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Palm Epiphyll Cover Shifts to Higher Elevations in Tropical Cloud Forest, Indicating Local Climate Change

by Maya Spaur
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ABSTRACT:

Intensifying patterns of weather and climate as caused by anthropogenic climate change have already caused extensive species extinctions, migrations, and range contractions in endemic species (Parmesan 2006), and pose the potential to induce substantial biodiversity loss on a global scale (IPCC 2014). Such trends have proven exceptionally apparent in tropical montane forests, where the disappearance of range-restricted species indicates a lifting cloud base as caused by rising sea surface temperature (SST) (Pounds et al.1999). Epiphylls serve as a bioindicator of local climate change due to their heightened sensitivity to water availability (Drake 2005). An altitudinal transect of percent epiphyll cover was performed on *Geonoma* palms to study how epiphyllous distribution has changed over the last ten years, replicating Drake's (2005) methods. Decades of increasingly severe local drying caused a significant difference in epiphyll cover and strengthened the negative relationship between altitude and percent epiphyll cover. As climate change increases SSTs and propels moisture up mountains, epiphylls serve as an indication of what to expect in the very near future, where species disappear at lower elevations and follow the lifting cloud bank upwards.

INTRODUCTION

Global climate change has triggered alterations unparalleled in recent history on natural habitats worldwide. Anthropogenic activities have exacerbated historical patterns of global warming, in which rising sea surface temperatures (SSTs) now stimulate augmented evaporation and production of water vapor (Pounds et al.1999). When increased amounts of water vapor condense, atmospheric warming advances more rapidly, propelling widespread, long-lasting, and significant change to the local climate of terrestrial ecosystems (Pounds et al.1999). Though local climate patterns vary with elevation, climate change has unequivocally caused global atmospheric and oceanic warming; increased and more frequent warm temperature extremes; fewer cold temperature extremes; more frequent, more extreme weather events; greater seasonality; and nonuniform precipitation changes (IPCC 2014). The effects of climate change are exacerbated in the tropics, which contain the highest terrestrial plant and animal species richness and biodiversity on the planet, and relatively high endemism (Brown 2014). Many species thrive within a narrow range of ideal abiotic conditions and cannot survive in temperature and seasonality extremes that exceed or fall below those limits (Brown 2014). Average annual temperature in the Caribbean has increased 0.5°C, and projections anticipate even drier weather patterns will occur based on convection zones and rain patterns over the last 15 years (Olaya 2009). Climate change has already pushed climate and weather patterns outside of range-restricted species' tolerable ranges, a trend amplified at high elevations on tropical mountains (Pounds 1999). Climate change has forced many terrestrial species to shift their

geographical ranges (IPCC 2014). The lifting-cloud-base hypothesis explores the negative relationship between rising SSTs induced by anthropogenic climate change, and patterns of dry season mist frequency on tropical mountains. The striking increase in SSTs correlates with the decline in dry season mist frequency since the mid-1970's. Rising temperatures and decreased moisture at lower elevations propel moisture upwards and raise average altitude of the orographic cloud bank base (Pounds et al.1999).

Such trends towards desiccation may influence the phenology, abundance, and distribution of tropical plants that thrive in or rely upon consistently wet conditions. In tropical montane cloud forests, changes in local drying patterns and dry-season mist frequency have been observed over the past few decades, exacerbating extinction rates of endemic species and causing species to shift their local ranges to higher elevations (Pounds et al.1999). Increases in local drying, quantified by the number of long dry runs of five or more continuous days, serve as an important stimulant for the upward migration or even extinction of certain plants. Though annual, seasonal, and monthly precipitation in Monteverde does not show significant trends from 1973 to present, dry days have increased significantly in frequency and converge increasingly into runs, from 5 to 16 continuously dry days (Pounds et al.1999).

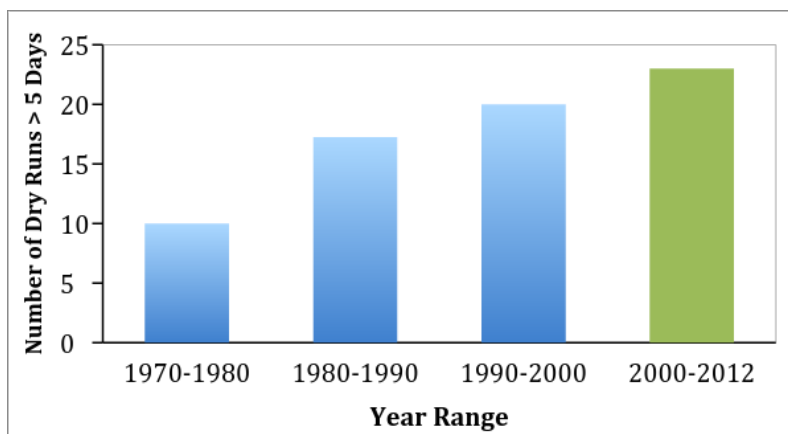


Figure 1. Number of extended dry runs of five days of more per decade from 1970 to 2012 in Monteverde Cloud Forest Preserve, Puntarenas, Costa Rica. Number of long dry runs has more than doubled since 1970, and can be attributed to local drying induced by climate change. Source: Alan Pounds (personal communication).

Epiphylls have shown promise as bioindicators of local mist and climate conditions in tropical montane forests in Costa Rica (Drake 2005). Data has shown that epiphytes inhabit climate-defined ecospace that encompass a narrower range of abiotic conditions in comparison to co-occurring species, such as the supporting tree. The unique mechanistic characteristics of epiphytes and reliance on near-constant precipitation render them particularly sensitive to changes in climate, particularly drying (Benzing 1998) and a decline in dry season mist frequency (Drake 2005). Nonvascular epiphylls lose moisture and capacity to perform photosynthesis promptly in dry atmospheric conditions; furthermore, their positive carbon budgets necessitate continual high humidity and persistent moisture (Benzing 1998). Epiphytes also play an integral role in influencing nearby biota and system processes, such as energetics,

hydrology, and mineral cycling. Epiphytes possess the unique capacity to indicate from an early stage the effects of climate change on tropical montane forests (Benzing 1998).

In comparison to nutrient and light availability, water supply has the strongest influence on epiphyll growth and proves the most limiting growth factor. Improved water supply increased relative growth rate (RGR) for all sizes of vascular epiphylls, and small and intermediate-sized bromeliad epiphylls demonstrated significant correlation between in situ growth rate and annual precipitation (Laube and Lotz 2003). This trend would be exaggerated for nonvascular epiphytes, as their growth is more restricted to a consistently wet environment. Increasingly, continual wetness is found only at higher elevations along tropical mountain ranges (Pounds et al. 1999), when Montane Wet Forest transitions to Rain Forest. Thus, past studies would support the prediction that epiphylls will be found at increasingly higher altitudes within the cloud bank, and will be more susceptible to extremes in growth limiting factors at lower elevations, below the lifting cloud base. With the establishment of epiphyll cover as a bioindicator of climate change (Drake 2005), this study seeks to record the changes in epiphyll cover across an altitudinal gradient over the past ten years. This study investigates if decades of increasingly severe, climate change-induced local drying caused significant upward shifts in epiphyll cover on a Costa Rican montane cloud forest.

MATERIALS AND METHODS

Study Site

Data were collected at seven different altitudinal zone ranges along the principal trail at the Estación Biológica in Monteverde, Puntarenas, Costa Rica (10°18' N, 84°48' W). This site is classified as Lower Montane Wet Forest from 1450 to 1600 m, and Lower Montane Rain Forest from 1550 to 1850 m (Bolaños and Watson 1993, in Haber 2000). Lower Montane Wet Forest receives mean annual rainfall 1850-4000 mm, with mean annual temperature 12 to 17°C and canopy height 25 to 35 m. Lower Montane Rain Forest receives mean annual rainfall 3600-8000 mm, with mean annual temperature 12 to 17°C and canopy height 20 to 30 m. The dry season lasts for 0 to 3 months for both life zones (Haber 2000). Altitudinal transects were performed between 1505 and 1817 m elevation during the wet season, from July 15th to July 30th, 2015. Though this study occurred during an El Niño, data indicate it was weak in strength and did not have significant or widespread effects on global climate and weather patterns (NOAA 2015). The methods for this study replicated Drake's (2005) experimental design to enable accurate analysis of epiphyll cover change over time.

Study Organism

Epiphyll cover was obtained from 186 *Geonoma spp.* (Araceae); identification did not discriminate between species of *Geonoma* as field guides did not lend comprehensive guidance on species composition within Monteverde cloud forest. An average of 26.6 *Geonoma* palms were analyzed for each altitudinal zone, centering around 50m increments from 1500 to 1800m elevation.

Altitudinal Transect of Epiphyll Cover on *Geonoma spp.* Palms

Leaflets were selected based on a simple visual analysis of epiphyll cover distribution. The youngest leaflets were located higher on each palm, and the older leaflets were lower, closer to the ground. To control for height and age, in which it may be assumed that older fronds provide greater time for epiphyll colonization than younger fronds, selection favored the middle leaflet or leaflet that best represented average epiphyll cover. A fine chicken wire grid was placed over an area of the leaflet that demonstrated the palm's average epiphyll cover, and a digital picture was taken 30 cm away. Altitude and proportional rank, the ratio of frond number to total number of fronds, were recorded.

Frond number is calculated by counting from newest, topmost frond to selected frond. The following equation, as stipulated by Drake (2005), ascertains frond age to account for time available for epiphyll colonization. Age (in weeks) = $-1.43 + (\text{proportional rank} * 83.6)$ (Daniels 1998).

Digital pictures were analyzed on a computer to quantify percent epiphyll cover for 25 grid cells. A cell demonstrated significant epiphyll cover if epiphyll growth covered at least one third of the cell. Percent cover constitutes the area occupied by epiphylls (the number of cells with significant epiphyll growth) divided by the total area (25 cells) sampled.

Additional Observations Though the majority of *Geonoma* palms surveyed were trunkless, six palms surveyed at higher altitudinal zones contained trunks and one trunked palm in the lowest altitudinal zone was noted.

RESULTS

Altitudinal Transect

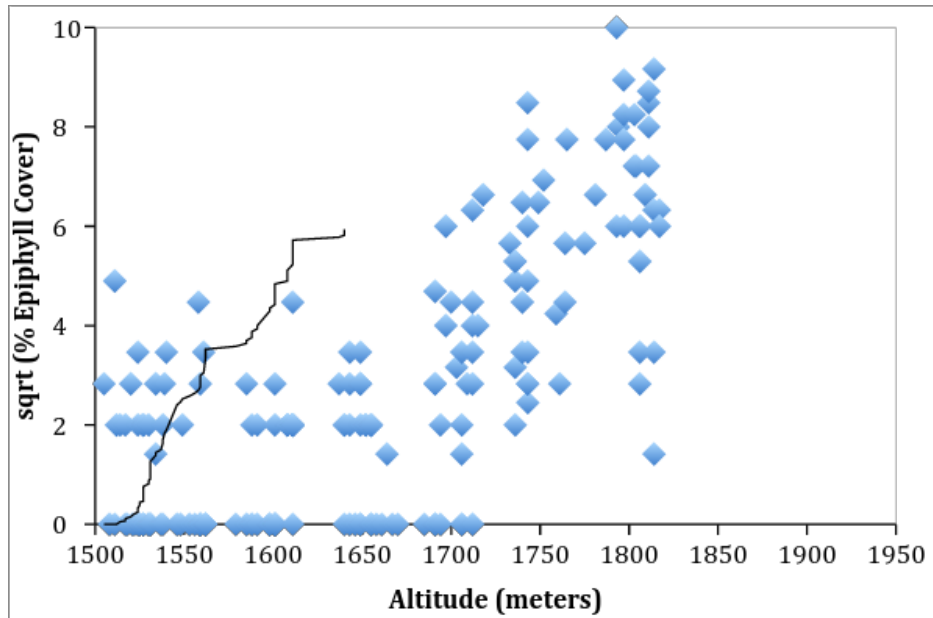


Figure 2. Square root of percent epiphyll cover on *Geonoma spp.* to altitude (meters). Epiphyll cover was calculated by number of cells with significant epiphyll coverage (at least one third of cell covered) divided by total area (25 cells) using a fine chicken wire grid. $N = 186$. $Y = 0.0196x - 29.713$. $R^2 = 0.52316$. As altitude increased, epiphyll cover on *Geonoma spp.* palms increased significantly with $p < 0.05$.

Square root of percent epiphyll cover increased significantly (ANOVA, $p < 0.05$; d.f. = 1; $F = 202.96814$) with increasing altitude, as demonstrated above in a linear regression. In subsequently higher altitudinal zones, a higher proportion of *Geonoma spp.* palms exhibited more epiphyll coverage. A stronger R^2 was found for this data, (Regression, $R^2 = 0.52316$), than quantified for Drake (2005) data (Regression, $R^2 = 0.49698$).

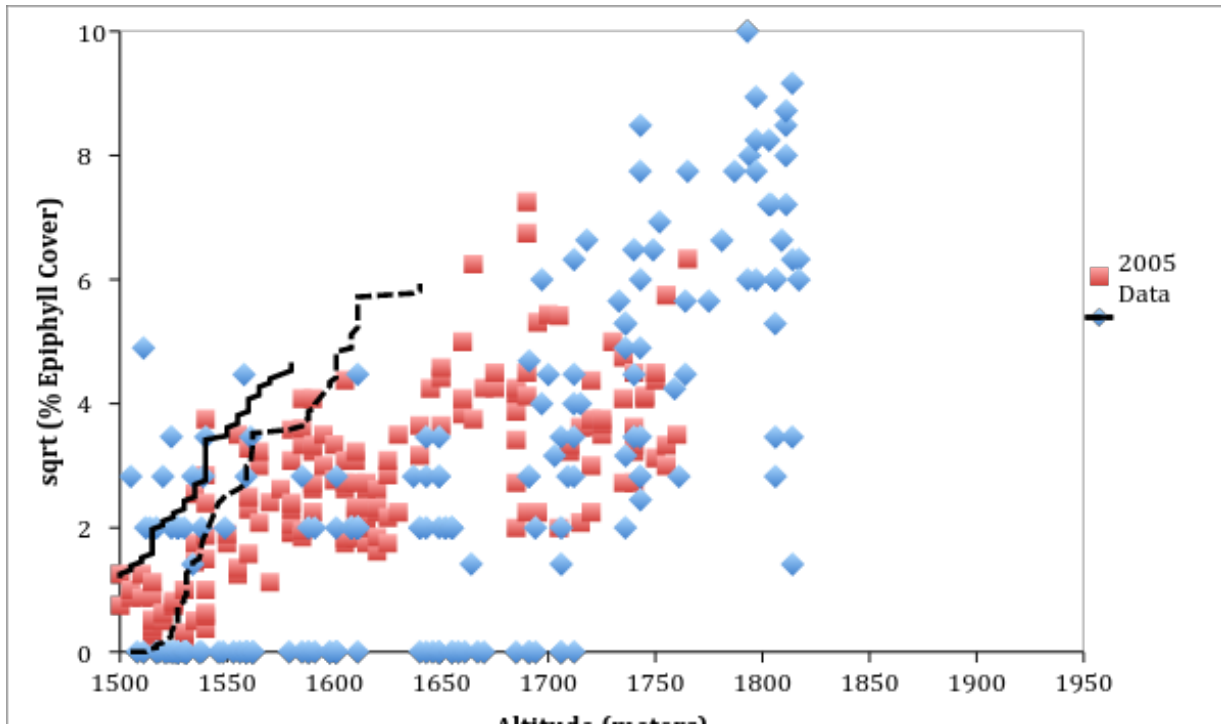


Figure 3. Square root of percent epiphyll cover on *Geonoma spp.* to altitude (meters), comparison between Drake (2005) data in red versus data collected from this study in blue. Solid line represents the linear trendline for Drake data, $N = 160$. $Y = 0.0131x - 18.483$. $R^2 = 0.49698$. Drake Figure 2 (2005) was printed and manually analyzed to obtain data points. Dashed line represents linear trendline for 2015 data, $N = 186$. $Y = 0.0196x - 29.713$. $R^2 = 0.52316$. Slopes were significantly different (ANOVA).

Lower altitudes contained greater percent epiphyll cover in 2005 than at present. Over the past ten years, the slope of the linear relationship between percent epiphyll cover and altitude has increased/ grown steeper, as the 2005 slope of $.0131 < 2015$ slope of 0.0196 . Though both Drake (2005) and this study found significant results in the linear relationship (Drake found $p < 0.0001$), R^2 increased from 2005 to present data. The data manually obtained from a print of Drake's Figure 2 lent an $R^2 = 0.49698$, but Drake (2005) reported an $R^2 = 0.517$. As this study found a stronger R^2 (Regression, $R^2 = 0.52316$) the difference between slopes and linear regressions is significant (ANOVA).

spp. palms with a stronger regression and slope (ANOVA Test) than ascertained in 2005 (Drake 2005). While epiphylls are increasingly found at higher altitudinal zones within tropical cloud forests, they have largely disappeared from lower elevations. The upslope migration of epiphylls to higher altitudes with consistently cooler, wetter climates was supported by the significant difference in linear regression slopes from 2005 to today (ANOVA Test). This trend may be attributed to local drying and decline in dry season mist frequency as stipulated by the lifting-cloud-base hypothesis (Pounds et al.1999). Weather data reporting the more than twofold increase in number of extended dry runs in Monteverde Cloud Forest Preserve from 1970 to 2012 reinforces the long-term trends of local climate desiccation as caused by rising SSTs (Figure 1).

This study reinforces the conclusions drawn in other studies regarding both the lifting-cloud-base hypothesis and percent epiphyll cover as a bioindicator of climate change, based on nonvascular epiphylls' unique vulnerability to fluctuations in climate patterns. Past studies show that water availability represents the most limiting factor for epiphyll growth; as dry season mist frequency declines with increasing number of dry days and continuous dry runs, water becomes less available to nonvascular epiphylls. The results for this study suggest that the intensification of local drying conditions over the past ten years have stripped the lower altitudinal zones of adequate moisture to support nonvascular epiphyll growth on *Geonoma* palms.

Potential Limitations

An interesting point to consider is the discrepancy between Drake's (2005) measurements, taken from 1490 to 1765 m along the principal trail, to this study site from 1505 to 1817 m. Though the data for this study start and end at higher elevations, the slope would remain consistent if limited to 1765 m. Additionally, Drake's (2005) data did not report any zero epiphyll coverage. As Drake's (2005) methods do not indicate preference for selecting only *Geonoma* palms with epiphyll cover, it would be assumed that Drake did not encounter any palms lacking epiphylls to obtain an unbiased sample.

Another limitation involves the difficulty in differentiating between *Geonoma spp.* and *Calypstrogyne spp.*, an understory palm highly similar in appearance and often found to occupy the same area as *Geonoma* palms. A comprehensive analysis of the physical attributes and differences between each genus was conducted to ensure correct identification in the field. As field guides did not provide information on the two species of *Geonoma* studied by Drake, *G. eludis* and *G. hoffmaniana*, this study did not attempt to discriminate between *Geonoma* palms on a species level and only identified to the genus. As Drake (2005) did not find significant difference in percent cover between *G. eludis* and *G. hoffmaniana*, his findings did not separate between host species and were reported to the genus level. This enabled accurate comparison of data at the genus level, however a degree of uncertainty remains regarding accurate distinction between *Geonoma* versus *Calypstrogyne* palms.

To control for the effects of frond age on epiphyll percent cover, a linear regression of fronds between 35 to 45 weeks old was run, excluding all other data. The average age of those fronds equaled 39.8 weeks. As Drake (2005) selected for fronds closest to 40 weeks in age, the linear regression confirmed that the total data, ranging from 12.503 to 82.17 weeks old, did not have a significantly different slope from the control data (ANOVA, $p = .8788$). Hence, frond age did not significantly affect the negative relationship between altitude and epiphyll cover and

comparison of total data versus Drake (2005) data remains valid (ANOVA). Despite limitations, the methods for this study constitute a reliable way of measuring the change in percent epiphyll cover over seven altitudinal zones from 2005 to present.

Further Research

To account for the effect of gap dynamics and canopy height on sun exposure variation and light availability for photosynthesis, future research might compare epiphyll relative growth rates (RGR) in sun versus shade. Past growth experiments conducted in Panamanian tropical moist forest have proved ambiguous on vascular epiphyte RGR in different light conditions, favoring analysis of water availability as the most important attribute and the effects of nutrient availability dependent on water supply (Laube and Lotz 2003). Despite prominent self-shading, Laube and Lotz (2003) unexpectedly found that increased light caused a decrease in RGR but difference was not significant. High vapor pressure deficits induced under high light conditions cause stomata to partially close, decreasing RGR. Further studies expanding on Laube and Lotz's (2003) research might discern whether *Geonoma spp.* demonstrate the same trends as *Vriesea sanguinolenta*, a tank-forming bromeliad. As canopy height in the Monteverde cloud forest decreases transitioning from the Montane Wet Forest to the Montane Rain Forest (Haber 2000), epiphylls may also receive greater sun exposure at higher elevations.

Seasonal variation in precipitation and mist frequency might also play a significant role in epiphyll growth. As Drake (2005) collected data during the end of the dry season from April to May, reduced precipitation and other weather variables characteristic of the dry season differ markedly from conditions during the wet season. This study, conducted in the wet season during latter half of July, was based on long-scale local drying trends spanning decades, negating the impact of seasonal or year-to-year variations in weather patterns. Further research would replicate the methods performed for the altitudinal transect during the dry season, to ascertain if linear relationship for upward migration proves equivalent or significantly different during the dry season versus wet season.

Current climate change projections predict that SSTs will continue to warm, and the strongest warming will be observed in tropical and Northern Hemisphere subtropical regions (IPCC 2014). As warming is predicted to affect precipitation patterns differently around the globe, future studies would ascertain whether patterns of intensified local drying continue in the Monteverde Cloud Forest Preserve, of conditions in comparison to the Estación Biológica, and whether the negative relationship grows stronger if the highest radiative forcing scenario (RF 8.5) proves accurate (IPCC 2014).

Conclusion

Overall, this study demonstrates the significant shift in epiphyll cover on *Geonoma* palms to higher elevations in the Monteverde cloud forest over the past ten years. This study suggests that the lifting cloud base, as caused by rising SSTs and local drying due to climate change, promotes this trend and will exacerbate decline in epiphyll cover at increasingly higher altitudes in future years.

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