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PALM EPIPHYLLS RESPONSE TO ELEVATION AND MIST FREQUENCY IN A COSTA RICAN CLOUD FOREST: A POSSIBLE BIOINDICATOR OF LOCAL CLIMATE CHANGE

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ABSTRACT

Recent extinctions coupled with climate changes in montane cloud forests of Costa Rica have highlighted the need to understand the biological consequences of local drying and decreased mist frequency in these ecosystems. With the intent of identifying a bioindicator of mist frequency, I performed an altitudinal transect of epiphyll cover on *Geonoma* fronds and an experimental manipulation of mist conditions on epiphylls of *Chamaedorea* fronds. Epiphyll cover on *Geonoma* was found to increase linearly with elevation ($p < 0.0001$). Percent cover of epiphylls did not respond to added mist, but the variation in epiphyll cover increased significantly with experimentally added mist (F-test, $p < 0.05$). The ratio of liverworts to lichens was high in dry conditions and low in conditions of experimentally added mist. This ratio shows promise as a bioindicator of mist conditions in tropical montane cloud forests.

RESUMÉN

Las extinciones recientes se emparejaron con cambios de clima en bosques de nube de montane de Costa Rica ha destacado la necesidad de entender las consecuencias biológicas del secado local y la frecuencia disminuida de la niebla en estos ecosistemas. Con la intención de identificar un bioindicador de la frecuencia de la niebla, yo realicé un transect de altitudinal de la cubierta de epiphyll en trundas de *Geonoma* y una manipulación experimental de condiciones de niebla en el epiphylls de trundas de *Chamaedorea*. La cubierta de Epiphyll en *Geonoma* se encontró para aumentar linealmente con elevación ($P (0,0001)$). Por ciento cubierta de epiphylls no respondió a la niebla agregada, pero a la variación en la cubierta de epiphyll aumentó apreciablemente con niebla experimentalmente agregada (la F-PRUEBA, $P < 0.05$). La proporción de hepáticas a líquenes era alta en condiciones secas y bajo en condiciones de la niebla experimentalmente agregada. Esta proporción muestra la promesa como un bioindicador de condiciones de niebla en bosques tropicales de nube de montane.

INTRODUCTION

Compelling evidence of a variety of forms now exists documenting changes in global climate. Some global trends such as a 0.6°C rise in average annual temperature (Walther et al. 2002) and an increasing concentration of atmospheric CO_2 are also clearly evident. In fact, 3 Pg of carbon are added to the atmosphere annually (Allen et al. 2000). Such changes in global climate have led to calls for natural history study to understand biological responses and establishing conservation priorities (May 1994, Wilson 2000).

The threat of climate change on biodiversity is real. Thompson et al. (2004) surveyed 1,100 species and estimated that 15-37% will be “committed to extinction” because of habitat loss to climate change by the year 2050. Phenology changes in bird mating are evident (Brown et al. 1999), butterfly species are moving towards the poles following regional warming (Parmesan et al. 1999), and birds in the northern hemisphere

are moving their ranges northward (Thomas and Lennon 1999). It is likely that local warming and increasingly variable winter snow accumulation is altering wolf hunting behavior on Isle Royale, MI, affecting ecosystem processes by modifying top-down control of primary production (Post et al. 1999). Variable snow cover is also changing the foraging behavior of northern browsers such as deer and muskoxen (*Ovibos moschatus*), which also affects the primary producers (Post and Stenseth 1999). Janzen (1994) demonstrated that the painted turtle (*Chrysemys picta*) is at risk of local extinctions in a variety of places because of the skewed sex ratio produced by warmer temperatures. Warming near Antarctica has caused dramatic ice-melting events that have impacted penguin populations (Taylor and Wilson 1990). These examples demonstrate the wide geographic and taxonomic distribution of biological consequences of changing climate as well the specificity of these biological responses to local conditions. Thus, it is the local climatic changes that will exert real forces on actual communities.

Pounds et al. (1999) provide a detailed description of changing climatic conditions for the cloud forest community in Monteverde, Costa Rica, the site of this study. He demonstrates that the number of completely dry days during the January- May dry

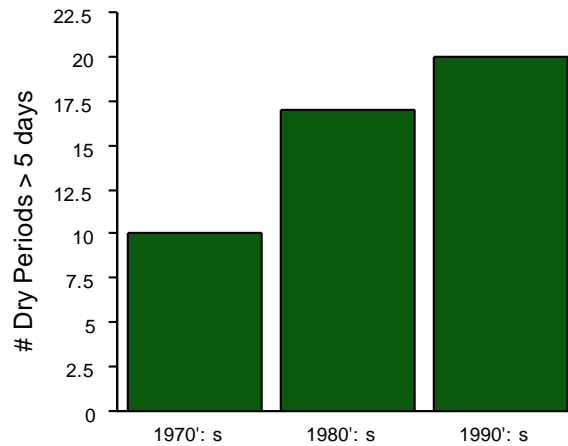


Figure 1. Number of relatively long dry periods from Jan-May in Monteverde in recent decades. This is related to a general increase in the number of total dry days in the area. Data from Pounds and K. Masters (personal communication).

season has increased since the 1970's and that these dry days increasingly run together into longer periods of dryness (Fig 1). Total rainfall has stayed more or less constant. However, roughly 10% of dry season days from 1975-1980 showed zero mist deposition, whereas roughly 35% of the days from 1993-1998 showed zero mist deposition. Pounds et al. (1999) correlates this drying with an upslope range changes for a 17 of 202 birds and sharp declines in 20 of Monteverde's 50 anurans. It also appears that an increase in the number of five-day dry spells is a plausible explanation for the famous extinction of the golden toad, *Bufo periglens* (Pounds and Crump 1994). This drying could be even further problematic to the cloud forest community as many epiphytic plants rely on nearly continuous precipitation to persist (Benzing 1998) and because pacific lowland organisms from bees to birds migrate upslope during the dry season to take refuge in the constantly wet cloud forest (Guindon 2000, Hanson 2000). According to Guindon (2000), 16 of 24 bird dispersed plants species in forest fragments in Costa Rica are exclusively dispersed by Black Guans, Keel-billed Toucans, Resplendent Quetzals, and Three-wattled Bellbirds; all of which rely on cloud forest refuges as the only place to find ripe fruit during the dry season. If the climate of cloud forest communities dries enough to decrease the fruit set of trees that produce large bird-dispersed fruit (e.g. Lauraceous

trees) these birds and the trees they disperse could be in major trouble. Cloud forests face major challenges because of climate change.

Still et al. (1999) demonstrated that climate change in cloud forest habitat is probable. They modeled future climate on tropical mountains based global climate models (GCM's) and concluded that the orographic cloud bank will rise hundreds of meters as the atmospheric CO₂ increases. They predict that major cloud bank changes could occur as early as 2050. It follows that cloud forests biologists desperately need to know whether or not these processes are a current reality for the local biota. We should attempt to answer this question with studies focusing on taxa that depend on frequent water availability: "first-responders" that can speak to current biological consequences of drying.

Regarding plants, epiphytic species that have no access to terrestrial water stores and are thus dependant on precipitation and mist have been recognized as being quick responders to the change in mist deposition. Thus, a considerable amount of research has focused on epiphytes (reviewed by Benzing 1998). I believe that non-vascular epiphylls (leaf dwelling organisms) are at higher risk to local drying than vascular epiphytes such as bromeliads and orchids because epiphylls lack the physical adaptations to store and conserve water present in these vascular families. Non-vascular plants require a nearly-omnipresent pool of available water in order to maintain a positive carbon balance (Coxson 1991, cited in Benzing 1998) as well as to disperse flagellated gametes (Schofield 1985).

Experimental evidence also exists for the use of bryophytes as indicators of climate. Gignac (2001) has effectively justified the use of bryophytes as bioindicators of changing water availability in northern peat bogs. He argued that vascular plants in the same community could tolerate changes in water availability by relying on water stores and increasing water use efficiency; bryophytes lacked these abilities, causing their growth to mirror water availability. Zartman (2003) demonstrated that forest fragmentation in the central Amazon reduced epiphyllous bryophyte diversity and abundance: 100 ha fragments had 25 times the mean abundance as one ha fragments. He argued that epiphyllous bryophytes had quick generation times, were sensitive to changes in light and water, were conspicuous, spatially delimited, and easily quantified. While non-vascular, they could indicate general plant responses on a short, measurable timescale. He thus called epiphyllous bryophytes an "ideal plant group" with which to study biological consequences of habitat fragmentation. As forest fragments are subject to more intense edge effects including warmer, dryer conditions (Lovejoy et al. 1986) it is reasonable to generalize Zartman's conclusion: epiphyllous bryophytes are likely to be ideal organisms with which to study drying climate conditions.

Other studies also point to epiphylls as bioindicator. Sandvik and Heegaard (2002) used a specific liverwort species to demonstrate a biological response to a temperature increase predicted by a global climate model in a subarctic ecosystem, and Hilmo and Holien (2001) demonstrated a growth response of epiphytic lichens to local drying conditions due to edge effects in a boreal forest in Norway. Coley et al. (1993) demonstrated a significant increase in epiphyll cover following a water-addition regime in tropical Panamanian forests, indicating that epiphylls respond to water availability. At my actual site, a cloud forest in Monteverde, Costa Rica, Mitchel (1996) was able to demonstrate an increase in epiphyll cover with increasing elevation.

I conclude that non-vascular epiphyllous plants are excellent study organisms for questions regarding the biological effects of the changing local climate in Monteverde. I use an altitudinal transect of epiphyllous cover on *Geonoma* (Arecaceae) pinnae and a mist addition experiment on *Chamaedorea* (Arecaceae) pinnae to explore the idea of using epiphyllous organisms as indicators of local drying in Monteverde.

METHODS

Data were collected for this study from April 16th to May 8th 2005 in a private forest owned by the Estación Biológica de Monteverde (EBM), Puntarenas, Costa Rica. This study site is classified as Lower Montane Wet Forest (Holdridge, 1967) and lies between 1500 and 1800 m elevation on the western slope of the Cordillera de Tilaran mountain range (10° 18' N, 84° 48' W). The study site is ecologically similar and adjacent to the forest of the Monteverde Cloud Forest Reserve, described by Murray and Garcia (2002) and Pounds et al. (1999). The time of data collection corresponds to the end of the dry season that is characterized by prevailing NE trade winds that prevent upslope movement of wet air from the Pacific Ocean, reducing precipitation (Haber et. al 2002).

Altitudinal Transect of Epiphyll Cover

Percent cover by epiphylls was measured for 172 *Geonoma* palms (*G. edulis* and *G. hoffmanniana*) between 1490 and 1765m elevation on a single ridge to the north of the principal trail in the EBM forest. To control for frond age and, thus, the length of time available for epiphyll colonization, I used the following equation to select the frond closest to 40 weeks in age for each individual: Age (weeks) = -1.43 + (proportional rank*83.6) $R^2 = 0.86$, $p < 0.01$ (Daniels, 1998). Proportional rank corresponds to the frond number (counted starting with the top, newest frond) relative to the total number of fronds. For each frond sampled, I selected a pinna representative of the frond's average epiphyll cover by simple visual inspection. I placed a fine chicken wire grid (cell area = 0.137 cm²) over an area representative of the average epiphyll coverage of the pinna and took a digital picture at a distance of 30 cm. The photos for each pinna were visually examined on a personal computer: percent cover was quantified for 25 chicken wire cells as the area occupied by epiphylls divided by the total area sampled.

Mist Addition Experiment

Thirty *Chamaedorea* (Aracaceae) individuals were marked with uniquely labeled flagging tape within a 900 m² area at an elevation of 1530 m in the EBM forest. I only included individuals with > 1% epiphyll coverage in this sample. A paired design was used: two pinnae of similar size and epiphyll cover were chosen for analysis and randomly assigned to either the experimental or control condition. Pinnae area was estimated by modeling each pinna as an ellipse (area = 0.5 π *ab) by measuring the major (a) and minor (b) axes to the nearest 0.01 cm with metal calipers. Initial measurements were taken on the 16th of April. Using a transparent herbivory grid with small cells (cell area = 0.0405 cm²) I measured the number of cells with >50% epiphyll cover and the number of cells with epiphyll presence. The estimate of pinnae area was used to calculate the total number of cells for each pinna. Percent cover was defined as the number of cells with >50% epiphyll cover divided by the total number of cells. I also recorded the abundance of seven recognizable morphospecies for each pinnae.

To collect mist, I constructed two mist collectors by suspending vertical strands of fishing-line in a cylindrical arrangement from an inverted plastic jar. A funnel was connected at the bottom of these strings, which was connected by a plastic tube to a collecting bottle that sat on the ground. These mist collectors were suspended by rope from trees in my study site. I checked the mist collectors twice a day, at roughly 8:30 am and 3:30 pm. At each time, when no mist was found in the collectors, I sprayed each experimental pinna with collected mist until the pinna was saturated and a drop of water ran off of the terminal end of the pinna. Tap water was used when collected mist was unavailable. No mist was ever added to the control group. This misting procedure was repeated everyday until the 8th of May, when I measured percent cover, presence, and morphospecies abundance as describe previously.

RESULTS

Altitudinal Transect of Epiphyll Cover

Epiphyllous cover increased significantly in linear relationship with elevation ($p < 0.001$). Percent cover data was significantly non-normal (Kolmogorov-Smirnov test, $p = 0.0384$). Data were normalized (Kolmogorov-Smirnov test, $p = 0.999$) by taking the square root of percent cover (Fig. 2). No significant difference of percent cover existed between *Geonoma* species between the 1610 and 1625 m elevation (Mann-Whitney U test, $N = 10$ per species, $p = 0.82$). Thus, data were not separated based on host species for the linear regression (Fig. 2).

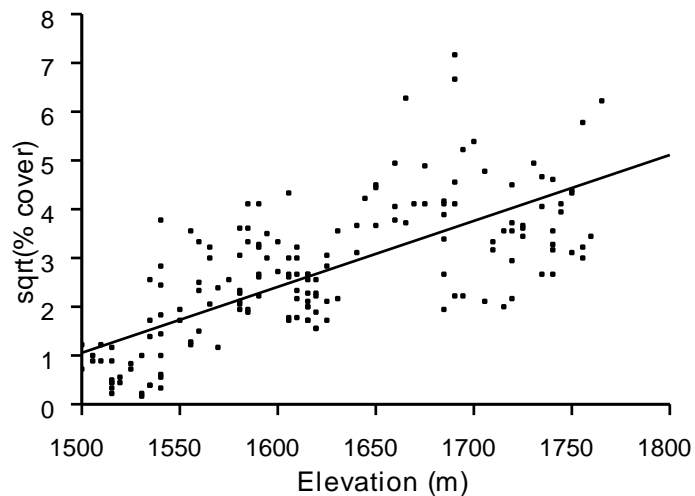


Figure 2. Epiphyllous cover on *Geonoma* palm fronds, altitudinal transect. $N = 172$. $Y=0.013x-19.125$. $R^2=0.517$, $p<0.0001$.

Mist Addition Experiment

I measured collected mist five times out of the 42 times I checked the collectors. There was a general decrease in percent epiphyll cover and an increase in epiphyll presence over time. This was true of both the experimental and control condition (Table 1), though the experimental condition was significantly more variable than the control for both measurement types (Fig 3; F test, $p < 0.05$). There was no significant difference between the change in cover between the experimental and control conditions (paired t-test, $N = 29$, $df = 28$, $p = 0.79$). There was also no significant difference between the control and experimental conditions for the epiphyll presence data (paired t-test, $N = 29$, $df = 28$, $p = 0.74$).

The change in abundance was not constant across all taxa surveyed (Fig. 4). The number of liverwort individuals in the control group increased significantly following treatment ($X^2 = 18.49$, $df = 1$, $p < 0.001$) but did not for the experimental group ($X^2 = 0.011$, $df = 1$, $p > 0.95$). On the other hand, the number of lichens in the experimental group increased while the number of lichens in the control group decreased following treatment, but neither trend was significant (experimental group: $X^2 = 2.152$, $df = 1$, $p > 0.10$; control group: $X^2 = 1.739$, $df = 1$, $p > 0.10$).

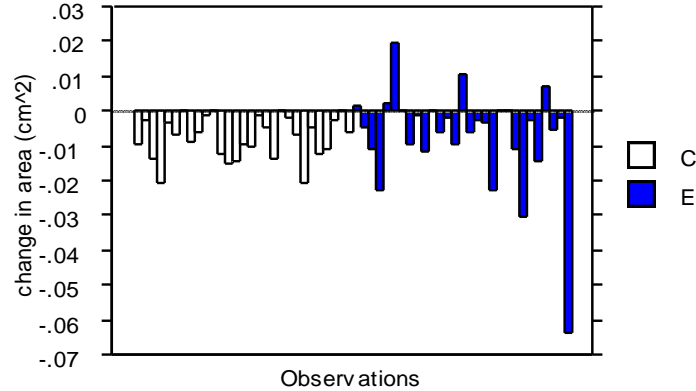


Figure 3. Variation in change of epiphyll cover between conditions. C= control, E= experimental. N=29 for both groups, each bar is one individual. Standard deviation: control = 0.00602 cm^2 , experimental= 0.01475 cm^2 .

Table 1. Presence and area data for epiphylls. Ratio presence data is number cells occupied final / number cells occupied initial. Change in area = cm^2 covered final – cm^2 covered initial. Units for ratio presence data are # cells occupied. Units for change area data are cm^2 .

	Mean	Std. Dev.	N	Range
Ratio presence E	0.01268	0.06385	29	0.30494
Ratio presence C	0.01590	0.02303	29	0.08928
Change area E	-0.00698	0.01475	29	0.08319
Change area C	-0.0078	0.00602	29	0.02067

DISCUSSION

The increase in epiphyll cover with elevation suggests that epiphyll growth or colonization is correlated with the decreasing temperature and/or the increasing moisture associated with the higher elevations of the Monteverde area (Clark et al. 2000). Clark et al. (2000) also indicate that Monteverde receives roughly 22% of its annual precipitation in the form of cloud deposited mist. However, I discovered no distinct threshold of epiphyll growth with respect to altitude, as was expected from predictions based on the orographic cloud bank (Pounds et al. 1999, Still et al. 1999). It is reasonable, however, for the base of the cloud bank to vary in altitude throughout the dry season and with normal weather fluctuation. As this study occurred on a relatively small spatial scale, it is not surprising that I did not find evidence for a distinct cloud bank base. Perhaps a

threshold of epiphyll cover would be found in a study encompassing a greater range of altitude.

It is also possible that epiphylls simply do not respond strongly, or primarily, to mist availability. Temperature declines more-or-less constantly with increasing elevation (Holdridge 1967); epiphylls could respond primarily to temperature. The linear relationship of figure 2 is consistent with this idea. It is not possible to distinguish between causal factors from these data. It is likely that epiphylls respond, at least to a degree, to both water availability and temperature. The linear increase of epiphylls with elevation found in this study (Fig 2) is of similar magnitude to that measured by Mitchel (1996), suggesting that drastic up-slope movements of epiphylls has not occurred in the past 9 years.

While this study and Mitchel (1996) used different methodology, the similarity in our findings is good news: it suggests that the cloud forest of Monteverde is not currently experiencing a drying crisis.

The high variance in growth and colonization (as measured by the change in presence data) in the experimental condition is most likely attributable to pinnae microhabitat differences. This interpretation is supported by Daniels (1998), who demonstrated that microhabitat differences were important in determining colonization and growth rates of epiphylls on *Geonoma edulis* in a cloud forest adjacent to my study site. Microhabitat differences were apparently less important in the less variable control condition, possibly because water availability was limiting the growth and establishment processes which are affected by microhabitat heterogeneity. Adding water to the experimental group could have removed this water limitation, allowing microhabitat to exert effects. Another possibility is that mist was not added to the experimental condition often enough to mimic natural conditions of intense mist. Wet, misty days in the cloud forests in Monteverde are characterized by mist deposition for a period of hours; mist

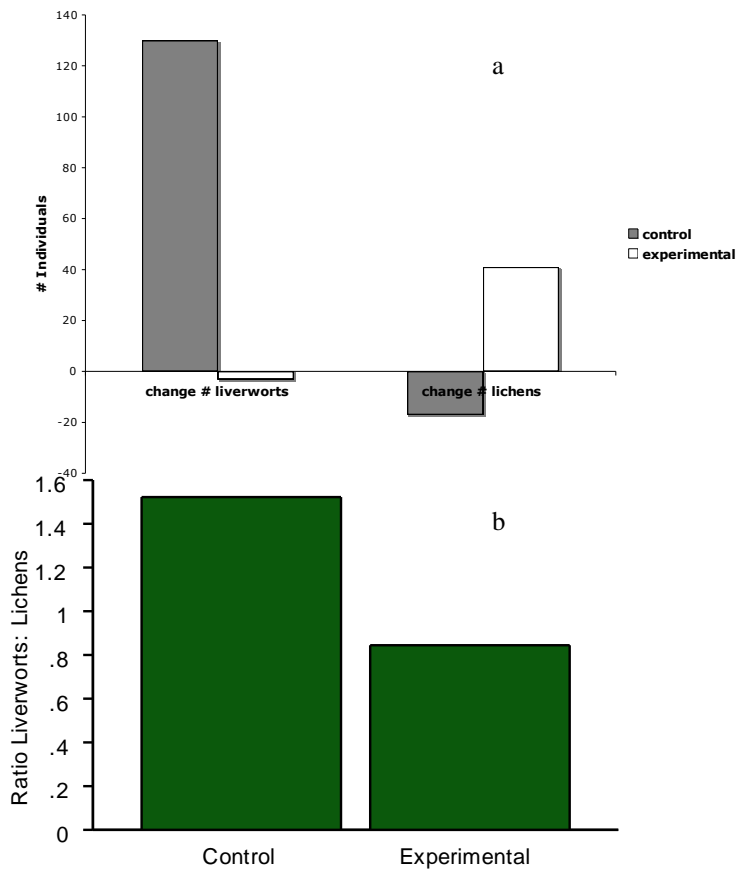


Figure 4. Differential change in number of individuals across taxa, summed for each condition (a). Ratio of Liverworts to Lichens for the final measurements on May 8th (b).

does not naturally deposit moisture in two distinct bursts throughout the day. Furthermore, epiphylls probably do not respond solely to mist, but are also affected by temperature and light availability. This reduces the plausibility of the use of epiphylls as a bioindicator of changes in mist conditions.

More than simple measurements of percent epiphyll cover, the ratio of liverwort to lichen abundance on palm fronds shows promise as a bioindicator of mist conditions in tropical cloud forests. The drier, less frequently misted fronds of the control condition had more liverworts than lichens, and therefore had a liverwort: lichen ratio that was greater than one. The wetter, more frequently misted fronds of the experimental condition were just the opposite, with a liverwort: lichen ratio that was less than one. Thus, it appears that mist frequency is controlling this ratio, which possibly provides us with an easy-to-measure parameter with which to indirectly compare mist frequencies across sites.

The differential success of liverworts to lichens is, however, seemingly at-odds with previous research. Olarinmoye (1974) demonstrated a higher growth rate of epiphyllous liverworts at wetter sites and during wetter periods in western Nigeria, suggesting that adding water should have benefited liverworts in the experimental group. Perhaps adding water in this way pushed the liverworts in this study over a threshold of water tolerance not reached in western Nigeria. Species-specific responses to water could also explain this discrepancy. The differential success by taxa also seemingly contradicts results obtained by Coley et al. (1993) who demonstrated that experimentally adding water increased the cover of epiphyllous liverworts and decreased the cover of epiphyllous lichens in low to mid-elevation tropical Panamanian forests. This makes biological sense, as lichens are known to tolerate drying out periodically (Brodo et al. 2001), whereas bryophytes are less capable of tolerating drought stress (Schofield 1985, Coxson 1991, cited in Benzing 1998).

These studies, combined with the highly variable growth responses observed in the current study, reduce the plausibility of using epiphylls as bioindicators of changing mist conditions. While the liverwort to lichen ratio shows a degree of promise in this regard, it is also possible that variation in this ratio will make informative surveys impossible without large sample sizes.

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