December 2003

Family composition of vascular epiphytes varies by directional quadrant

David N Bums

Family composition of vascular epiphytes varies by directional quadrant

David N. Bums

Department of Environmental Studies, Bates College, Lewiston, ME 04240

ABSTRACT

Vascular epiphytes are an extremely diverse and prevalent plant-form of neotropical cloud forests, and are strongly affected by abiotic factors including light and moisture. The goal of this study was to determine whether the family composition and diversity of vascular epiphytes living on pasture tree trunks differed by quadrant (northeast, northwest, southeast, and southwest). It was hypothesized that the northeast quadrant would exhibit the greatest diversity due to the mist-laden trade winds blowing from that direction. Twenty trees in a pasture surrounded by lower montane wet forest in Monteverde, Puntarenas, Costa Rica were divided into four quadrants and sampled for vascular epiphytes (N = 597 plants), which were tallied by family. A Chi-squared analysis revealed that there was a nonrandom frequency of families across quadrants (x^2 = 29.445, df = 12, P = 0.0034). The family diversity of the northeast (H' = 2.067) was significantly higher than the diversity of the southwest (H' = 1.817; t = 2.497, df = 263.04). Additionally, there were more bromeliads in the northeast than expected (54 observed, 34.7 expected), and less than expected in the southeast (15 observed, 22.1 expected) and southwest (7 observed, 18.4 expected). Also, there were more Pteridophytes in the southwest than expected (45 observed, 36.8 expected) and less than expected in the northeast (54 observed, 69.5 expected). These differences may be due to a combination of abiotic and biotic factors related to moisture acquisition by the epiphytes.

RESUMEN

Las epífitas vasculares son una forma vegetal extremadamente diversa y frecuente en los bosques nubosos neotropicales, y son afectadas fuertemente por factores abióticos incluyendo luz y humedad. La meta de este estudio fue determinar si la composición de las familias y la diversidad de las epífitas vasculares que vivían en troncos de árboles en potreros diferenciaron por cuadrante (noreste, noroeste, sureste, y sudoeste). La hipótesis fue que el cuadrante noreste exhibiría la mayor diversidad debido a los vientos alisios cargados de humedad en esa dirección. Veinte árboles en un potrero pasto rodeado de bosque húmedo montano bajo en Monteverde, Puntarenas, Costa Rica fueron dividido en cuatro cuadrantes y muestreados para la existencia de epífitas vasculares (N = 597 plantas), que fueron identificadas por familia. Un análisis Chi-cuadrado reveló que había una frecuencia no al azar de familias a través de los cuadrantes (x^2 = 29.445, df = 12, P = 0.0034). La diversidad de familias del noreste (H'= 2.067) era perceptiblemente más alta que la diversidad del sudoeste (H' = 1,817; t = 2,497, df=263.04). Además, había *más* bromelias en el noreste que lo esperado (54 observados, 34,7 esperados), y menos que lo esperado en el sureste (15 observados, 22,1 esperados) y en el sudoeste (7 observados, 18,4 esperados). También, había más pteridófitos en el sudoeste que lo esperado (45 observados, 36,8 esperados) y menos que lo esperado en el noreste (54 observados, 69,5 esperados). Estas diferencias pueden ser debido a una combinación de factores abióticos y bióticos relacionados con la absorción de humedad por las epífitas.

INTRODUCTION

An important feature of neotropical forests is the abundance and diversity of vascular epiphytes. Worldwide, there are over 23, 000 species of vascular epiphytes in 876 genera and 84 families, representing some ten percent of all vascular plants (Lesica & Antibus 1990; Zimmerman & Olmsted 1992). Epiphytes account for up to 35% of vascular flora in some neotropical wet forests, and in some montane rain forests, their biomass can equal half of all tree leaf biomass (Ingram & Nadkarni 1993). In the neotropical lower montane wet forest of Monteverde, Costa Rica, epiphytes are the most species-rich growth form, with 878 identified species (Haber 2000).

There has been increasing attention given to canopy communities, especially in cloud forests. They are important subsystems in ecosystem-level interactions between terrestrial and atmospheric processes because they can retain atmospheric nutrients and pollutants (Ingram & Nadkarni 1993). Additionally, epiphytes are useful climatic indicators and may aid ecological assessment of forests (Hietz-Seifert et al. 1995).

One highly studied phenomenon is that epiphytic growth is strongly influenced by abiotic factors, including substrate texture and size, light, nutrients taken from the atmosphere, and moisture. These resources are limiting and epiphytes may compete for them (Hopcus 1999; Haber 2000). Studies have shown that epiphyte growth in wet forests is influenced most strongly by light and moisture availability (Veblen 1996). Hietz-Seifert et al. (1995) found that trees with greater exposure to cool and humid winds from the north had more epiphytes than trees receiving hot and dry winds from the south.

While ter Steege and Cornelissen (1989) have proposed that tree bases and humid understory areas are typically poorer in epiphyte diversity than the canopy, Veblen (1996) argues that the canopy conditions of abundant wind, light, and moisture conditions are experienced by trees in the hillside pasture behind the Estación Biológica Monteverde in Costa Rica. Two of the above conditions, wind and moisture, have been studied in this pasture, and it is known that mist-laden trade winds blow southwest (Meisner-Bagdahn 2003).

As more neotropical forests are converted to cropland or pastures, it is becoming clearer that a better understanding of these altered ecosystems is needed. Often, a few isolated trees are left following deforestation and these may play an important role in maintaining biodiversity. Hietz-Seifert et al. (1995) found that the numbers of epiphytic species per tree in pastures were within the range of those found in studied forests. Thus, they may serve as nuclei for reestablishment of forest species (Hietz-Seifert et al. 1995).

The goal of this experiment was to determine whether the family composition and diversity of vascular epiphytes living on pasture tree trunks differed by quadrant (northeast, northwest, southeast, and southwest). It was hypothesized that the northeast facing quadrant would exhibit the greatest diversity of epiphytic families, as the trade winds from the northeast bring the most mist to that quadrant during the dry season (Meisner-Bagdahn 2003, Ingram & Nadkarni 1993). This would provide the most favorable growing conditions for vascular epiphytes. Conversely, the southwest side receives the least mist in the dry season, and will support the least diversity of vascular epiphytes. This study, relating vascular epiphytic family diversity to tree quadrant based on fine-scale mist frequencies is a novel concept, and thus far, has received little attention from the tropical scientific community.

METHODS

Study Site

The trees sampled were located in a hillside pasture of approximately 2.5 ha, behind the Estación Biológica Monteverde, Puntarenas, Costa Rica. This site lies at approximately 1570m in elevation, and is surrounded by Lower Montane Wet Forest on all sides except the southwest (Levine 1999). Total annual precipitation is about 2-2.5m of rain and an additional 0.5-2m is contributed by mist (Ingram & Nadkarni 1993). The majority of this mist is delivered between November and May by trade winds from the northeast (Ingram & Nadkarni 1993). The majority of this mist is delivered between November and May by trade winds from the northeast (Ingram & Nadkarni 1993, Meisner-Bagdahn 2003).

Tree Selection

Eighteen of the 20 host trees used in this study were those previously sampled in Meisner-Bagdahn's orchid study (2003), with the other two being new additions. Mist frequency and abundance for the trees has been recorded (Meisner-Bagdahn 2003). These trees were originally chosen, regardless of identity, on the basis that they contained over ten pleurothalid individuals and were at least 30 cm in dbh (Meisner-Bagdahn 2003). The two newly sampled trees were chosen on the bases of having over 30 vascular epiphytes and a dbh of at least 30cm.

Tree Preparation & Experimental Design

Each of the 20 trees was divided into four quadrants, representing the northeast, northwest, southeast, and southwest-facing sides of those trees. These quadrants were created by hanging string from nails placed on the north, east, south, and west sides of the tree. Many of the trees were on a slope, and it was necessary to mark the lower limit of the quadrants by placing a string around the circumference of the bole, level with the ground on the north side. The height of the quadrants was two meters above the lower limit on the north side.

The area of each quadrant was measured by multiplying the height (two meters) by the average width of that quadrant. Branches, deep clefs, and the area between trunks whose bole split below the two-meter line were not included in the quadrants.

In each quadrant, all occurrences of vascular plants were tallied by family, excluding Orchidaceae. Plants with runners were only counted once per quadrant, however, if they crossed over into another quadrant, their occurrence was also tallied there. Plants rooted outside of the quadrant, but who were in contact with the tree and shaded the quadrant were also tallied. It was indicated that these plants were from outside of the quadrant however.

Analysis

Differences in community composition and diversity were analyzed for each quadrant, across all 20 trees, using a contingency table analysis. Only those families with greater than 20 individuals across all trees were included. Although Acanthaceae had more than 20 individuals across all trees, it was not included because it is not typically an epiphytic family (Gentry 1993), and those individuals found were non-liana herbs growing low on the tree trunks. Additionally, a second contingency table analysis was created, omitting those plants rooted outside of the quadrants. A post hoc test was also run for each.

Diversity parameters, including number of individuals (N), species richness (S), Margalef indices (S_{marg}), Shannon-Weiner indices (H'), and evenness (E) were run for each quadrant. H' values were then compared for variance of diversity using t-tests. Family similarities across the quadrants were also compared using a Sorenson quantitative measure of similarity (C_N). Finally, a one-way ANOVA was run to determine whether the quadrants differed in mean area.

RESULTS

There was a significant difference found in family composition between quadrants by the Chi-squared analysis (X^2 = 29.445, df = 12, P = 0.0034). Additionally, the analysis revealed that a higher number of bromeliads were present in the northeast than expected, and a lower number than expected was found in the southeast and southwest (Table 1, Table 2). There were also higher numbers of Pteridophytes found in the southwest than expected, and less than expected found in the northeast (table 1, table 2). The exclusion of those plants rooted outside of the quadrant boundaries did not change this trend (X^2 = 28.550, df = 12, P = 0.0046 (Appendix 1, Appendix 2). The observed frequencies for all families are seen in Table 3. Individuals rooted outside of the quadrant boundaries have been removed from the family frequencies shown in Table 4.

Diversity parameters for each quadrant across all trees are shown in Table 5. Number of individuals and family richness were greatest in the northeast quadrant (N = 208, S = 17) and lowest in the southeast (N = 102, S = 10). Additionally, the Margalef index for the northeast quadrant (S_{marg} = 2.998) was higher than that of the southwest (S_{marg} = 1.946). The family diversity of the northeast (H' = 2.067) is also significantly higher than the diversity of the southwest (H' = 1.817; t = 2.497, dF = 263.04), as seen in Table 6. No other Shannon-Weiner indices were significantly different.

Finally, the northeast and southwest have the least similar family compositions across quadrants (C_N = 0.619), while the two southerly quadrants have the most similar family compositions (C_N = 0.873) (Table 7). It should also be noted that there were no significant differences in quadrant area across the trees sampled.

DISCUSSION

These results indicate that there was a significant difference in the community composition and diversity of vascular epiphytes on the different directional faces of tree trunks in a lower montane wet pasture, supporting the hypothesis. More specifically, the greatest differences were between the northeast and southwest facing quadrants, with the northeast having the greatest familial diversity of any quadrant (H' = 2.067) and the southwest having the least (H' = 1.817).

Vascular epiphytes are most likely to establish on the northeast side of tree trunks, as trade winds bring the majority of mist during the otherwise potentially desiccating dry season (Ingram & Nadkarni; 1993, Meisner-Bagdahn 2003), and moisture is a limiting factor of epiphyte growth (Veblen 1996). These results are consistent with the Hietz-Seifert et al. study (1995), which found that trees with a higher exposure to cool and humid winds from the north had more epiphytes than trees receiving hot and dry winds from the south. Similarly, Levine (1999) suggests that orchids establishing on a northeastern facing site may have advantage over the potentially more water-stressed epiphytes pointing other compass directions. One conclusion drawn from this is that differences in community composition and diversity of vascular epiphytes among the intercardinal points are the result of abiotic factors.

As seen in Table 1, there was a higher number of bromeliads present in the northeast than expected, and a lower number than expected in the southeast and southwest. Interestingly though, there were a higher numbers of pteridophytes found in the southwest than expected, and less than expected found in the northeast (Table 1). The pattern of bromeliad growth can be explained using the previous argument of the importance of abiotic factors. The higher amount of mist reaching the north side of the tree facilitates germination and growth. Additionally, the higher abundance of bromeliads on the north-facing side leads to a higher seed rain there, and more of these seeds germinate than in other quadrants due to the favorable conditions. The pattern of pteridophytic growth requires an alternate explanation however. One possible explanation may be avoidance of competition and horizontal niche partitioning.

Resources such as light and moisture are limiting resources for vascular epiphytes, leading to high competition (Veblen 1996; Hopcus 1999; Haber 2000). This competition may lead to niche partitioning, in which plants have evolved to occupy different microhabitats in order to utilize the available resources and thereby minimize competition (Begon et al. 1990). Most epiphytic plants, including atmospheric bromeliads, can only absorb water in liquid form. Some tropical epiphytic fern species however, are poikilohydric, and can take water from saturated air. These plants can quickly absorb water over the entire surface of their leaves, but can lose it rapidly as well. In a drier atmosphere, the leaves curl up, and expand when moist conditions return (Richards 1996). As it may be possible for some pteridophytes to live in more xeric conditions than other epiphytes, those who do so will avoid competition for other abiotic factors like space and light.

As greater amounts of tropical land are being converted into pastures, research needs to be directed toward understanding and accurately describing how epiphytes partition resources among themselves. Epiphytes form important centers of biodiversity in pastures and can act as useful climatic indicators, as they retain atmospheric nutrients and pollutants. In order to utilize them as climatic indicators and sites of forest reestablishment in conservation efforts though, a better understanding of how they are affected by and respond to both abiotic and biotic factors is needed.

ACKNOWLEDGEMENTS

Foremost, I'd like to thank Karen Masters for helping me to develop this project after all of the previous frustrations. It could not have been done without her plant identifications. A big thanks also to Alan Masters for running such an amazing program. Cheers to Andrew Rodstrom for critiquing my paper, spending the time to teach me to climb, and for caring so much about the whereabouts of my ladder. Matt and Carmen, your statistical help was a big help, thank you. I'd also like to thank the Estación Biológica Monteverde, for allowing me to conduct my research on its land. Additionally, I'd like to thank Sarah for editing and being the nicest person in the world, Catherine Ross for reviewing my paper, Chelsea Beebe for letting me use her map when mine blew away, and Alyson for moving like a Jellyfish. A special final thanks to the Solis family, who graciously allowed me to live with them and gave me the amount of support I would expect from my own family.

LITERATURE CITED

Begon, M., J.L. Harper, and C.R. Townsend. 1990. *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Boston.

Catling, P.M. and L.P. Lefkovitch. 1989. Association of vascular epiphytes in a Guatemalan cloud forest. Biotropica 21: 35-40.

Gentry, A.H. 1993. *A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru)*. The University of Chicago Press, Chicago; pg. 205 – 212.

Haber, W.A. 2000. “Plants and Vegetation” In: Nadkarni, N.M. and N.T. Wheelwright, eds. *Monteverde: ecology and conservation of a tropical cloud forest*. Oxford University Press, New York; pg. 55

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

Hopcus, J. 1999. “Competition between epiphytic congeneric orchids *Oncidium bracteatum* and *Oncidium bryolophotum*”. CIEE Fall Tropical Ecology and Conservation.

Ingram, S.W. and N.M. Nadkarni. 1993. Composition and distribution of epiphytic organic matter in a neotropical cloud forest, Costa Rica. Biotropica 25: 370-383.

Lesica, P. and P.K. Antibus. 1990. The occurrence of mycorrhizae in vascular epiphytes of two Costa Rican rain forests. Biotropica 22: 250-258.

Levine, M.T. 1999. Niche partitioning of congeners in two orchid genera, *Scaphyglottis* and *Epidendrum*. CIEE Spring Tropical Ecology and Conservation.

Meisner-Bagdahn, Hanna. 2003. Climate change and microclimate variation: Effects on fitness and abundance of cloud forest orchids. American Colleges of the Midwest Spring Program.

Richards, P.W. 1996. *The Tropical Rain Forest*. Cambridge University Press, Cambridge; pg. 142-143.

Ter Steege, H. and J.H.C Cornelissen. 1989. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. Biotropica 21: 331-339.

Veblen, K. 1996. Comparison of epiphytes on stumps in a pasture and in the forest. CIEE Summer Tropical Ecology and Conservation.

Zimmerman, J.K. and I.C. Olmsted. 1992. Host tree utilization by vascular epiphytes in a seasonally inundated forest (Tintal) in Mexico. Biotropica 24: 402-407.

Table 1. The number of observed and expected vascular epiphytes by family, on 20 trees, across the four directional quadrants. N= 504 vascular epiphytes.

Family	NE		NW		SE		SW	
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
Araceae	10	11.13	6	8.91	10	7.07	7	5.89
Bromeliaceae	54	34.74	27	27.79	15	22.07	7	18.39
Ericaceae	21	20.91	15	16.73	13	13.29	13	11.07
Piperaceae	31	33.73	27	26.98	24	21.42	18	17.86
Pteridophyta	54	69.48	61	55.59	46	44.14	45	36.79

Table 2. Post Hoc test results of contingency table analysis. N = 504 vascular epiphytes.

Family	NE	NW	SE	SW
Araceae	-0.431	-1.178	1.285	0.521
Bromeliaceae	4.50	-0.198	-1.904	-3.286
Ericaceae	0.025	-0.529	-0.094	0.683
Piperaceae	-0.645	0.004	0.700	0.042
Pteridophyta	-2.968	1.105	0.410	1.943

Table 3. The abundance of vascular epiphytes and shading vascular plants by family, across the four directional quadrants on 20 trees. Italicized values were those used in the contingency table analysis. N = 597 vascular plants.

Family	**NE**	**NW**	**SE**	**SW**	Totals
Araceae	10	6	10	7	33
Bromeliaceae	54	27	15	7	103
Ericaceae	21	15	13	13	62
Piperaceae	31	27	24	18	100
Pteridophyta	54	61	46	45	206
Gesneriaceae	8	4	1	3	16
Clusiaceae	4	1	0	0	5
Asteraceae	1	1	1	0	3
Mimosaceae	1	0	0	0	1
Acanthaceae	10	6	4	2	22
Moraceae	1	0	0	0	1
Rubiaceae	3	2	1	1	7
Poaceae	3	5	2	0	10
Rosaceae	0	1	1	1	3
Fagaceae	0	0	1	0	1
Smilacaceae	0	0	5	5	10
Solanaceae	0	0	1	0	1
Passifloraceae	2	0	1	0	3
Araliaceae	0	1	0	0	1
Lauraceae	2	2	0	0	4
Melastomataceae	2	0	1	0	3
Anacardiaceae	1	0	0	0	1
Cunoniaceae	0	1	0	0	1
Total	208	160	127	102	597(504)

Table 4. The abundance of vascular epiphytes, omitting individuals rooted outside of quadrant boundaries, across the four directional quadrants on 20 trees. Italicized values were those used in the contingency table analysis. S = species richness. N = 578 vascular plants.

Family	**NE**	**NW**	**SE**	**SW**	**Totals**
Araceae	10	6	9	7	32
Bromeliaceae	54	27	15	7	103
Ericaceae	21	15	12	13	61
Piperaceae	31	27	23	18	99
Pteridophyta	54	61	46	45	206
Gesneriaceae	8	4	1	3	16
Clusiaceae	4	1	0	0	5
Asteraceae	1	1	1	0	3
Mimosaceae	0	0	0	0	0
Acanthaceae	10	6	3	2	21
Moraceae	1	0	0	0	1
Rubiaceae	2	2	0	0	4
Poaceae	3	5	0	0	8
Rosaceae	0	1	1	1	3
Fagaceae	0	0	0	0	0
Smilacaceae	0	0	5	5	10
Solanaceae	0	0	1	0	1
Passifloraceae	2	0	1	0	3
Araliaceae	0	1	0	0	1
Lauraceae	0	0	0	0	0
Melastomataceae	1	0	0	0	1
Anacardiaceae	0	0	0	0	0
Cunoniaceae	0	0	0	0	0
Total	202	157	118	101	578(501)
S	14	13	12	9	18

Table 5. Diversity parameters for each quadrant, with all individuals present. N = 597 vascular plants.

Parameter	**NE**	**NW**	**SE**	**SW**
N	208	160	127	102
S	17	15	16	10
Smarg	3.00	2.76	3.10	1.95
Shannon-Weiner	2.07	1.91	1.98	1.82
Evenness	0.73	0.70	0.71	0.79

Table 6. Results of t-test for differences in diversity of Shannon-Weiner Index values (H'). Var H' = 0.0047 for the northeast, 0.0068 for the northwest, 0.0083 for the southeast, and 0.0053 for the southwest. N= 597 vascular plants.

Quadrants Compared	t-test Value	**DF**	**Significant**
NE: SW	2.50	263.04	Yes
NW: SW	0.80	259.39	No
SE: SW	1.35	226.08	No

Table 7: Values for Sorenson quantitative measure of similarity (CN). Higher values indicate that those quadrants are more similar in family composition. N = 597 vascular plants

Quadrants Compared	C_N
NE: NW	0.804
NE: SE	710
NE: SW	0.619
NW: SE	0.794
NW: SW	0.733
SE: SW	0.873

Appendix 1. The number of observed and expected vascular epiphytes by family, omitting individuals rooted outside of quadrant boundaries, across the four directional quadrants on 20 trees. N = 501 vascular epiphytes.

Family		NE		NW		SE		SW
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
Araceae	10	10.86	6	8.69	9	6.71	7	5.75
Bromeliaceae	54	34.95	27	27.96	15	21.59	7	18.5
Ericaceae	21	20.7	15	16.56	13	12.78	12	10.96
Piperaceae	31	33.59	27	26.87	23	20.75	18	17.78
Pteridophyta	54	69.9	61	55.92	46	43.17	45	37.01

Appendix 2. Post Hoc test results of contingency table analysis omitting individuals rooted outside of quadrant boundaries. N = 501 vascular epiphytes.

Family	NE	NW	SE	SW
Araceae	-0.331	-1.104	1.03	0.596
Bromeliaceae	4.448	-0.239	-1.789	-3.313
Ericaceae	0.087	-0.479	-0.263	0.727
Piperaceae	-0.614	0.032	0.621	0.063
Pteridophyta	-3.049	1.037	0.631	1.891