenerating forests is often low. Hickey found an average of only 1.5 epiphytic fern species per 25 m^2 on plots in 20–30-year-old regenerating forests in contrast to 5.5 species in old-growth forests (Hickey 1994). A plantation of *Alnus acuminata* in Mexico supported 21 vascular epiphyte species, in contrast to 39 on the same number of trees and in a similar plot area in an adjacent old-growth cloud forest (Hietz 1998). Fifteen-year-old forest fallows had 60–70 % fewer species than neighboring natural forests in Bolivia (Krömer & Gradstein 2003), and 0.25 ha of a 32-year-old plantation of *Cedrela montana* had only 13 compared with 119 species in 0.1 ha of primary forest in Venezuela (Barthlott *et al*. 2001). Four selectively logged forest plots of 625 m^2 had 31 vascular epiphyte species in contrast to 50 species in undisturbed plots in a lowland forest in northern India (Padmawathe *et al*. 2004), but it is unclear if the species decline is a result of fewer trees available for colonization or if the number of epiphytes per tree was also lower. A larger study comparing 16 forests in southern Mexico found a negative correlation between disturbance, quantified as the proportion of sprouted oak trees, and the number of epiphytes on 35 trees of the same size classes (Wolf 2005). That study also reports epiphyte biomass per tree decreasing with disturbance, but neither species richness nor biomass was correlated with the stem basal area of the forests. In contrast, epiphyte biomass on branches of

isolated remnant trees was almost twice as high as on forest trees in another study in Mexico, probably because the more abundant light reaching the branches of isolated trees made for stronger epiphyte growth (Flores-Palacios & García-Franco 2003).

In our study, five out of eight epiphytes were found at lower densities in the disturbed plot. This can be an effect of the lower basal area in the disturbed plot, with generally less substrate available for epiphytes to grow on. Also, a higher rate of disturbance means that the substrate is available for less time and fewer individuals will have become mature. Differences in host species composition is another possibility, but unlikely to account for the lower densities in the disturbed plot, where *Quercus* spp., generally a good host for all species investigated, are over-represented in basal area. Finally, the microclimate is likely to differ and the within-canopy distribution of epiphytes offers clues to preferred microhabitats. As *Lycaste aromatica* showed a strong preference for thick branches of the lower canopy in Plot 1, the drier conditions most plausibly explain its complete absence from Plot 2. There was some stratification also in the distribution of the other species, but their position within Plot 1 was not very helpful in predicting the abundance in the more open plot.

Three bromeliads out of eight species grew at higher densities in the disturbed plot, as a consequence of which the total density of all epiphytes studied was about three times higher. Bromeliads have been classified according to their light demand and photosynthetic adaptations, which is reflected in their distribution within the canopy and in a wider geographical area (Pittendrigh 1948; Griffiths & Maxwell 1999). While it can be expected that shade-demanding species will find less suitable habitat in open forests, sun-loving epiphytes should find the high light environment in the disturbed forest equally represented in the upper canopy of the closed forest. Which factors, then, can be responsible for the high abundance of bromeliads on the disturbed plot? Species that, for whatever reason, grow better on *Quercus* could be favored on Plot 2, where *Quercus* accounted for 66 % of the total basal area, as opposed to 33 % on Plot 1. In fact on Plot 2, *Quercus* carried 82 % of individuals of the three *Tillandsia* species that had higher densities on Plot 2, but only 54% of individuals of the other species. A host effect, however, cannot be the only cause since the abundance of the three *Tillandsia* spp. was also higher per individual oak tree (Fig. 2). If tree growth rates differed, slow-growing

trees would have been available for a longer time to be colonized and carry more epiphytes on reaching a given size, but it is unlikely that trees in the more open plot would grow more slowly. Given the very close proximity of the two plots, we regard differences in pollinator presence or dispersal as very unlikely. The open nature of the forest on Plot 2 where a few remaining large trees emerge from the mass of smaller trees provides a rougher canopy surface, which means that a larger volume of the canopy is close to the canopy surface, the exchange of air between the forest and the surroundings is faster, and the air is consequently drier. Atmospheric bromeliads in particular are known to be sensitive to high humidity because the adpressed trichomes of a wet leaf surface impede gas exchange (Benzing *et al.* 1978), and they could thus be favored by disturbance. Furthermore, the large oak trees in the closed forest do not emerge from the other trees as in the disturbed plot, and since these carry the bulk of epiphytes, sun-loving species may find the exposed oak trees of the disturbed forest more suitable than the sheltered trees in the closed forest.

Our results were obtained from a single pair of plots and may not be generally valid, but other studies also found bromeliads to be either more diverse (Barthlott *et al.* 2001) or with more biomass (Flores-Palacios & García-Franco 2003) in disturbed plots or on isolated trees. The surprisingly fast colonization of secondary forests by bromeliads in a Costa Rican cloud forest, where their biomass increased 5- to 46-fold between four-year-old and eight-year-old plots (Merwin *et al.* 2003), further supports the notion that at least some bromeliad species are favored by disturbance. Using data from the proportion of reproductive individuals of the eight species (Table 2), the 4129 reproductive individuals per ha translate to *ca.* 45 000 individuals of all age classes on Plot 1, and to *ca.* 102 000 on Plot 2. Given that the species studied account for *ca.* 59 % of all epiphyte individuals (Hietz 1997), we arrive at a total density of 77 000 individual vascular epiphytes on Plot 1. The second extrapolation cannot be applied to the disturbed plot, where bromeliads are relatively more abundant than on Plot 1, but even allowing for a decrease in the density of individuals from other families, the much higher abundance of the three commonest bromeliads means that the total density of vascular epiphytes is also higher in the disturbed plot, which has not been reported previously. For the forest studied, abundance also translates to biomass because the common bromeliads are larger than most other species and bromeliads strongly dominate epiphyte biomass at this altitude (Hietz & Hietz-Seifert 1995a).

In contrast to most previous studies, we compared epiphyte abundance rather than species numbers, which may be a more sensitive indicator of environmental and specifically microclimatic changes. Species lists from the two plots studied here are incomplete but indicate that the number of species was about 10 % lower in Plot 2 than in Plot 1, whereas individual densities differed more than two-fold in six out of eight species. In an Indian lowland forest, the abundance of epiphytic pteridophytes and non-orchid angiosperms reached only 21 and 15 % respectively of the primary forest, though their species numbers differed less (Padmawathe *et al.* 2004). Interestingly, and contrary to our and other studies from the Neotropics, on both counts orchids were the least affected group.

This study is too limited to allow general conclusions but shows that disturbance affects species differently and may result in an increase of epiphyte biomass. The effect disturbance has on epiphyte diversity and abundance is complex and dependent on many factors, including epiphyte and host tree species. Hence more studies are required for a clearer picture to emerge.

ACKNOWLEDGMENTS

REFERENCES

Acebey, A., Gradstein, S.R., & T. Krömer. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. J. Trop. Ecol. 19: 9–18.

Arditti, J., & A.K.A. Ghani. 2000. Tansley review No. 110 – Numerical and physical properties of orchid seeds and their biological implications [Review]. New Phytol. 145: 367–421.

Barthlott, W., Schmit-Neuerburg, V., Nieder, J., & S. Engwald. 2001. Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. Plant Ecol. 152: 145–156.

Benzing, D.H. 1990. Vascular epiphytes. General biology and related biota. Cambridge Univ. Press, Cambridge.

Benzing, D.H., Seemann, J., & A. Renfrow. 1978. The foliar epidermis in Tillandsioideae (Bromeliaceae) and its role in habitat selection. Amer. J. Bot. 65: 359–365.

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

Flores-Palacios, A., & J. García-Franco. 2001. Sampling methods for vascular epiphytes: their effectiveness in recording species richness and frequency. Selbyana 22: 181–191.

Flores-Palacios, A., & J.G. García-Franco. 2003. Effect of isolation on the structure and nutrient budget of oak epiphyte communities. Plant Ecol. 1736: 259–269.

Griffiths, H., & K. Maxwell. 1999. In memoriam CS Pittendrigh: does exposure in forest canopies relate to photoprotective strategies in epiphytic bromeliads? Funct. Ecol. 13: 15–23.

Hickey, J.E. 1994. A floristic comparison of vascular species in Tasmanian oldgrowth mixed forest with regeneration resulting from logging and wildfire. Aust. J. Bot. 42: 383–404.

Hietz, P. 1997. Population dynamics of epiphytes in a Mexican humid montane forest. J. Ecol. 85: 767–775.

Hietz, P. 1998. Diversity and conservation of epiphytes in a changing environment. Pure Appl. Chemistry 70: 2114.

Hietz, P. 2005. Conservation of vascular epiphyte diversity in Mexican coffee plantations. Cons. Biol. 19: 391–399.

Hietz, P., & U. Hietz-Seifert. 1995a. Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. J. Veg. Sci. 6: 487–498.

Hietz, P., & U. Hietz-Seifert. 1995b. Intra- and interspecific relations within an epiphyte community in a Mexican humid montane forest. Selbyana 16: 135–140.

Hietz-Seifert, U., Hietz, P., & S. Guevara. 1996. Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz, Mexico. Biol. Cons. 75: 103–111.

Holdridge, L.R. 1967. Life Zone Ecology. Tropical Science Center, San José.

Holz, I., & R.S. Gradstein. 2005. Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica - species richness, community composition and ecology. Plant Ecol. 178: 89–109.

Isaza, C., Betancur, J., & J.V. Estévez-Varón. 2004. Vertical distribution of bromeliads in a montane forest in the eastern Cordillera of the Colombian Andes. Selbyana 25: 126–137.

Krömer, T., & S.R. Gradstein. 2003. Species richness of vascular epiphytes in two primary forests and fallows in the Bolivian Andes. Selbyana 24: 190–195.

Merwin, M.C., Rentmeester, S.A., & N.M. Nadkarni. 2003. The influence of host tree species on the distribution of epiphytic bromeliads in experimental monospecific plantations, La Selva, Costa Rica. Biotropica 35.

Morisita, M. 1962. Id-Index, a measure of dispersion of individuals. Researches on Population Ecology 4: 1–7.

Nieder, J., Engwald, S., Klawun, M., & W. Barthlott. 2000. Spatial distribution of vascular epiphytes (including hemiepiphytes) in a lowland amazonian rain forest (Surumoni crane plot) of southern Venezuela. Biotropica 32: 385–396.

Padmawathe, R., Qureshi, Q., & G.S. Rawat. 2004. Effects of selective logging on vascular epiphyte diversity in a moist lowland forest of Eastern Himalaya, India. Biol. Cons. 119: 81–92.

Peterson, R.L., Uetake, Y., & C. Zelmer. 1998. Fungal symbioses with orchid protocorms. Symbiosis 25: 29–55.

Pittendrigh, C.S. 1948. The bromeliad-Anopheles-malaria complex in Trinidad. I. The bromeliad flora. Evolution 2: 58–89.

Rzedowski, J. 1986. Vegetación de México. 3rd edition. Mexico, D.F., Editorial Limusa.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., & D.H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

Simard, S.W., & D.M. Durall. 2004. Mycorrhizal networks: a review of their extent, function, and importance. Can. J. Bot. 82: 1140–1165.

Sinclair, D.F. 1985. On tests of spatial randomness using mean nearest neighbor distance. Ecology 66: 1084–1085.

ter Steege, H. 2003. Long-term changes in tropical tree diversity: Studies from the Guiana Shield, Africa, Borneo and Melanesia. Wageningen, the Netherlands, Tropenbos. Tropenbos Series 22.

Van Dunné, H.J.F. 2002. 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). J. Trop. Ecol. 18: 193–213.

Williams-Linera, G., & J. Tolome. 1996. Litterfall, temperate and tropical dominant trees, and climate in a Mexican lower montane forest. Biotropica 28: 649–656.

Winkler, M. 2005. Population dynamics of epiphytes related to canopy structure in a Mexican humid montane forest. Doctoral thesis, Universität für Bodenkultur, Vienna.

Wolf, J.H.D. 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. For. Ecol. Manag. 212: 376–393.

Zotz, G., Laube, S., & G. Schmidt. 2005. Long-term population dynamics of the epiphytic bromeliad, *Werauhia sanguinolenta*. Ecography 28: 806–814.

Zotz, G., & G. Schmidt. 2006. Population decline in the epiphytic orchid *Aspasia principissa*. Biol. Cons. 129: 82–90.