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PATCHINESS, DIVERSITY, AND ABUNDANCE RELATIONSHIPS OF VASCULAR EPIPHYTES

BRADLEY C. BENNETT

Department of Biology, University of North Carolina,
Chapel Hill, North Carolina 27514

ABSTRACT. Diversity and abundance relationships of vascular epiphytes were examined at several sites in southern Florida and Peru with reference to the patchiness of the epiphytic biotope. Mortality rates were measured for four epiphytic bromeliads in southern Florida. The number of main vertical stems produced by a tree was positively correlated with the number of epiphytic individuals supported. Stem diameter had no effect on epiphyte abundance or diversity. The average annual mortality rate approaches 30 percent for *Catopsis* and *Guzmania* in southern Florida. Several processes may account for the diversity of epiphytes including habitat diversity, niche differentiation, ecological equivalency, and mass effect (sensu Schmida & Wilson, 1985). Ecological equivalents are most likely maintained by high mortality rates. This, coupled with the inherently patchy biotope, results in highly discontinuous populations, especially when populations are small as with many epiphytic orchids. Evolutionary implications of this are discussed.

One characteristic of the tropics is the great diversity of plants and animals. The neotropics are especially noted for their species richness which is due, in part, to the abundance of vascular epiphytes (Dodson and Gentry, unpubl.). Perhaps 28,000 species of vascular plants in at least 65 plant families may occur as epiphytes (Madison, 1977; Kress, 1986). Taxa specifically adapted for life in the upper canopy, however, are restricted to a few families, particularly the Araceae, Bromeliaceae, Cactaceae, Gesneriaceae, and Orchidaceae.

Although vascular epiphytes are abundant in the tropics the epiphytic biotope is seldom filled. For example, in southern Florida I found an average of 33 epiphytic individuals per tree but many trees were unoccupied. In an African study, 50 percent or fewer of the individuals of 16 host species supported epiphytes (Johansson, 1974). A feature common to most epiphyte communities is the availability of habitable substrates.

The epiphytic biotope also is spatially heterogeneous or patchy. Patchiness can be defined as a heterogeneous environment in which an organism's chance of death varies according to its position in the environment (Wiens, 1976). Johansson (1974) classified epiphytes according to the position of the host that each occupied and showed that certain species carried more epiphytes than others. Benzing (1978, 1980) mentioned host preference and another type of patchiness—microsite preference. Patchiness of the epiphytic habitat may exist at several hierarchical levels as indicated by habitat preference, host preference, vertical stratification and microsite preference (Grubb et al., 1963; Johansson, 1974; Schlesinger & Marks, 1977; Benzing, 1978, 1980; Sugden, 1981; Bennett, 1984, unpubl.; Hassall & Kirkpatrick, 1985; Kelly, 1985).

Bark characteristics are important in determining the suitability of a host species (Oliver, 1930; Benzing, 1973; Johansson, 1974; Schlesinger & Marks, 1977). In addition the quantity and quality of nutrients leached from the canopy (e.g., Schlesinger & Marks, 1977) and deciduousness may be important. Epiphytes in southern Florida are more common on deciduous *Fraxinus* than on evergreen *Annona* (Bennett, unpubl.). Even on "optimum" hosts, epiphytes are not distributed randomly but are vertically stratified. *Catopsis berteroniana* is found at an average height of 5 m in the Fakahatchee Strand and 2 m in Everglades National Park, but in both cases in the upper canopy. Spatial heterogeneity exists within vertical zones on hosts. Some species are distributed nonrandomly with respect to compass orientation (Bennett, 1984, unpubl.). In addition, the presence of epiphytic mosses may increase the probability that a seed will adhere and germinate at a given site and also may diminish allelopathic effects on seedlings (cf. Pavone & Reader, 1985).

Schmida and Wilson (1985) recently offered four biological determinants of species diversity: niche differentiation, habitat diversity, mass effect, and ecological equivalency. In this paper I examine species richness of vascular epiphytes at several sites in Peru and southern Florida with reference to the four mechanisms of Schmida and Wilson.

MATERIALS AND METHODS

Epiphytes were examined in the Fakahatchee Strand State Preserve (FSSP; Collier County; 26°15′N, 81°30′W), Pine Jog Environmental Study Center (PJ; Palm Beach County; 26°40′N, 80°10′W), and Everglades National Park (ENP;

TABLE 1. Number of each species of epiphyte found in the sampled FSSP plots.

	Plots											
Taxa	1	2	3	4	5	6	7*	8	9	10	11	Total
Guzmania monostachia	0	0	0	202	543	495	56	23	75	50	0	1,444
Catopsis berteroniana	0	0	0	0	0	0	14	21	0	12	0	47
Catopsis floribunda	0	0	0	0	0	0	60	0	97	1	0	158
Catopsis nutans	109	8	2	0	0	0	0	0	0	0	128	247
Tillandsia balbisiana	0	0	0	0	0	0	—	1	0	1	0	2
Tillandsia fasciculata	0	0	0	0	0	0	—	1	0	0	0	1
Tillandsia setacea	0	0	0	0	0	0	—	214	169	51	159	593
Tillandsia virabilis	230	380	239	22	2	6	—	161	86	20	34	1,180
Encyclia cochleata	0	1	0	1	0	0	—	0	0	1	1	4
Encyclia tampensis	0	0	0	1	0	0	—	0	1	0	1	3
Epidendrum anceps	2	0	0	2	0	0	—	25	20	14	17	80
Epidendrum difforme	0	1	0	2	0	0	—	1	0	0	0	4
Epidendrum nocturnum	0	0	0	0	0	0	—	3	0	0	0	3
Epidendrum rigidum	4	5	1	0	0	0	—	5	1	0	1	17
Epidendrum strobiliferum	0	0	0	0	0	0	—	1	0	0	2	3
Campylocentrum pachyrrhizum	0	0	0	1	0	0	—	0	0	0	0	1
Pleurothallis gelida	0	0	0	0	0	0	—	0	1	0	0	1
Peperomia obtusifolia	0	0	0	1	0	0	—	0	0	0	0	1
Total	345	395	242	232	545	501	130	456	450	150	343	3,789

* Only *Catopsis* and *Guzmania* species were counted in plot #7.

Dade County; 25°15′N, 80°50′W) in southern Florida. Details on FSSP and PJ and sampling procedures can be found in Bennett (1984, unpubl.). The ENP site, located 15 km N of Flamingo in a Red Mangrove-spike rush community, supports *Catopsis berteroniana, Encyclia tampensis,* and several species of *Tillandsia.*

In the FSSP spatial distribution was determined by recording the habitat, host species, and position on the host of all epiphytes within 11 10 m × 10 m plots. Many of the host species in the FSSP produce several main, vertical stems from a single trunk. The number of stems per trunk or stems per clump was recorded as a measure of available space.

Populations of *Guzmania monostachia, Catopsis floribunda,* and *C. nutans* in FSSP and *C. berteroniana* in ENP were censused in May 1984. Each individual rosette was marked with a metal tag. These populations were recensused in October 1984. Because of time constraints only *C. berteroniana* was counted in March 1985.

A final epiphyte community near Ura Ayllo, Puno, Peru (14°8′S, 69°32′W) was studied in August 1985. The study site, at 3,200 m, is located 150 km N of Puno and 50 km W of the Bolivian border. All sampled individuals were growing in a monotypic stand of an unidentified host tree on a south facing slope. The number of epiphytes, by taxa, was recorded for 27 trees.

Linear regressions and analysis of variance of nontransformed data were used to examine the effects of several variables on species richness and abundance in the FSSP. All analyses are based on 116 observations and were done at the University of North Carolina with the GLM procedure of SAS (Goodnight et al., 1982). The ratio of bromeliad to orchid species was calculated from field data and from published floras. Ephemeral and accidental epiphytes were not counted. Epiphytic members of these two families have the greatest latitudinal distribution of any angiosperm epiphytes, ranging from the Carolinas to Chile. The ratio of bromeliad to orchid individuals was calculated from the FSSP and Ura Ayllo data.

Schmida and Wilson's (1985) determinants of diversity can be arranged in a hierarchical fashion as follows: habitat diversity, niche differentiation, and ecological equivalency. Mass effect may operate at any level. Epiphytes sampled in the FSSP were classified with respect to these mechanisms based on spatial distribution, light preference, and reproductive data.

In most cases light preference was determined with respect to the vertical position of an epiphyte relative to the canopy height. Quantitative measures of illumination for *Catopsis* and *Guzmania* also were used (Bennett, unpubl.). This "habitat partitioning" is actually a measure of habitat diversity by Schmida and Wilson's (1985) terminology, at least for epiphytes. Species groups within each zone arise from niche differentiation. Species within each ecological group are ecological equivalents. I make these assessments based on joint occurrences and morphological similarities and do not imply that other niche factors such as pollination, dispersal, and nutritional re-

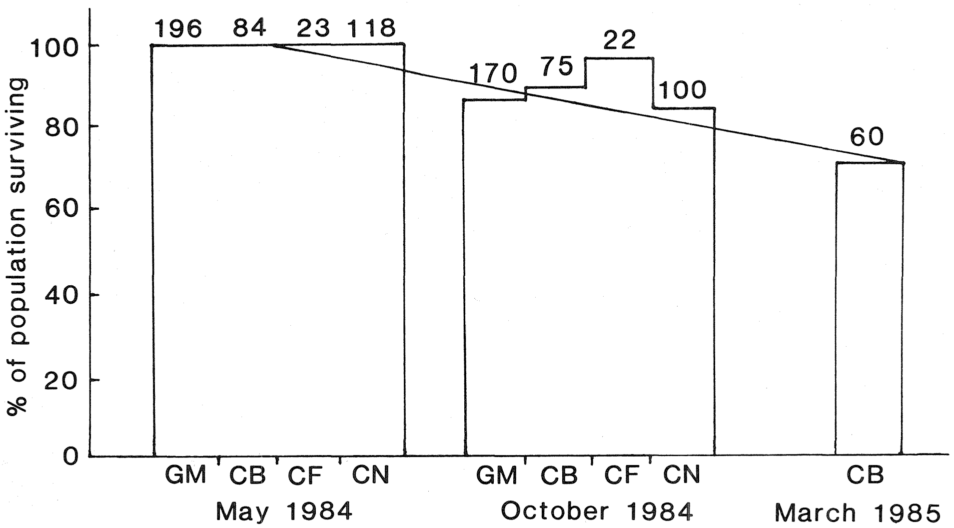

FIGURE 1. The number and percentage of individuals of *Guzmania monostachia* (GM), *Catopsis berteroniana* (CB), *C. floribunda* (CF), and *C. nutans* (CN) initially marked and the number and percentage remaining at two subsequent dates. The solid line is the average depletion rate for all four species.

lationships are not important. Rather, "ecological equivalents" have similar habitat requirements. Seldom does one dominate at the exclusion of the others. Finally, some species are rare in the sampled plots and seldom produce seeds when they do occur there. These species are maintained by mass effect—the establishment of species in habitats in which they cannot reproduce. Seeds may be derived from individuals in adjacent zones or from surrounding plant communities.

RESULTS

A total of 3,789 epiphytes were sampled in the FSSP (TABLE 1). These occurred on 11 different host species. The number of individuals per host was strongly correlated with the number of vertical stems produced by the host (F = 163.93, $P < 0.001$, $R^2 = 0.59$). Host species ($F = 2.54$, $P = 0.014$, $R^2 = 0.16$) and the number of epiphyte species supported by an individual ($F = 12.18$, $P < 0.001$, $R^2 = 0.10$) also were correlated with epiphyte abundance but to a lesser degree. Diameter at breast height (DBH) had no effect on abundance ($F = 3.47$, $P = 0.065$, $R^2 = 0.03$).

Species diversity per host tree was correlated with the species of the host but accounted for only 16 percent of the variability ($F = 2.46$, $P = 0.018$, $R^2 = 0.16$). The number of stems per clump ($F = 5.89$, $P = 0.017$, $R^2 = 0.05$) and the number of individuals per clump ($F = 12.18$, $P < 0.001$, $R^2 = 0.10$) also were significantly correlated with diversity but each accounted for 10 percent or less of the variability. DBH had no significant effect on epiphyte diversity ($F = 0.16$, $P = 0.690$, $R^2 < 0.01$).

Between May and October 1984 mortality ranged from 4 percent for *C. floribunda* to 16 percent for *C. nutans*. By March 1985, 30 percent of the rosettes of *C. berteroniana* had perished (FIGURE 1). This is equivalent to a turnover of the entire population in less than 3.5 years.

The ratio of bromeliad to orchid individuals in FSSP was 31.66 and 1.66 in Ura Ayllo. The ratio of epiphytic bromeliad to orchid species from field data and seven floras ranged from 0.22 to 1.00 and with the exception of the Carolinas all values were less than one (TABLE 2). More significantly, lowest values are found in areas where epiphytes are best represented.

The 18 epiphyte species sampled in FSSP have been arranged into three zones (a measure of habitat diversity for epiphytes). Two to eight ecological groups occur within each vertical zone (niche differentiation) and one to six species occur within each group of ecological equivalents (TABLE 3). In this study zone II, with intermediate light intensities, is most diverse. Several species occur within the sampled plots or within a particular zone as a result of mass effect.

DISCUSSION

In the FSSP the number of stems per clump is significantly correlated with the number of epiphytes supported but DBH, another measure of available space, is not. This result suggests that

TABLE 2. Ratio of bromeliad to orchid species from field data and published floras.

Location	Bromeliad species	Orchid species	Ratio	Reference
BCI, Panama	17	79	0.22	Croat, 1978
Jamaica	52	127	0.41	Adams, 1972
Bahama Islands	15	30	0.50	Correll & Correll, 1982
Puerto Rico	29	55	0.53	Liogier & Martorell, 1982
Southern Florida	31	16	0.53	Long & Lakela, 1971
Central Florida	12	19	0.63	Wunderlin, 1982
Ura Ayllo, Peru	2	3	0.67	this study
FSSP, Florida	8	9	0.89	this study
Carolinas	1	1	1.00	Radford et al., 1968

although space is an important resource limiting epiphyte distribution, other factors are more important—perhaps the aerodynamic aspects of seed dispersal. Boundary layers are partly a function of stem size. The advantage of more area may be offset by the decreased probability of lodging on a large trunk. Host species also was significantly correlated with abundance and diversity but less so than in other studies (e.g., Schlesinger & Marks, 1977).

Turnover rates were higher than expected for plants found in nutrient-poor and water-stressed sites. In less than a year 30 percent of the rosettes in a population of *C. berteroniana* were lost (FIGURE 1). At this rate the entire population would be replaced every three to four years. Vegetatively produced rosettes flower earlier than those which grow from seed. Thus, there should be strong selection for efficient vegetative propagation.

The ratio of bromeliad to orchid individuals was greater than one in southern Florida and in Peru. Conversely, the ratio of bromeliad to orchid species was less than one, except for the Carolinas. This pattern has been noted by others (e.g., Atwood, 1984; Kelly, 1985). Not only are there fewer orchid individuals but they are distributed among a greater number of species. There are exceptions to this trend, especially near the end of environmental gradients, where there are more bromeliad species as well as individuals. In the Valdivia region of Chile (40°S) only one epiphytic bromeliad, *Fasicularia bicolor,* and no orchids are found (Bennett, unpubl.). At Pine Jog in southern Florida eight species of *Tillandsia* (Bromeliaceae), but only one orchid, *Encyclia tampensis,* were present. In addition to the inherently discontinuous nature of the epiphytic biotope the small population size of orchids results in greater spatial isolation in comparison to other epiphytic groups.

Vertical stratification of epiphytes represents habitat diversity. Taller trees provide longer environmental gradients and thus are expected, a priori, to have higher diversity (but see Johansson, 1974, for an exception). Within each vertical zone there are various degrees of resource partitioning or niche differentiation, particularly with respect to microsites and mineral nutrition. Taxa within each group are ecological equivalents (cf. Benzing, 1981). For example, eight ecological groups are recognized in zone II (TABLE 3). Five bromeliad species are found in the second group in this zone. All are tank epiphytes and though different in size, are morphologically similar. Members within each of the other groups in each zone are morphologically similar and utilize the spatial niche in a similar fashion. Ecological equivalents can coexist because of high mortality and slow growth rates.

Mass effect operates at several levels. For example, *Guzmania* is most abundant in zone I but is sometimes found in zone II. Its persistence in this zone, however, is due to recruitment from zone I. Individuals higher in the canopy are more susceptible to cold damage and are less likely to flower (pers. obs.). Though common elsewhere *T. fasciculata* is rare in the sampled FSSP plots. Again, mass effect is the mechanism by which diversity is increased; in this example it is due to recruitment from a different host-plant community.

Mechanisms that maintain species diversity, especially vertical stratification and high mortality rates, may contribute to the origin of epiphyte diversity. The Bromeliaceae and Orchidaceae dominate many epiphyte communities in the neotropics. With 20,000–30,000 species, Orchidaceae is the largest family of flowering plants and Bromeliaceae, comprised of more than 2,000 species is the largest family confined to the neotropics. The great number of taxa found in these two families is no doubt related to their epiphytic existence. Patchiness of the epiphytic biotope results in discontinuous populations that have great potential for reproductive isolation and thus for speciation. Few data are available on gene flow and community structure in epiphyte commu-

TABLE 3. Epiphyte species found in the sampled FSSP plots and arranged into three light preference classes (habitat diversity) and ecological groups (niche differentiation). Species within each group are ecological equivalents and those marked by an asterisk are maintained by mass effect.

Low light	Medium light	High light
Group 1. *Guzmania monostachia* *Catopsis nutans**	Group 1. *Peperomia obtusifolia*	Group 1. *Tillandsia balbisiana**
Group 2. *Peperomia obtusifolia*	Group 2. *Guzmania monostachia** *Catopsis nutans* *Tillandsia virabilis* *Tillandsia fasciculata** *Catopsis floribunda*	Group 2. *Encyclia tampensis**
	Group 3. *Epidendrum nocturnum* *Epidendrum anceps* *Epidendrum difforme* *Epidendrum rigidum* *Epidendrum strobiliferum* *Encyclia cochleata*	Group 3. *Tillandsia fasciculata** *Tillandsia virabilis**
	Group 4. *Tillandsia balbisiana**	Group 4. *Tillandsia setacea**
	Group 5. *Tillandsia setacea*	Group 5. *Catopsis berteroniana*
	Group 6. *Encylcia tampensis**	
	Group 7. *Campylocentrum pachyrrhizum**	
	Group 8. *Pleurothallis gelida*	

nities. Certainly, the trapline behavior of certain hummingbird and euglossine bee pollinators increases gene flow and thus reduces the effects of spatial isolation (cf. Handel, 1983). On the other hand, many pollinators forage in distinct vertical strata. This, coupled with the vertical stratification of epiphytes may prevent gene flow even between individuals on the same tree. The smaller population sizes of orchids in contrast with bromeliads may further reduce gene flow and be responsible, in part, for the great number of species in this family.

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