The effects of elevation on epiphyte richness and density on cloud forest tree ferns (Cyatheaceae and Dicksoniaceae)

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ABSTRACT

Epiphytes play an integral role in nutrient cycling in tropical rainforests and are often found on the trunks of tree ferns. This study examined the role of elevation on epiphyte load on tree ferns. Ninety-six tree ferns were examined along an elevational gradient, and data were collected regarding the identity and dimensions of the trees as well as their elevations and the number and type of epiphytes on their trunks. Epiphyte abundance was not significantly correlated with elevation, but epiphyte load was significantly related to tree fern morphology. The Alsophila, whose spines likely provide a prime habitat for epiphytes, possessed a significantly larger epiphyte load than Cyathea, which does not possess spines (P = 0.0062). Further study regarding tree fern morphologies and epiphyte load should be conducted.

RESUMEN

Las epífitas juegan un rol integral en el ciclo de nutrimentos en el bosque lluvioso tropical y a menudo se encuentran en los troncos de helechos arborescentes. Este estudio examinó el rol de la elevación en la carga de epífitas en los helechos arborescentes. Noventa y seis helechos arborescentes fueron examinados a lo largo de un gradiente altitudinal y se colectó datos con respecto a la identidad y dimensiones de los helechos así como con respecto a sus elevaciones y al número y tipo de epífitas en sus troncos. La abundancia de epífitas no estuvo significativamente correlacionada con la elevación, pero la carga de epífitas estuvo significativamente relacionada con la morfología del helecho arboresco. Alsophila, cuyas espinas probablemente proveen un mejor habitat para las epífitas, tuvo una carga significativamente mayor de epífitas que Cyathea, la cual no tiene espinas (P = 0.0062). Debe de estudiarse la morfología de los helechos arborescentes y de la respectiva carga de epífitas.

INTRODUCTION

Scientific research has recently begun focusing on the enormous biodiversity of canopy organisms and their contributions to the ecosystem. Epiphytes comprise a significant portion of the canopy biomass, and their integral role in uptake, storage and release of minerals play a noteworthy part in the mineral cycling of the ecosystem (Coxson and Nadkarni 1995). No other place on earth has as great a diversity or abundance of epiphytes as the Neotropics. Epiphytes are the most species-rich life form in the Monteverde flora, with 878 species including ferns, orchids, and bromeliads, among others (Haber 2000).

Typically found in the canopy, epiphytes in the cloud forest are often associated with low-growing tree ferns, which are abundant in the cloud forests of Monteverde and are often found in clearings as light-gap pioneers (Gómez 1983). The trunks of tree ferns
are composed of a fibrous layer known as the root mantle, which is a good substrate for many epiphytes. Moran et al. (2003) found that some epiphytic ferns occurred exclusively on tree ferns. The limited maximum height of tree ferns (about ten meters) provides an opportunity for a unique study on the relationship of epiphytes and tree ferns.

Due to epiphyte requirements for high aerial moisture and nutrient availability, it has been observed that epiphyte density and abundance drop dramatically with a decrease in elevation on the Pacific slope of the Tilarán mountain range (Haber 2000). High humidity and rainfall favor the increased presence of vascular epiphytes and bryophytes in mid-elevation cloud forests in the tropics (Vázquez 1998); however, the abundance of epiphytes on tree ferns along an elevational gradient has not yet been studied.

The purpose of this study was to gain information on epiphyte abundance and richness on tree ferns. Epiphytic density (abundance related to available surface area for growth) and richness on different tree fern species was compared along an elevational gradient. It was hypothesized that epiphyte load on tree ferns would be positively correlated with elevation. Dimensions of tree size (DBH, height) and percent of canopy coverage were also hypothesized to be positively related to epiphyte abundance and richness.

**MATERIALS AND METHODS**

This study was conducted in the forest adjacent to the Estación Biológica de Monteverde in Puntarenas, Costa Rica from July 15 to August 6, 2004. The study area included primary forest located on the Pacific slope of the Tilarán mountain range between the elevations ranging from 1500 m to 1800 m above sea level, within the lower montane rain forest life zone. This area receives an average of 2.5 meters of precipitation per year, with an additional 25% meters in mist; the mean temperature is 18.8° C (Clark et al. 2000). Ninety-six tree ferns located along trails were sampled along the elevational gradient. The tree ferns were identified to species, and data were collected only on those taller than 1.3 meters. The following data were recorded for each tree: circumference at breast height (CBH), tree height, elevation and percent canopy coverage. Tree height was calculated from the base to the lowest frond. Surface area of the trunk was extrapolated from CBH and height. Elevation was measured using the altimeter on a SUUNTO Vector watch. Epiphytes on the trunks were identified to morphospecies on each tree fern sampled and their individual abundance recorded. Percent coverage of the canopy was estimated by standing directly next to the trunk of the tree fern and looking up at a 90° angle from the horizontal.

Epiphyte richness and abundance along the elevational gradient were compared using simple regressions between the independent variables (CBH, height, surface area, elevation and canopy coverage) and the dependent variables (richness, abundance, density and adjusted species richness). Species richness was determined only for epiphytes on individual tree ferns. Density was calculated by dividing the number of individuals by surface area, and adjusted species richness was calculated on individual tree ferns by dividing the species richness by surface area. The data for all the tree ferns were statistically analyzed by simple regressions; *Cyathea caracasana*, *C. delgadii* and *C. onusta* were analyzed individually using simple regressions as well.
A one-way ANOVA was used to compare species richness and density between the three aforementioned species. A Kruskal-Wallis test was used to compare species richness and density among the following most common species: *Alsophila erinacea*, *A. polystichoides*, *C. caracasana*, *C. delgadii* and *C. onusta*. Unpaired t-tests were used to determine if there was a significant difference in the mean epiphyte density and mean adjusted species richness of *Alsophila sp.* and *C. caracasana*. Finally, unpaired t-tests compared mean epiphyte density and mean adjusted species richness between *Alsophila sp.* and 19 randomly selected *Cyathea sp.* individuals.

**RESULTS**

Ninety-six total individuals of eight different species of tree ferns were identified in the study area (E. Cruz, pers. comm.), including 10 *Alsophila erinacea*, 9 *Alsophila polystichoides*, 26 *Cyathea caracasana*, 20 *Cyathea delgadii*, 20 *Cyathea onusta*, 3 *Cyathea poeppigii*, 3 *Shaeropteris brunei* and 4 *Dicksonia gigantea* (Table 1).

When testing all tree ferns together, elevation was not found to be significantly correlated with epiphyte abundance or richness. A significant positive correlation was found between epiphyte abundance and tree fern surface area ($R^2 = 0.324, P < 0.0001$), tree height ($R^2 = 0.211, P < 0.0001$) and CBH ($R^2 = 0.283, P < 0.0001$). Similarly, a significant positive correlation was found between species richness and surface area ($R^2 = 0.238, P < 0.0001$), tree height ($R^2 = 0.211, P < 0.0001$) and CBH ($R^2 = 0.202, P < 0.0001$) (Figure 1).

A significant positive correlation was found between surface area of *C. caracasana* ($N = 26$) and epiphyte abundance ($R^2 = 0.244, P = 0.0088$) as well as between CBH and abundance ($R^2 = 0.302, P = 0.0030$) (Figure 2). A significant positive correlation was also found between the surface area of *C. delgadii* ($N = 20$) and species richness ($R^2 = 0.228, P = 0.0333$) in addition to elevation and CBH ($R^2 = 0.3, P = 0.0124$). Further analysis showed that elevation and adjusted species richness were positively correlated ($R^2 = 0.203, P = 0.0463$) (Figure 3). A significant positive correlation between adjusted species richness and elevation were also found for *C. onusta* ($N = 20$) ($R^2 = 0.293, P = 0.0137$), although this species was only found at elevations over 1730 m. Furthermore, abundance on this species was positively correlated with surface area ($R^2 = 0.322, P = 0.0090$) and tree height ($R^2 = 0.454, P = 0.0011$). In addition, species richness was positively correlated with tree height ($R^2 = 0.348, P = 0.0061$), surface area ($R^2 = 0.487, P = 0.0006$) and CBH ($R^2 = 0.332, P = 0.0078$) (Figure 4).

There was no significant difference between either epiphyte density (one-way ANOVA, $P = 0.0957$) or adjusted species richness (one-way ANOVA, $P = 0.1106$) on *C. caracasana*, *C. delgadii* and *C. onusta*. A significant difference was found among *A. erinacea*, *A. polystichoides*, *C. caracasana*, *C. delgadii* and *C. onusta* with regards to epiphyte density (Kruskal-Wallis, $P = 0.0055$) but not adjusted species richness (Kruskal-Wallis, $P = 0.2239$). Based on the means, the *Alsophila sp.* had the greatest epiphyte density. When comparing *Alsophila sp.* and *C. caracasana*, a significantly greater mean epiphyte density was found on the *Alsophila* (unpaired t-test, $t = 3.062, P = 0.0037$), but not in the mean adjusted species richness (unpaired t-test, $t = 0.364, P = 0.7174$). Finally,
Alsophila sp. was found to have a significantly higher mean epiphyte density than Cyathea sp. (unpaired t-test, t = 2.906, P = 0.0062), but this was not found in adjusted species richness (unpaired t-test, t = 0.751, P = 0.4575).

DISCUSSION

Epiphyte abundance and richness were found to have no significant correlation with elevation of tree ferns. This is in conflict with prior studies regarding increased epiphyte abundance and richness with increased elevation. Perhaps this has to do with the vertical distribution of epiphytes on their host plants. Epiphytes tend to concentrate in the canopy, but tree ferns are primarily found in the understory and in light gaps. It seems that the elevational distribution of epiphytes may vary when vertical distribution is limited.

A positive correlation was found between epiphyte abundance and species richness when compared to tree height, CBH and surface area. This indicates that tree dimension is more important than elevation in the frequency of epiphytes on tree ferns. Taller, thicker trunks are colonized by more epiphytes. This may be because the tree itself is larger and therefore its surface can sustain a larger population. Additionally, the larger trunks indicate increasing age. It may take time for epiphytes to become established on tree ferns, so those that are older would be more likely to possess a greater abundance of epiphytes as well as more species.

Among the individual Cyathea species, tree dimension may also be more influential on epiphyte load than elevation. Larger trees with larger surface areas possess larger environments. There is less competition for resources so more epiphytes are able to become established.

Elevation could only be correlated with adjusted species richness on two species of tree ferns, *C. delgadii* and *C. onusta*. The latter was only found over a 65 meter range from 1730 m to 1795 m which is not representative of the entire elevational gradient of the study site. Furthermore, there was no significant difference among the three *Cyathea* spp. regarding epiphyte density or adjusted species richness. Belonging to the same genus, the surface of the trunks are similar which is reflected by comparable epiphyte compositions.

There is some indication that epiphyte abundance and richness may be more strongly correlated with morphological characteristics on various species of tree ferns. In order to distinguish epiphyte load according to possible morphological differences, the five most represented tree ferns were compared statistically at the genus level, *Cyathea* and *Alsophila*. There was a significant difference between the genera with regard to epiphyte density. These two genera exhibit strikingly unique morphologies which may play a role in their epiphyte load. *Alsophila* are easily recognized by its spiny trunk, whereas *Cyathea* are without spines (Rojas 1999). These spines’ primary purpose serves to protect the tree fern from herbivory, but their uneven surface may serve as a prime substrate for epiphyte growth. The spines offer increased surface area, protection and a horizontal surface on which the epiphytes can grow.

There could also be a chemical reason for the reduced number of epiphytes on *Cyathea*. In Mexico, it has been found that while orchids and other epiphytes are
abundant on some oak species, they are virtually absent on others. Experiments showed that toxicity in the bark inhibited orchid growth (Richards 1996). It could be possible that in some way the Cyathea produce a chemical response which help to limit the epiphytic load, but not much is known on this topic.

The data indicates that possibly tree fern morphologies, rather than elevation, have a greater effect on epiphyte density, abundance and richness. For future study, it is suggested that a closer look be taken at various morphologies of tree ferns in cloud forests with respect to epiphyte abundance and richness, while at the same time holding elevation constant.

Individual epiphytic ferns are often difficult to differentiate; their roots may extend throughout the tree fern trunk, tangling with one another, forming mats of the epiphyte. Additionally, many epiphytes such as mosses were overlooked in this study due to the difficulty in counting individuals. It would be interesting to perform a similar study measuring epiphyte coverage area of the tree fern trunk. Lianas and vines were also found to inhabit tree fern trunks, and perhaps this variable could be incorporated into future studies as well.

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LITERATURE CITED


## TABLES

**Table 1:** Relative abundance of families and species of 96 tree ferns sampled between 1500 m and 1800 m in forest adjacent to the Estación Biológica, Monteverde.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyatheaceae</td>
<td><em>Alsophila erinacea</em></td>
<td>10</td>
</tr>
<tr>
<td></td>
<td><em>Alsophila polystichoides</em></td>
<td>9</td>
</tr>
<tr>
<td></td>
<td><em>Cyathea caracasana</em></td>
<td>26</td>
</tr>
<tr>
<td></td>
<td><em>Cyathea delgadi</em></td>
<td>20</td>
</tr>
<tr>
<td></td>
<td><em>Cyathea onusta</em></td>
<td>20</td>
</tr>
<tr>
<td></td>
<td><em>Cyathea poepzig</em></td>
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</tr>
<tr>
<td></td>
<td><em>Shaeropteris brunei</em></td>
<td>3</td>
</tr>
<tr>
<td>Dicksoniaceae</td>
<td><em>Dicksonia gigantea</em></td>
<td>4</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>96</td>
</tr>
</tbody>
</table>
Figure 1. Simple regressions showing the significant relationships between three physical measurements of tree ferns (N = 96) and the two major indicators of epiphyte load (abundance and richness). A) Epiphyte abundance increased with tree fern trunk surface area ($R^2 = 0.324$, $P < 0.0001$) ($Y = 1.74 + 0.002 \times X$). B) Epiphyte abundance increased with tree fern trunk height ($R^2 = 0.211$, $P < 0.0001$) ($Y = -5.786 + 9.648 \times X$). C) Epiphyte abundance increased with tree fern CBH ($R^2 = 0.283$, $P < 0.0001$) ($Y = -15.272 + 1.297 \times X$). D) Epiphyte species richness increased with tree fern trunk surface area ($R^2 = 0.238$, $P < 0.0001$) ($Y = 1.984 + 2.722E-4 \times X$). E) Epiphyte species richness increased with tree fern trunk height ($R^2 = 0.211$, $P < 0.0001$) ($Y = 0.852 + 1.21 \times X$). F) Epiphyte species richness increased with tree fern CBH ($R^2 = 0.202$, $P < 0.0001$) ($Y = 0.078 + 0.147 \times X$).
Figure 2. Simple regressions for *Cyathea caracasana* (N = 26) showing the significant relationships. A) Epiphyte abundance increased with trunk height ($R^2 = 0.244$, $P = 0.0088$) ($Y = -1.88 + 0.002 \times X$). B) Epiphyte abundance increased with trunk CBH ($R^2 = 0.302$, $P = 0.0030$) ($Y = -14.83 + 1.132 \times X$).
Figure 3. Simple regressions for *Cyathea delgadii* (N = 20) showing significant relationships. A) Epiphyte species richness increased with trunk surface area ($R^2 = 0.228$, $P = 0.0333$) ($Y = -0.886 + 0.001 \times X$). B) CBH increased with increasing elevation ($R^2 = 0.3$, $P = 0.0124$) ($Y = -17.748 + 0.026 \times X$). C) Adjusted species richness increased with elevation ($R^2 = 0.203$, $P = 0.0463$) ($Y = -0.002 + 1.772E-6 \times X$).
Figure 4. Simple regressions for *Cyathea onusta* (N = 20) showing significant relationships.  
A) Epiphyte adjusted species richness increased with elevation ($R^2 = 0.293, P = 0.0137$) ($Y = -0.027 + 1.552E^{-5} * X$).  
B) Epiphyte abundance increased with trunk height ($R^2 = 0.322, P = 0.0090$) ($Y = 5.839 + 0.002 * X$).  
C) Epiphyte abundance increased with trunk surface area ($R^2 = 0.454, P = 0.0011$) ($Y = -4.198 + 9.319 * X$).  
D) Epiphyte species richness increased with trunk height ($R^2 = 0.348, P = 0.0061$) ($Y = 0.439 + 1.509 * X$).  
E) Epiphyte species richness increased with trunk surface area ($R^2 = 0.487, P = 0.0006$) ($Y = 1.246 + 4.935E^{-4} * X$).  
F) Epiphyte species richness increased with trunk CBH ($R^2 = 0.332, P = 0.0078$) ($Y = -1.393 + 0.242 * X$).