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ABSTRACT

Many studies have been done regarding vascular epiphyte communities in the tropics; however all of the previous studies have neglected the canopy branch tips due to their limited accessibility (Nieder *et al.* 2004, Freiberg and Freiberg 2000, Zotz *et al.* 1999, Hietz 1997, Freiberg 1996, Ingram and Nadkarni 1993). The purpose of this study was to evaluate differences in family richness, and diversity of previously unstudied branch tip epiphyte communities vs. those of secondary branch bases. Data were gathered about community composition of vascular epiphyte families and climbers on the branch tips of canopy trees in a Neotropical, lower montane rainforest in Costa Rica. Branches were accessed from suspension bridges ranging from 32-65 m, in Selvatura Park, Costa Rica. The number of individuals from each family and total branch area covered by each family were recorded. Branch tip and base communities were compared using S, H', E, N, and Smarg parameters (Magurran 1988), and diversity indices were compared using a t-test. Additionally a pair-wise comparison was carried out on each branch base and tip pair using a sign test (Ambrose et al. 2002). Counts of number of individuals per family were deemed to be inaccurate due to the difficulty in identifying individual ferns. As such, coverage area data were used to draw conclusions. Branch tips (H' = 0.27) were found to have a significantly higher diversity than branch bases (H' = 0.71) (p-value < 0.001). However, branch bases were found to have a significantly higher family richness even when differences in abundance were controlled for. It was noted that almost all branches surveyed showed high dominance of the Division Pteridophyta on both branch bases and tips. Future studies of epiphyte communities in canopy branch tips should address the issue of identifying individual ferns when root systems are covered in humus and bryophyte mats, as was observed in this study.

RESUMEN

Muchos estudios se han hecho con respecto a comunidades vasculares del epífitas en los trópicos, no obstante todos los estudios anteriores han descuidado las puntas de las ramas en el dosel debido a su limitada accesibilidad (Nieder y otros 2004, Freiberg y Freiberg 2000, Zotz y otros 1999, Hietz 1997, Freiberg 1996, Ingram y Nadkarni 1993). El propósito de este estudio fue evaluar diferencias en la riqueza de familias, y diversidad de las comunidades de epífitas en las puntas de las ramas del dosel, contra los de las bases secundarias de la rama. Los datos fueron recopilados sobre la composición de la comunidad de las familias de epífitas y de plantas trepadoras en las extremidades de la rama de los árboles en un Bosque pluvial Montano Bajo en Costa Rica. Las ramas fueron alcanzadas desde los puentes en suspensión que se encontraban entre los 32-65 m, en el parque de Selvatura, Costa Rica. El número de individuos de cada familia y el área total de la rama cubierta por cada familia fueron registrados. Utilizando los parámetros S, H', E, N y Smarg se compararon a las comunidades de la punta y de la base de la rama (Magurran 1988), y los índices de la diversidad fueron comparados usando una prueba T. Adicionalmente se utilizó una comparación pareada entre la base y la punta de las ramas utilizando una prueba de muestra (Ambrose y otros 2002). El número de individuos por la familia fue determinado para ser inexacto debido a la dificultad en la identificación de helechos individuales. Como tal, los datos del área de la cobertura fueron utilizados para extraer conclusiones. Las puntas de la ramas (H = 0.27) presentan significativamente una mayor diversidad que la base de las ramas (H = 0.71) (< del p-valor; 0.001). Sin embargo, las bases de la

rama fueron presentan una mayor riqueza de familias incluso cuando las diferencias en abundancia fueron controladas para esto. Se observó que casi todas las ramas examinadas demostraron la alta dominancia de la de la división Pteridophyta en ambas, puntas y bases. Futuros estudios en las comunidades de epífitas en las puntas de las ramas deben considerar el hecho de la identificación individual de helechos cuando el sistema radical está cubierto en humos y briofitos, como se observó en este estudio.

INTRODUCTION

Tropical forests host the highest diversity of vascular epiphyte species in the world. They may comprise up to 50% of tree and leaf biomass in some montane rainforests (Ingram and Nadkarni 1993). Epiphytic organic matter plays an important role in the ecology of tropical rainforests by absorbing precipitation from rain and fog, capturing and retaining minerals and pollution from the air, and influencing the microclimate in the canopy (Freiberg and Freiberg 2000, Ingram and Nadkarni 1993). Rain forest canopies are also highly dynamic ecosystems, prone to frequent disturbance. This aspect may help to explain the high species richness in these ecosystems. Disturbances can help prevent any one species from dominating and open up space for new colonization, which fosters greater diversity (Hietz, 1997).

In their study of the spatial distribution of vascular epiphytes in a lowland rainforest, Nieder *et al.* (2004) noted that horizontal distribution was non-random. Similarly, other studies have found that there is a gradient of epiphyte growth that occurs laterally along branches with highest amounts of growth occurring close to the base of the tree (Freiberg and Freiberg 2000, Hietz 1997, Freiberg 1996, Ingham and Nadkarni 1993). In all of these studies it was asserted that differences in epiphyte distribution were the result of bryophyte and humus build-up required for germination and nutrient acquisition, as well as branch size, angle, and age. Results have consistently shown that the highest species richness and abundance of vascular epiphytes is found on older, larger, substrate covered branches, which seem to provide the optimum environment for colonization Ingham and Nadkarni 1993). Many studies have been done regarding vascular epiphyte communities in the tropics; however, previous studies have neglected the canopy branch tips due to their limited accessibility (Nieder *et al.* 2004, Freiberg and Freiberg 2000, Zotz *et al.* 1999, Hietz 1997, Freiberg 1996, Ingram and Nadkarni 1993).

Although branch tips have not been studied, previous results lead me to hypothesize that there is a difference in diversity, family richness, and abundance between secondary branch tips and branch bases in the canopy of lower montane rainforests. It was predicted that a higher abundance, richness, and diversity of vascular epiphyte families would be observed on canopy branch bases than on branch tips, as the decreased size and age of branch tips do not provide the optimum micro-habitat for epiphyte colonization.

For this study data were gathered on the diversity, richness, and abundance of vascular epiphyte families and ferns on the branch tips of canopy trees in a Neotropical, lower montane rainforest in Costa Rica. Branch tip data were compared to data collected from the base of the contiguous secondary canopy branches. Hemiepiphytes and climbers were included in this study, as much of their life cycle occurs under the same conditions as true epiphytes (Ingram and Nadkarni 1993). The purpose of this study was to evaluate differences in family richness, and diversity of branch tip epiphyte communities vs. those in secondary branch bases.

METHODS

Study Site

The site was situated on the Atlantic slope of the Tilarán mountain range in Costa Rica. Data were collected in Selvatura Park, on the Atlantic slope (elevation 1600 m) where forest consists of intervened, secondary growth, lower montane rainforest. The site receives 3 m to 8 m of rain annually, and the mean annual temperature ranges between 12 and 17 ºC (Haber, 2000). Access to the canopy was achieved by a series of suspension bridges ranging in height from thirty two to sixty five meters off the ground.

Sampling Method

Branch samples were chosen based on level in the canopy, branch base diameter, branching angle, and proximity to the bridges. Tree species were not taken into account. Only trees comprising the uppermost level of the canopy were surveyed. A total of 12 branches were sampled. All were secondary branches with diameters between 8 cm and 20 cm with branching angle no more than 45 degrees from horizontal.

Epiphyte growth on the first meter from the branching point and the last meter from the branch tip was surveyed for each branch. Diameter and length measurements were visually estimated. Diameter measurements were taken for the base of the branch and the thickest part of the branch tip. The one-meter sample sites at the branch bases were assumed to be regular cylinders and the one-meter branch tip sites were assumed to be regular cones for the purpose of calculating surface area.

Epiphyte and climber angiosperm families were identified by morphological characteristics with the aid of binoculars and a digital camera. Ferns (Division Pteridophyta) were identified only to the Division level, The number of individuals present from each family (or Division, in the case of ferns) and the branch surface area covered by each family was recorded for each base and tip respectively. Because many ferns can reproduce by vegetative budding or send up new shoot from rhizome runners (Moran 2004), and because roots and bases of epiphytes were often obscured by bryophyte growth, continuous mats of fern growth were considered as a single individual for the purpose of this study. Data were collected from July 15, 2008 through August 2, 2008.

Statistical Analysis

The parameters of species richness (S), Shannon-Wiener diversity index (H'), evenness (E), abundance (N) and Margelef index of species richness (Smarg) were calculated using standard methods and equations (Magurran 1988). However, in this report, S and Smarg are referred to as F and Fmarg to denote that epiphytes were identified to the family level (or to division in the case of ferns), not to the species level. Parameters were computed for the number of individuals per family observed in the meta-community (all 12 branches sampled) and for the surface area covered by each respective family in the meta-community. The meta-community H' diversity indices for branch bases and tips

were compared using t-tests. Additionally, pair-wise comparisons were performed on each of the 12 sample branches using a sign test (Ambrose et al. 2002). The pair-wise comparison was performed based on relative numerical abundances.

RESULTS

Results from meta-community analysis based on relative numerical abundance of each family (or division in the case of ferns) show strong evidence to indicate that branch bases (H' = 1.66) have a higher diversity than branch tips (H' = 1.17) (p = value < 0.001). Evenness (E) was very similar for branch bases (E = 0.63) and tips (E = 0.65), but abundance, family richness, and Margelef index of family richness were all higher in branch bases (Figure 1).

Conversely, results from the meta-community analysis based on relative area of coverage suggest that there is strong evidence to indicate that branch tips (H' = 0.71) are more diverse in coverage than branch bases (H' = 0.27) (p-value < 0.001). Evenness is greater in branch tips, but family richness, total area covered, and Margelef diversity index was greater in branch bases than in tips (Figure 2).

All results from the pair-wise comparison (Table 1) corroborated previous results, with the exception of the Margelef index of family richness (Fmarg). The sign test results for Fmarg indicate that there is not a significant difference in family richness on Branch bases vs. branch tips when differences in abundance are controlled for.

DISCUSSION

The comparison of family diversity using relative numerical abundance offers a result that conflict with the family diversity using relative areal abundance. The former indicates that the branch base diversity is greater, whereas the latter says that the diversity of branch tips is higher. Since family richness remains constant for both of these tests, the conflicting results are the product of differences in family evenness between the different regions of a branch (Figures 1 and 2). The unevenness of aerial coverage in both branch locations can be explained by the dominance of Pteridophyta. Many of the branches sampled were covered in dense mats of fern growth, however these mats were observed to cover a greater proportion of the branch surface on bases than on tips. Many species of Pteridophyta have the ability to reproduce by vegetative budding, or send up new shoots from creeping rhizomes (Moran 2004). Since roots and bases of epiphytes are often obscured by bryophyte growth on branches, it is impossible to distinguish individual plants in a dense mat (Freiberg (1996). For this reason, continuous mats of fern growth were considered as a single individual in this study. As a result, relative numerical abundance of ferns was likely underestimated. Since the Shannon-Wiener diversity index takes into account richness and evenness, the outcome of such an error could be a false conclusion of greater diversity in branch bases than tips. Therefore relative area measurements were deemed to be more accurate. As such, more emphasis is placed on the results of that meta-community analysis and the conclusion was drawn that branch tips have significantly higher family diversity than branch bases.

The conclusion reached here can be supported by the previous findings that individuals on branches less than 6cm in diameter experienced higher turnover rates than

individuals living on larger branches (Heitz 1997). More frequent disturbances in branch tips may lead to higher mortality rates, which may inhibit any one species from dominating the area, and thus increasing the overall diversity on branch tips compared to branch bases (Hietz, 1997).

Relative area for branch tips and bases were both dominated by ferns, followed by orchids. However, in both cases the relative coverage of orchids was more than eight times less than that of ferns, and the next most abundant family covered about three times less area than orchids. (Table 2). These results are not congruent with results from Ingram and Nadkarni (1993) in which they found no strong dominance in angiosperm species. However, ferns were not considered in their study, and it was conducted at a lower elevation on the Pacific slope of the Tilarán mountain range, which may have markedly different climate than the Atlantic slope site studied here.

It was also observed that, in general, less of the total surface area of the branch tips was covered by epiphytic growth. In contrast, many of the branch bases sampled were completely covered in large fern mats. Therefore, fern coverage was more dominant on branch bases than branch tips, leading to the lower evenness noted in the meta-community analysis based on relative area. This observation of higher fern coverage on branch bases is corroborated by previous studies. Heitz (1997) found that ferns and orchids tend to grow in higher abundance on thicker branches. While Freidberg (1996) proposed that smaller branches have lower richness and abundance because their decreased branch top surface area leads to a high instance of epiphyte growth slipping off of the branch.

Although diversity was found to be higher on branch tips, branch bases had a higher family richness (figure 1 and Figure 2). Only 6 out of the 15 families (including the division Pteridophyta) observed were found on branch tips, while all but one family (Asteraceae) was found on branch bases (Table 2). These results have been corroborated by results of past studies. Freiberg (1996) found that species richness was highest at the base of branches in the middle of the crown.

However, while both meta-community analyses illustrate that branch bases have higher family richness than branch tips (Figure 1 and Figure 2), results of the pair-wise comparison imply that there is no difference in family richness between branch bases and tips (table 1). This discrepancy is most likely the result of limitations in the sign test analysis. The sample size of 12 branch tip/base pairs is small, and sign tests do not pick up subtle differences. For this reason overall interpretation of species richness and Fmarg should be based on meta-population calculations, not on the sign test calculations. Therefore, it can be concluded that branch bases displayed an overall higher family richness than branch tips. All other results from the pair-wise comparison corroborated the meta-population results (Table 1).

Future investigations may wish to address the experimental limitations of this study by physically identifying the exact number of Pteridophyta species present on each sample branch. However, obtaining a definite number of fern individuals would require physical access to canopy branch tips as well as removal of the bryophyte substrate, and thus would be difficult to achieve and would heavily impact the microhabitat. It is also worth noting that although fern growth dominated the surface area of both branch bases and branch tips, most large fern mats were comprised of short, delicate ferns that did not seem to obscure growth of larger vascular epiphytes. If disturbing the habitat is not an

issue, future studies may choose to follow techniques outlined by Ingram and Nadkarni (1993), in which branches are stripped and species abundance and diversity is compared based on dry weight.

During data collection it was observed that branches without much moss cover tended to have less epiphytes growing on them. These results were consistent with previous observations that scarcity of bryophytes and humus build-up impedes epiphyte colonization and succession (Nieder *et al.* 2004). Bryophyte coverage provides a medium for epiphytes to germinate and take root and Substrate characteristics determine the composition and availability of resources. In the future a study could be conducted to test the relationship between epiphyte growth and the type or thickness of bryophyte coverage for the upper canopy and branch tips. Freidberg and Freidberg (2000) found that the thickness of bryophyte and humus cover was generally higher on larger, central branches than on smaller peripheral branches. They proposed that the lower species richness and abundance found in the periphery of the crown is due to low amounts of humus and bryophyte cover on the branches. A study on the effects of bryophyte colonization on branch tip epiphyte communities would be particularly interesting, as high exposure to abiotic pressures and increased rate of disturbance may result in a tight correlation between moss coverage and vascular epiphyte succession (Freiberg 1996).

This study was designed as a preliminary attempt to collect branch tip epiphyte data that has never been accessed before. Family richness results are congruent with the results from previous studies. However the conclusion that branch tips have higher diversity than branch bases runs counter to the trends noted in previous epiphyte reports. This conclusion could change if data at the species level was collected, as the more in depth sat could pick up differences in species richness that did not register at the family level. Future studies are encouraged to gather additional branch tip data, identifying individuals to the species level, if access allows, in order to gain more in depth insight into the little known world of canopy branch tips.

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Literature Cited

Ambrose, H. W., K. P. Ambrose, D. J. Emlen, and K. L. Bright. 2002. A handbook of biological investigation. Hunter Textbooks Inc., Winston-Salem, North Carolina.

Freiberg, M., E. Freiberg. 2000. Epiphyte diversity and biomass in the canopy of lowland and montane forests in Ecuador. J. Trop. Ecol. 16: 673-688.

Freiberg, M. 1996. Spatial distribution on vascular epiphytes on three emergent canopy trees in French Guiana. Biotropica. 28: 345-355.

Haber, W. A., Plants and vegetation. *In* N. M. Nadkarni, and N. T. Wheelwright (Eds.). Monteverde, Ecology and Conservation of a tropical cloud forest, pp. 39-94. Oxford Univ. Press, New York, New York.

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

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

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton Univ. Press, Princeton, New Jersey.

Moran, R. C. 2004. A natural history of ferns. Timber Press Inc, Portland, Oregon.

Nieder, J., S. Engwald, M. Klawun, and 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.

Zotz, G. P. Bermejo, H. Dietz. 1999. The epiphyte vegetation of *Annona glabra* on Barro Colorado Island, Panama. J. Biogeography. 26: 761-776.

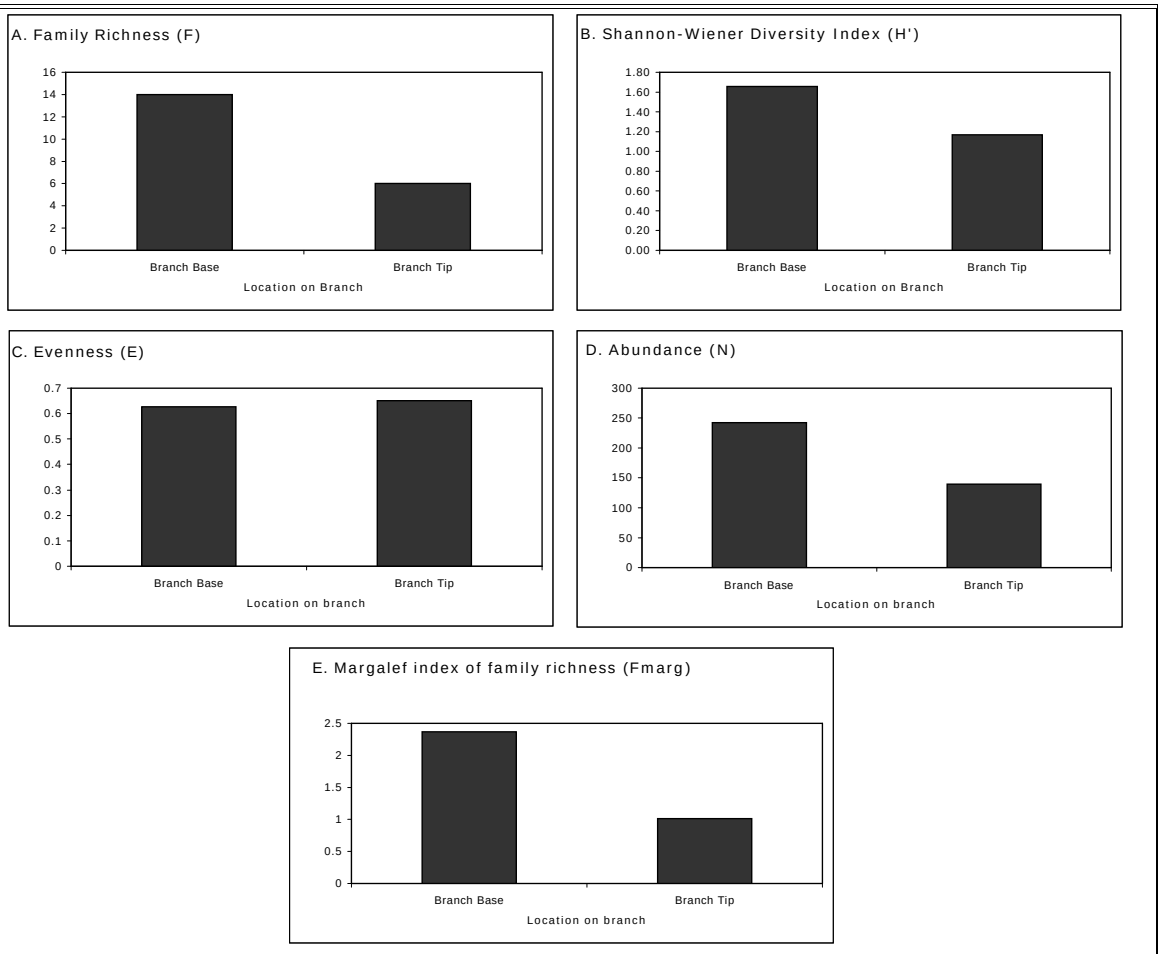

Figure 1. Summary results of F, H', E, N and Fmarg for the number of individuals per family observed on branch bases vs. branch tips. (A) Overall Branch bases had higher family richness than branch tips. (B) The Shannon-Weiner diversity index shows a higher diversity of epiphyte families on branch bases. (C) The evenness was very similar for branch bases and branch tips. (D) Branch bases were observed to have a higher abundance of individual epiphyte plants than branch tips. (E) The Margelef index of family richness revealed that branch bases are more diverse than tips, even when differences in abundance are controlled for. Based on 12 branches.

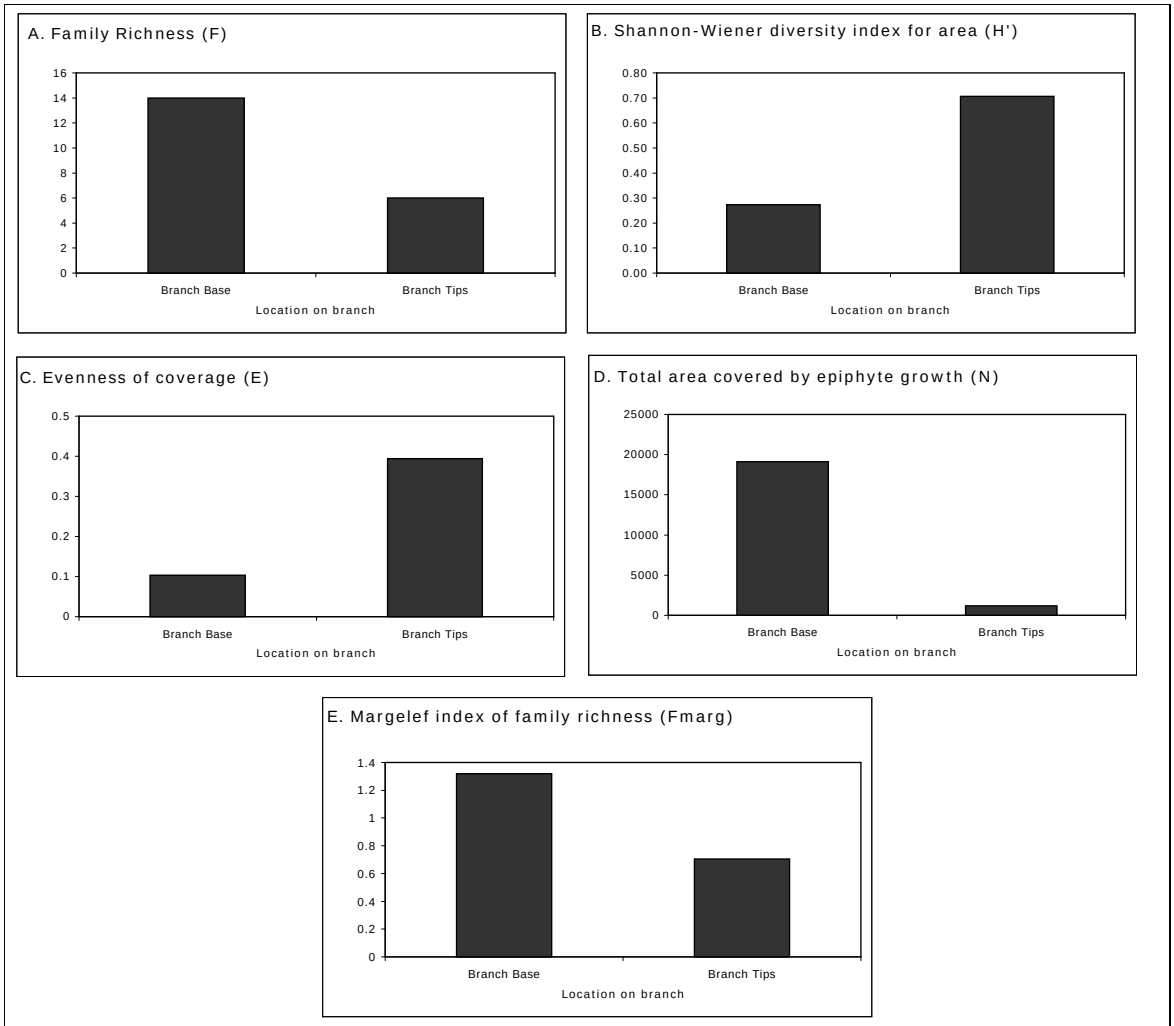

Figure 2. Summary results of F, H', E, N and Fmarg using relative area covered of epiphyte coverage on branch bases vs. branch tips, for 12 branches. (A) Overall there were more families represented branch bases than branch tips. (B) The Shannon-Weiner diversity index for area covered suggests that branch tips are more diverse in their coverage than branch bases. (C) Evenness of coverage was greater in branch tips than in branch bases, although neither location showed high overall evenness. (D) The total area covered by epiphyte growth was higher in branch bases than branch tips. (E) The Margelef index of family richness shows that even when differences in the coverage area are controlled for, branch bases still have greater family richness than branch tips.

Table 1. Results of pair wise comparisons (sign test) of branch bases vs. branch tips for all branches sampled. To the right are the significance values for each comparison. All values corroborate previous results with the exception of Fmarg.

Community index	*Number +*	*Number -*	*Number Ties*	*Significance*
F	10	0	2	$P < 0.05$
H'	11	1	0	$P < 0.05$
E	7	5	0	$P > 0.05$
N	10	1	1	$P < 0.05$
Fmarg	8	4	0	$P > 0.05$

Table 2. Families (and division in the case of ferns) observed on sample branches, including two unidentified epiphytes. The right-hand columns represent the relative area covered by each family on branch tips and bases respectively.

Family (or Division)	Branch bases (cm)	Branch tips (cm)
Orchidaceae	386	111
Bromeliaceae	145	41
Ericaceae	103	71
Pteridophyta	18192.23	975.58
Araceae	150	0
Cyclanthaceae	35	0
Cluseaceae	38	0
Melastomataceae	2	0
Rubiaceae	20	0
Smiliaceae	10	0
Gesnariaceae	5	0
Asteraceae	0	2
Piperaceae	5	5
Unknnown #1	3	0
Unknown #2	5	0
Total area covered	19099.23	1205.58