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INTRA- AND INTERSPECIFIC RELATIONS WITHIN AN EPIPHYTE COMMUNITY IN A MEXICAN HUMID MONTANE FOREST

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ABSTRACT. Studies on epiphytic vegetation are scarce. Most have been made on a regional scale or by comparing different host trees or locations within a tree. We present an analysis on a very small scale, which may be a powerful tool for describing and understanding community structure and organization. One hundred and eight photographs of oak branch or stem sections, some 50 to 100 cm long, were analyzed, and the nearest neighbors of the 1,843 specimens of vascular epiphytes, belonging to 39 species, were recorded. The non-randomness of species associations was calculated as χ^2 values of 2×2 contingency tables. Not surprisingly, many species were their own nearest neighbors. The significance of having a neighbor of the same species, i.e., the degree of clustering, however, differed between groups and may be interpreted in terms of mobility of diaspores and specificity of substrate requirements. Generally, clustering decreased in the following order: orchids, *Peperomia* spp., most bromeliads, and non-creeping ferns. Three orchid species showed an extremely high incidence of interspecific association, which we suppose to be the result of sharing the same mycorrhizal partner. Weaker associations of different species may be explained by their preferring similar zones in the trees or, possibly, by some species serving as seed traps or nurse plants.

INTRODUCTION

Describing the spatial distribution of epiphytes not only requires canopy access techniques, but also methods of vegetation registration and analysis different from those used and well established for the study of ground-rooted vegetation. On the one hand, epiphytes are distributed in three-dimensional space, and on the other, their distribution depends on the architecture of the trees upon which they grow. Nychka and Nadkarni (1990) analyzed the three-dimensional distribution of tank bromeliads related to tree architecture. They found derivation from completely random patterns both in the direction towards clustering and towards hyperdispersion (regularity) and suggested fungal associations with epiphyte roots or organic matter associated with branch substrate may be the underlying causes.

Several authors have recorded the distribution of epiphytes in various zones within the host trees (Johansson 1974, Kelly 1985, ter Steege & Cornelissen 1989, van Leerdam *et al.* 1990) or on branch diameter classes (Zimmerman & Olmsted 1992). These studies show that the distribution is influenced by microclimatic gradients within the canopy and by substrate qualities. Such studies are valuable for describing the autecological requirements of the species and in some extent to classify communities. However, they will reveal little about possible biotic causes of the community structure, and intra- or interspecific relations.

Sampling small plots of several decimeters^2 on the stem or branch has successfully been applied for the analysis of epiphytic moss and lichen communities (Kenkel & Bradfield 1986, Kantvilas & Minchin 1989, Wolf 1993). As most vascular epiphytes show low constancies in plots of this size, larger plots or a very high number of samples would be necessary to accurately describe their distribution and the composition of communities. For ground-rooted vegetation this problem is overcome by enlarging the area sampled. On trees, plots of one m^2 or more would be too heterogeneous due to changing branch diameter, inclination, or other characteristics within the plot that affect the composition of the epiphytic community.

Hazen (1966) measured the distance between individuals along branches and found no deviations from randomness in the distribution of epiphytes. His analysis strongly suffers from the fact that the branching system of the tree was converted to a linear system that did not correctly represent the distances between individuals or even their order along branches.

Yeaton and Gladstone (1982) evaluated nearest neighbors of four orchids in a Costa Rican dry forest and found each species to be its own nearest neighbor.

We present an analysis of nearest neighbors of a larger data set, evaluating the significance of a

TABLE 1. F-values of χ^2-tests of combinations between the 23 more frequent species. Only significant relationships between species ($F < -3.8$ or >3.8) and all intraspecific relationships are shown. Values <15 and all intraspecific relationships are boldfaced, values <100 are boldfaced and underlined. Negative values indicate significant non-co-occurrence. A: Araceae, B: Bromeliaceae, F: fern, O: Orchidaceae, P: Piperaceae.

Group	Species	Individ.	*A. scan.*	*C. angu.*	*C. schi.*	*C. nuta.*	*C. sess.*	*C.* spp.	*D. negl.*	*E. ochr.*	*J. leuc.*	*J. tere.*	*L. arom.*	*P. 4-lea.*
A	*Anthurium scandens*	8	**0**											
F	*Campyloneurum angustif.*	7	8	**0**										**50**
O	*Campylocentrum schiedei*	10			**118**									
B	*Catopsis nutans*	14				**0**	6							
B	*Catopsis sessiliflora*	38					**4**	9						
B	*Catopsis* spp.	62					5	**11**						
O	*Dichaea neglecta*	26							**0**					
O	*Encyclia ochracea*	27								**340**				
O	*Jacquiniella leucomelana*	11									**34**	**16**		
O	*Jacquiniella teretifolia*	22									**16**	**217**		
O	*Lycaste aromatica*	44											**980**	
P	*Peperomia* 4-leaved	12		**50**						11				**2**
P	*Peperomia* sp01	135												
P	*Pepe.* aff. *quadrifolia*	29												
P	*Peperomia* spp.	44												
P	*Peperomia tetraphylla*	295							6					
F	*Phlebodium areolatum*	9												
F	*Pleopeltis crassinervata*	122												4
F	*Polypodium furfuraceum*	19							6					**17**
F	*Polypodium plesiosorum*	22							5					
F	*Polypodium polypodioides*	14												
O	*Scaphyglottis livida*	11									**34**	**157**		
B	*Tillandsia* broad-leaved	171												
B	*Tillandsia butzii*	18							7					
B	*Tillandsia deppeana*	8												
B	*Tillandsia multicaulis*	28												
B	*Tillandsia punctulata*	206											−4	
B	*Tillandsia* narrow-leaved	102				5								
B	*Tillandsia* spp.	237											−5	

species having a conspecific nearest neighbor and being associated with a different species.

MATERIALS AND METHODS

The study site is located at 1,350 m elevation above sea level in a small reserve adjacent to the Instituto de Ecología, 2.5 km south of Xalapa, in central Veracruz, Mexico. Average temperature at this altitude is about 19°C. Annual precipitation is ca. 1,500 mm, 79% of which falls in the wet season between May and October. According to the Holdridge life zone system, the forest is at the transition between premontane moist forest and lower montane moist forest and is commonly classified as "bosque mesófilo de montaña" (mesophilous montane forest, Rzedowski 1984) in Mexico. While most dominant trees (*Quercus* spp., *Liquidambar macrophylla*) of this forest type are of temperate origin, the shrub and herb layers include many tropical elements. Canopy height is ca. 20–25 m. Epiphytes, especially bromeliads, ferns and orchids, are very abundant and 66 species of vascular epiphytes have been recorded in the reserve (unpublished data).

In August 1992, 108 photos of branch and stem sections, typically 50–100 cm long, were taken on seven oaks at a height between 2 and 20 m above ground. The photos are representative for the microsites available to epiphytes on these trees and include stems, thick branches, and thin twigs of various inclinations and light levels. Photos of the same branches taken one year later for demographic studies facilitated the identification of individuals, some of which had, by that time, grown or produced inflorescences. On the photos of 1992, 1,843 individuals could

TABLE 1. Extended.

P. sp01	*P. quad.*	*P.* spp.	*P. tetr.*	*P. areo.*	*P. cras.*	*P. furf.*	*P. ples.*	*P. poly.*	*S. livi.*	*T. br-lea.*	*T. butz.*	*T. depp.*	*T. mult.*	*T. punc.*	*T. na-lea.*	*T.* spp.
				6												
															5	
			−5													
			4								7					
						6										
									192							
									46							
			−5											−4		−5
5			**16**					14							−5	−12
	0						15	8								
7		**139**						5						−4		
18	−4		**12**	**33**	13			11		−9				14		**−20**
				0												
					−3					10						
						1					10					
							6									
7		5						**0**				3				
									0							
			−4		**35**					**27**						
											1					
												0				
													0			
7		−4	**21**		7									**22**		−14
−5													7		**26**	
−11			**−17**		**28**									**−16**	−5	**188**

be distinguished. Of these, 1,213 individuals belonging to 39 species were identified, and all but one individual could be identified to the genus level. Individuals which could only be attributed to genera were mostly bromeliads. Where it was not possible to decide whether shoots or leaves belonged to one or more individuals, we conservatively counted only the number of individuals we could positively distinguish.

The nearest neighbor of each individual was identified and the randomness of all possible species pairs was evaluated by χ^2-tests of 2 × 2 contingency tables (Zar 1984).

RESULTS

F-values of the χ^2-tests are presented in TABLE 1. To reduce the size of the table and to avoid random errors due to low sample size, only the more frequent species are presented. Note that the matrix is not symmetric, as the fact that individual A is nearest neighbor to individual B does not imply that B is nearest neighbor to A. Significant positive intraspecific associations (diagonal of the matrix) indicate that a species has a clustered distribution. Five orchids (*Campylocentrum schiedei, Encyclia ochracea, Lycaste aromatica, Jacquiniella leucomelana* and *J. teretifolia*) showed very high significances of clustering. The two orchids which did not were *Scaphyglottis livida,* which was found with only 11 individuals, and was mostly associated with *Jacquiniella spp.*, and *Dichaea neglecta,* whose creeping shoots form dense mats and individuals could therefore not be delimited. Equally, the non-significance of clustering observed for the long-creeping ferns *Phlebodium areolatum, Pleopeltis crassinervata* and *Polypodium polypo-*

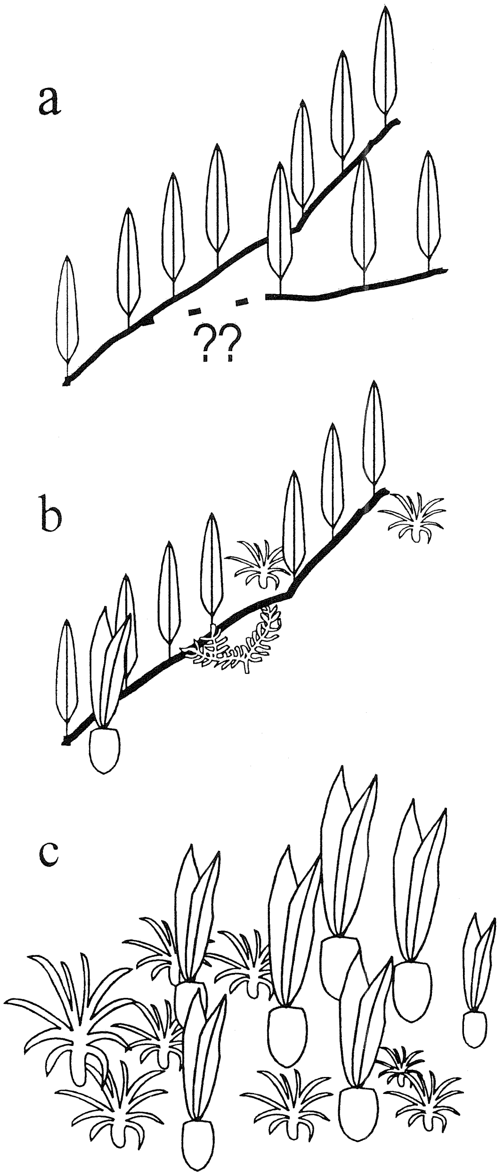

FIGURE 1. Problems and possible sources of error of nearest neighbor registration. a. Individuals, especially of long-creeping forms, are sometimes impossible to delimit. In case of doubt, such groups were conservatively counted as one individual, therefore underestimating possible aggregations. b. Long-creeping plants may be nearest neighbors to several others, but only one plant will be attributed to the as neighbor. If this results in a strong bias, the matrix of correlations will be asymmetric for such species. c. Clusters of two species growing close together by chance will result in a high number of inter-species counts.

dioides could be a result of the fact that we could not always distinguish between individuals. On the other hand, no clustering was found for the non-creeping ferns *Campyloneurum angustifolium* and *Polypodium furfuraceum,* of which individuals are readily distinguished. *Asplenium sphaerosporum* and *Polypodium plesiosorum* (not shown in TABLE 1) were significantly clustered, but were present in low numbers only.

The two most common species of *Peperomia* (*P. reflexa* and *P.* sp.1) were clustered with significances much lower than those of orchids.

Among bromeliads there was no significance of intraspecific co-occurrence, except for *Tillandsia punctulata* and *Catopsis sessiliflora.* Juvenile bromeliads (in contrast to the other epiphytes present), however, are difficult to identify and could often be assigned only to species groups (e.g., broad-leaved *Tillandsia, Catopsis* sp.). Therefore, many juveniles growing close to adults of the same species may have been assigned to species groups, resulting in low or no significant clustering of species. Indeed, all species groups used for bromeliads were strongly aggregated.

No species showed a significantly negative intraspecific correlation. The highest interspecific relationships were found among the three orchids *Jacquiniella leucomelana, J. teretifolia,* and *Scaphyglottis livida.*

Weaker relationships were found, among others, between *Peperomia* sp.1, *P. reflexa* and *Tillandsia punctulata,* between *Dichaea neglecta* and *Peperomia reflexa,* between *P. reflexa* and *Phlebodium areolatum,* and between *Polypodium polypodioides* and *Peperomia* spp.

DISCUSSION

Possible sources of error—The results of this analysis are not entirely free from systematic errors and should be interpreted with some caution.

As it was impossible to follow the rhizomes or stems of many long-creeping plants, individuals of these could not always be delimited (FIGURE 1a). This was the case for *Dichaea neglecta, Phlebodium areolatum, Pleopeltis crassinervata, Polypodium polypodioides,* and *P. plesiosorum,* and for these species a possible clustering may have gone unrecorded. Furthermore, not all individuals of plants growing in dense clusters could be distinguished. This was the case only with a few large groups of *Encyclia ochracea* and *Lycaste aromatica,* and, could the error have been avoided, significances for intraspecific relations of these two species would be still higher than those presented in TABLE 1. As many juveniles of bromeliads and some of *Peperomia* could not be identified to the species level, some significance of intraspecific relations may have been lost for these groups.

Long-creeping plants have a high circumference and one individual is often the nearest neighbor to several others, whereas only one plant will be attributed as its nearest neighbor (FIGURE 1b). As a consequence, the significance of having a long-creeping plant as nearest neighbor may be overrated, but the probability of finding a compact species as nearest neighbor of a long-creeping species should not be affected. If this effect causes a bias, the matrix of significant associations will be strongly asymmetric for creeping species. This is indeed true for the more frequent species with creeping stems (*Pleopeltis crassinervata, Dichaea neglecta,* and *Polypodium polypodioides*).

If large clusters of two species happen to grow mingled (FIGURE 1c), this will automatically result in high numbers of interspecific neighbors registered and consequently in a significant interspecific correlation. With very large numbers of observations this error will be attenuated, but it may have had some effect on the results of this study.

Intraspecific correlation—In spite of these constraints, the results of this analysis are useful for understanding the structure of epiphyte communities and are confirming our impressions from the field.

Specific microhabitat requirements of a species may result in positive intraspecific relations, as individuals more or less restricted to a zone within the host tree will often be found growing together. As most species grow in a range of microhabitats within a tree, there is much overlap and significant nearest neighbor associations due to such preferences will be rather low. Much higher clustering may be expected for species with low seed mobility or with vegetative reproduction.

Peperomia reproduces easily by clonal growth and its seeds, although sticky and designed for exozoochory, will often simply drop and eventually germinate without being carried away. With the exception of *P.* aff. *quadrifolia,* significant clustering was detected in all species.

Tillandsia and *Catopsis* have plumed seeds that are more easily dispersed than those of *Peperomia.* The evidence of clustering in bromeliads is not quite unambiguous from our data due to the limitations explained above, but at least some species show significant clustering. In many cases, seeds, although plumed, appeared to have fallen and germinated close to the mother plant, and juveniles especially were often found growing in groups.

The two common species of non-creeping ferns, *Campyloneurum angustifolium* and *Polypodium furfuraceum,* which are dispersed by dust-like spores, were not clustered at all.

As *Anthurium scandens* was the only bird-dispersed species in our study, and found with only few individuals, our data do not allow an evaluation of the effect bird dispersal has on distribution and clustering of epiphytes.

The degree of clustering of the groups may be explained by diaspore mobility. Orchids however, have dust-like propagules and should be dispersed as easily as ferns. Orchids rely on fungi for germination and growth and the probability that a seed falls close to a potential symbiont is minimal (hence the numerous seeds). Yeaton and Gladstone (1982) found that among four orchids each species was its own nearest neighbor and attribute it to the fact that the chance of finding the necessary fungus is highest among the roots of the same species with an already established symbiosis. This will result in a strong clustering in spite of high seed mobility.

Interspecific correlation—Two epiphytic species may frequently be found close together if they prefer similar locations within the phorophyte, such as thick and shaded branches or exposed twigs. As most species grow in a wide range of zones within a tree, such preferences will result in low, if any, significances. If two species share more specific substrates, such as knot-holes or ant gardens, this may be expected to result in higher significances of correlation, but no such specialists were present on the trees studied.

Positive direct relations between species or indirect relations via a third agent will result in higher significances. The association observed between the three orchids *Scaphyglottis livida, Jacquiniella leucomelana,* and *J. teretifolia* was frequently confirmed in other locations of the area. In some places these species were so constantly growing together, that it was uncommon to find one of them alone. As orchids need mycorrhizal partners for growth, we suppose that these three species are associated with the same fungus. Harley and Smith (1983), reviewing an extensive literature, conclude that, although in many cases groups of plants have been more frequently found with certain groups of fungi, the association between host and mycorrhiza is generally not very specific and that there is indeed no described case of absolute species-to-species specificity. In our case a not very specific preference of the three species discussed for a group of fungi might explain the significances found.

Weaker interspecific associations may result from a plant finding favorable conditions for germination or growth in vicinity of another species. *Peperomia* sp.1 and *P. reflexa* were often found close to *Tillandsia,* especially *T. punctulata.* Possibly these plants obtain some protection by growing between the narrow leaves of the bromeliad or by extending roots into its dead but still attached leaf bases where nutrients and water are retained. *Tillandsia punctulata* may thus serve as a nurse plant for *Peperomia* sp.1 and *P. reflexa*. Also, bromeliads may function as seed traps, especially for *Peperomia,* whose seeds simply drop or adhere to any surface where they come in contact.

Despite the limitations discussed, nearest neighbor analysis may reveal patterns in the distribution of epiphytes and possible relationships between species, and can help to explain them. As the scale of registration is very small (a few cm to dm), some patterns in the distribution of species within a tree or a site may go unregistered or take very large data sets to detect. Larger scales such as the phorophyte zones used by Johansson (1974) and many others since, will be helpful in evaluating these patterns and in explaining some of the small-scale significances. For instance, the positive association between *Catopsis sessiliflora* and *C. nutans* is probably due to the fact that both species, habitually very similar, are usually found on rather thin twigs where few other epiphytes are common.

Evaluation of absolute distances (e.g., plants within 20 cm) rather than relative distances ("nearest") may also help avoid some of the restraints of the analysis presented here, but require a more laborious registration and more elaborate mathematical tools.

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