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The effects of rainfall and seasonality on epiphyte community composition

Introduction:

Tropical forests cover only seven percent of the world's land area, yet they contain 50 to 80 percent of the world's plant species. Given that accelerating rates of tropical deforestation are threatening these ecosystems, it is important to be able to recognize biodiversity hotspots in order to develop effective conservation policies. However, in many developing countries it is often difficult to take complete biodiversity inventories; therefore it is necessary to develop taxon-based mapping methodologies that allow us to predict biodiversity patterns based on abiotic factors such as climate and altitude (Müller *et al*. 2003).

It has always been a puzzle to scientists as to why the tropics can maintain such high levels of diversity. Part of the answer may lie in how the tropics are able to support extensive and diverse epiphytic communities because unlike temperate forests, neo-tropical rainforests have a vast amount of their biodiversity in epiphytic forms. Epiphytes are very sensitive to microclimate and disturbance and serve as good indicators for forestry management practices (Hietz 1998). Studying factors that affect epiphyte community composition and distribution should therefore allow us to make broader predictions about biodiversity.

In a study of vascular epiphytes in Western Amazonia, Kreft et al. (2004) found that climatic patterns of high annual rainfall and low seasonality were strongly correlated with high species richness. However, less is known about the interaction between rainfall and seasonality and which of these two climatic factors is more important in determining levels of species richness. Benzing (1998) suggests that areas that receive heavy but unevenly distributed rainfall are more likely to have smaller and less diverse epiphyte communities than areas with less total but more evenly distributed rainfall. More empirical evidence will enable us to create methodologies to more accurately predict biodiversity patterns based on climatic factors. This will also allow us to better determine how climate change, manifested as shifts in patterns of annual and seasonal rainfall, will affect the composition of tropical epiphyte communities (Benzing 1998).

In this study, we will explore how rainfall and seasonality interact to influence biodiversity by comparing the epiphyte community composition of two sites in Costa Rica, with different amounts of annual rainfall and varying dry season lengths. La Selva Biological Station has on average higher total rainfall but a more pronounced dry season than Sirena National Park (OTS/OET 2004, Vega 2005). Studying these sites allows us to test the model Benzing (1998) suggested – that rainfall, specifically its consistency throughout the year, is one of the greatest limiting factors on epiphyte diversity.

Our working hypotheses:

- La Selva will have higher total epiphyte diversity than Sirena as measured by number of phylogenetic groups.
    - $H_{\varnothing}$: There is no difference between the total number of epiphytic phylogenetic groups found at La Selva and Sirena
    - H_{A1}: Total number of epiphytic phylogenetic groups found at La Selva will be more than the number found at Sirena
    - H_{A2}: Total number of epiphytic phylogenetic groups found at La Selva will be less than the number found at Sirena
- Sirena will show a greater dominance of drought-adapted morphological forms than La Selva as measured by percent coverage within the epiphyte community.
    - $H_{\varnothing}$: There is no difference between the percent coverage of drought-adapted morphological forms within the epiphyte communities at La Selva and Sirena

- H_{A1}: Relative percent coverage of drought-adapted morphological forms within the epiphyte community at La Selva will be less than the relative coverage at Sirena
- H_{A2}: Relative percent coverage of drought-adapted morphological forms within the epiphyte community at La Selva will be more than the relative coverage at Sirena

Background on Proposed System:

Epiphytes: Epiphytes comprise 10 percent of all vascular plant species on Earth and might be the most species-rich life form in certain humid tropical areas (Hietz 1998). These commensalists use living hosts as substrates for growth, without parasitizing their host. While epiphytes present little benefit to their host directly, in many areas they provide valuable ecosystem services such as nitrogen fixation (Bermudes and Benzing 1991), rainfall interception and moisture retention (Andrade and Nobel 1997, Hoelscher *et al.* 2004). Additionally, tropical epiphytic communities increase the mineral and carbon storage capacity of the forests (Nadkarni 1984) and provide a source of substrate and food for many animal species (Hietz 1998, Benzing 1998).

Beyond these important ecological services recently there has been much interest in studying these communities as biological indicators. Epiphyte communities are very sensitive to changes in atmosphere and climate (Nadkarni, Wheelwright 2000) and are expected to be the first communities to show drastic responses to impending climate change (Gignac 2001, Nadkarni, Solano 2002). Already they have been used to indicate increasing levels of atmospheric pollution, as tools in forestry management and to recognize other anthropogenic changes to ecosystems (Benzing, Arditti et al. 1992, Garcia, Nash et al. 2000, Hauck 2003, Hietz 1998).

Thus epiphyte communities are excellent study systems to use to explore the forces affecting biodiversity maintenance. They represent a large portion of the world's biodiversity, provide valuable ecological services and with only slight changes in moisture availability or seasonality, they demonstrate recognizable changes in their community composition (Gignac 2001). For these reasons it is important to understand the factors that maintain these communities as they become increasingly threatened by anthropogenic changes. Furthermore, studying factors that affect epiphyte community composition and distribution therefore should allow us to make broader predictions about biodiversity.

Study sites: In this project, we plan to compare epiphyte communities between the La Selva and Sirena field sites in Costa Rica. These sites were chosen for this study because despite their high overall levels of annual rainfall, they have markedly different seasonal patterns (Table 1). This will potentially allow us to examine whether rainfall or seasonality is a more important factor in determining epiphyte diversity across habitats.

	Rainfall (mm)	
Month	**La Selva**	**Sirena**
January	353.3	176
February	257.8	26.3
March	137.7	82.4
April	240	200.9
May	521.9	505.6
June	543	616.5
July	528	505.5
August	481.8	594.7
September	276.8	767.7
October	366.5	914.6
November	435.5	819.7
December	532.4	357.6
Total	4674.6	5567.4

Table 1. Monthly rainfall totals for La Selva and Sirena field sites, averaged from 2000 to 2005. Sirena has a higher annual rainfall total, but a more pronounced dry season as evidenced by the rainfall totals for the months of February and March. **(Adapted by Orians from OTS/OET 2004, Vega 2005)**

Aside from having contrasting seasonal patterns, several other features of the La Selva and Sirena field sites make them appropriate for a comparative study of epiphyte biodiversity. Much of the literature about epiphyte communities examines how epiphyte distribution varies over broad geographical patterns and does not separate seasonality from its correlating altitudinal gradients (Benzing 1984, Cardelus, Benzing 1998, Kreft, Koester et al. 2004). On the other hand, La Selva and Sirena both have similar and constant elevations; Sirena is at sea level and La Selva is 30 m above sea level (OTS/OET 2004, Vega 2005). Therefore these two sites allow us to control for altitude as a factor influencing epiphyte community composition.

Furthermore, these two sites offer a choice of overlapping host tree species (Janzen 1983). By focusing on a single host species common to both La Selva and Sirena study sites, we can control for host species type as we compare epiphyte diversity across the two habitats.

Methods:

Our strategy for testing our two hypotheses is as follows. We will randomly select a subset of host trees, controlling for host species, host size/age and distance from trail/edge, and survey the epiphyte communities upon those selected trees controlling for ordinal direction. We will then count the number of phyla/families present (hypothesis 1) and estimate the percent coverage of each phylogentic group (hypothesis 2). Finally, we will analyze the data first using the Simpson's index of diversity to compute richness and percent cover into an index of diversity. Then we will compare the two sites using a similarity index (hypothesis 1) and an unpaired two-tailed t-test (hypothesis 2).

Host Tree Selection: In order to isolate the effects of seasonality on the epiphyte communities in these two sites, our aim is to collect a random sample that also controls for factors that affect epiphyte diversity from tree to tree rather than between sites. To this end we plan to randomly establish five 50 m transects at both study sites and to sample within 1 m of each transect. The transect location will be chosen by overlaying a grid on the site map and using a random numbers table to establish coordinates within that grid for the starting point.

Since lack of canopy cover has been shown to decrease the diversity of epiphytes within continuous forest stands (Kueper, Kreft et al. 2004, Mills, Macdonald 2004, Wolf 2003), we want to exclude the effects of reduced localized canopy cover. Therefore all points within 2 meters of the trail or forest edge will be excluded. Furthermore, it has been shown that the host species type can dramatically affect epiphyte communities, both in composition and in coverage (Gonzalez-Mancebo, Losada-Lima et al. 2003, Merwin, Rentmeester et al. 2003), so we want to control for both the type of host and its age. To this end we will survey only tree ferns (Cyatheaceae *sensu latu*) with diameters greater than 10 cm that fall along the transects. Tree ferns are known to carry a high diversity of epiphytes (Moran, Klimas et al. 2003) are sub-canopy trees and are found at both sites (Janzen 1983).

Survey of Epiphyte Communities: These surveys are intended to show a general measure of genetic diversity and morphological diversity. As the ordinal orientation of the host species can also affect the microclimate of the community and thus its diversity, we must control for ordinal direction as well as vertical placement and size of our survey plots. There are two basic methods to accomplish this. One is to choose one direction and survey in a vertical band on that side of the host tree. Alternately, one could survey a horizontal band around the main vertical stem, thereby including all ordinal directions. We plan to use the latter method, but this may be changed on site in order to maximize our sample size. For each tree we will characterize the epiphyte communities by surveying a 0.5 meter band centered at breast height around the circumference of the host. To establish community dominance, percent cover will be ranked for each phylogenetic group in 0.25 m wide sections at a time, using a 2x2 cm grid as a reference. Finally, we will estimate canopy cover by taking a light reading as an internal control for the effects of light availability.

Diversity: To test our first hypothesis, we will record all families of vascular plants and phyla of non-vascular plants observed within the study plot. We will record the overall percent epiphyte coverage, the number of phylogenetic groups observed, and the number of morphological forms observed. We will separate the morphological groups based solely on drought adaptive traits, there could be several ways of separating these groups, but the key is that they do not necessarily represent genetic similarity but a common selection pressure. So that groups that may be evolutionarily separate may converge to similar morphology. Conversely species related more closely to one another may have different morphological types based on selection pressures. While phylogenetic groups give us an indication of genetic diversity looking also at morphological types allows us to understand the selection pressures.

Percent Cover: To test our second hypothesis we will follow the same methodology, this time recording the number and percent coverage of drought adapted morphological forms and the percent coverage of vascular vs. non-vascular epiphytes. Drought adapted morphological form categories include spongy, tough, reduced leaf area, and heavy cuticles, and other traits established on site.

Data analysis: Since our purpose is to compare diversity and understand which climatic patterns influence this diversity we need to first convert the richness and percent cover data into a measure of diversity. Then we would like to know if the biodiversity index, the richness and total epiphyte cover or relative categorical representation at each site are significantly different. Transects will be summed and then the total percentage of each transect will be used as separate replicates. We will use the Simpson's index which measures both total richness and weights that by the percent representation of each category (Table 2). This is a good index for small sample sizes, and is simple to use with the information that we have collected. Then to compare the two sites we will use a similarity index which compares both richness and evenness. Then we will use two-tailed unpaired t-tests to look at differences the total percent cover and relative categorical representation, because we are looking between two groups, and do not have one-one matching pairs. To increase our ability to detect differences in each direction we chose the two-tailed t-test.

Table 2. The formula for calculating **Simpson's Index** (**D**), a measure of the probability that two individuals randomly selected from a sample will belong to the same category The value of **D** ranges between 0 and 1 (http://www.countrysideinfo.co.uk/simpsons.htm)

$D = \Sigma (n / N)^2$	$D = \frac{\Sigma\, n(n-1)}{N(N-1)}$
n = the total number of organisms of a particular species **N = the total number of organisms of all species**	

Predicted Results: We expect to find a greater number of epiphytic phylogenetic groups and greater total epiphyte coverage on the tree ferns in La Selva than in Sirena. This would support our hypothesis that although Sirena has greater total rainfall, its more pronounced dry season will have a stronger effect on limiting biodiversity. If the dry season is limiting the growth in Sirena, we would also expect to see a higher relative percent cover of drought adapted morphological forms at that study site. This would indicate that the reduction in biodiversity was at the cost of drought sensitive species. In general it will be interesting to see how these two factors combine to influence epiphyte biodiversity (Table 3). Even if no difference was found in total biodiversity but the relative abundance/coverage of drought-adapted forms was significantly different across study sites, this might indicate that drought-adapted forms are getting out-competed in the high rainfall, low seasonality system of La Selva. If no difference was found in either measure, this might indicate that the rainfall and seasonality factors are of equal importance and the opposite trends are actually canceling one another out, or that the 2 month “dry season” is not long enough to show pronounced limitations on biodiversity. Finally, if the outcomes were the opposite of our expectations, then it would seem to indicate that absolute rainfall is the greater limiting factor for epiphyte biodiversity.

Table 3. Various combinations of total species richness and the relative percent cover of drought adapted morphological types between La Selva and Sirena can be explained by assigning different levels of importance to climatic factors of rainfall and seasonality.

Total Richness	% Drought Morphology	Explanation
La Selva > Sirena	La Selva < Sirena	Seasonality is the limiting factor to biodiversity
No difference	La Selva < Sirena	Seasonality is the limiting climatic factor, but drought adapted forms are being out-competed by non-drought adapted forms in La Selva, thus there is no net different in diversity
No difference	No difference	Rainfall and seasonality are of equal importance -or- The dry season is not long enough to have a significant impact on diversity
No difference	La Selva < Sirena	Rainfall is the limiting climatic factor, but drought adapted forms are being out-competed in Sirena, thus there is no net difference in diversity
La Selva < Sirena	La Selva > Sirena	Rainfall is the limiting climatic factor

Significance: There have been many attempts to explain the immense biodiversity of epiphytes in the tropics (Barthlott *et al.* 2001; Benzing 1984; Cardelus 2002; Kroemer *et al.* 2004; Kueper *et al.* 2004, Monneveux and Belhassen 1996, Kreft *et al.* 2004). It has been supposed that high rainfall and low seasonality contribute to the high biodiversity of tropical epiphyte communities (Kreft *et al.* 2004). Furthermore, global biogeographical patterns indicate that it is in fact seasonality that most greatly affects biodiversity patterns. By comparing two sites that resemble each other in altitude, host species and canopy cover but show opposing trends in rainfall and seasonality, we are able to ask questions that isolate the importance of the latter two factors in contributing to the diversity of Costa Rica's epiphyte communities.

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