June 2006

Effects of weevil parasitismo n a Cecropia-Azteca mutualism

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Testing the Unified Neutral Theory using the epiphylls of *Geonoma spp.* (Arecaceae) as model communities

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ABSTRACT

This experiment tests the predictions of the Unified Neutral Theory of Ecology (Hubbell 2001) using epiphylls on leaves of the palm tree *Geonoma spp.* (Arecaceae) as local communities. The metacommunity is defined as the collection of leaves of one palm tree. The UNT assumes all species to be competitively equivalent and population sizes to remain constant overtime. It also asserts that community drift is strong and that for diversity to exist there must be factors that slow its progress. The UNT predicts that increases in connectivity of the metacommunity, community area, population size of local and metacommunities, as well as metacommunity area should slow the rate of community drift and favor increased species richness. The UNT also predicts that Dominance-Diversity relationships of each metacommunity will form a family of curves that will differ in slope in relation to differences in community richness, rates of immigration between communities, and community sizes. Data taken on the epiphyll richness of different *Geonoma spp.* leaves support predictions that community and metacommunity size are positively correlated with species richness. The data shows no evidence of the effects of connectivity or population size on species richness. The model communities provided Dominance-Diversity curves of which the slopes were negatively correlated with species richness, but community size had no significant effect. I found Hubbell's Unified Neutral Theory to be an insufficient model of epiphyll community richness and dominance on *Geonoma spp.* leaves in the cloud forest of Monteverde, Costa Rica.

RESUMEN

Esta investigación es un examen de las predicciones de la Teoría Neutral Unificada (UNT) de la Ecología (Hubbell 2001) usando epífilas en las hojas de la palma *Geonoma spp.* (Arecaceae) como comunidades locales. Se define metacomunidad como la colección de hojas de una palma. La UNT asume que todas las especies son competitivamente equivalentes y que el tamaño de la población permanece constante. También asume que la deriva de las comunidades es fuerte y que para que la diversidad sea posible deben existir factores que reduzcan su progreso. La UNT predice que los aumentos en las conexiones de la metacomunidad, el área de la comunidad, el tamaño de la población local y de las metacomunidades y el área de la metacomunidad debería reducir la tasa de deriva de communidades y favorecer el incremento de la riqueza de especies. La UNT también predice que las relaciones entre la dominancia y la diversidad de cada metacomunidad formará una familia de curvas que diferirá en pendiente en relación con las differencias en la riqueza de las especies, la tasa de inmigración entre las comunidades y el tamaño de las comunidades. Los datos sobre la riqueza de especies en diferentes hojas de *Geonoma spp.* apoyaron las predicciones de que el tamaño de las comunidades y de las metacomunidades está positivamente relacionado con la riqueza de especies. Los datos no muestan ninguna evidencía de los efectos ni de las conexiones ni del tamaño de la población sobre la riqueza de especies. Las comunidades modelo produjeron curvas de dominancia contra diversidad cuyas pendientes fueron negativamente correlacionadas con la riqueza de especies, pero el tamaño de la comunidad no tuvo un efecto significativo. Se concluye que la Teoría Neutral Unificada de Hubbell es un modelo insuficiente para describir la riqueza de especies y dominancia de epífilas en las hojas de *Geonoma spp.* en el bosque nuboso de Monteverde, Costa Rica.

INTRODUCTION

Biodiversity is regarded as one of the most valuable resources the natural world has to offer, a fact that is reflected in the choice and defense of conservation areas (Myers *et al.* 2000, Orme *et al.* 2005). Biodiversity has been shown to increase stability through its effect on productivity (Tilman, *et al.* 1996, Hector, *et al.* 1999) and protection against invaders (Naeem *et al.* 2000, Symstad *et al.* 2000). It is important to know how biodiversity is created and maintained in order to preserve it effectively. Hubbell (2001) posed an important stochastic theory, the Unified Neutral Theory, to explain patterns of biodiversity and community assembly. To test the UNT, I examined epiphyll communities on leaves of the palm *Geonoma spp.* (Arecaceae). I defined epiphylls as my ecological community. I delineated epiphylls on individual leaves of *Geonoma spp.* as local communities, and the collection epiphylls on an entire palm as a metacommunity.

The Unified Neutral Theory (UNT) assumes that all species have equal competitive abilities. This is an unrealistic assumption, and there have been many criticisms of this model with supporting data (Chave 2004, Harpole and Tilman 2006, Assaf 2005). However, in spite of its assumption, the model has successfully explained extensive experimental results (Hubbell 2001, Brown 2001). This disagreement in the literature provides reason for a small scale, straightforward test of the predictions of the UNT.

The UNT presumes that j and J, the total number of individuals in the local and metacommunity, respectively, never changes. That is, the birth rate plus immigration rate must equal the death rate plus emigration rate on both the local and community levels. From this, Hubbell (2001) states that every time an individual dies exactly one must replace it, and by competitive equivalence of species, it follows that chance will tend to choose a member of the abundant species to fill the hole more often than those of rare species. This leads, over time, to a new community where the abundant species are become increasingly abundant and the rare species become rarer. Continuing this pattern without allowing any immigration, emigration or speciation events, communities drift will cause communities to become monodominant, which is, composed of only one species. Hubbell (2001) terms this process the "random walk to extinction." In fact, natural communities hardly ever consist of one single species. To explain this apparent paradox, the UNT proposes that areas that have levels of high diversity must have mechanisms to slow down or counter the "random walk to extinction."

Specifically, the UNT makes five predictions for community assembly and diversity trends. (1) A higher level of connectivity between local communities will lead to greater local community species richness because of greater immigration rates, which counter the random walk by rescue effects. (2) A local community of greater area will provide room for more individuals, which slows the walk down and favors diversity. (3) A greater j or J, number of individuals in the local and metacommunities respectively will also decrease demographic stochasticity, thus reducing the rate of drift and favor diversity. (4) A larger metacommunity area will provide more opportunities for immigration and favor diversity. (5) The Dominance-Diversity curves produced from the collection of metacommunities will form a family of curves that will differ in slope. The slope of these curves should depend on rates of immigration, local community size, and metacommunity size. It is superficially predicted that these curves will have shallower slopes with increases in any one of these three factors.

I tested these five predictions of Hubbell's Unified Neutral Theory (2001) by examining the community of epiphylls on the leaves of individuals of the understory palm *Geonoma spp.* (Arecaceae). Epiphylls are photosynthetic organisms, usually bryophytes or lichens, which inhabit leaf surfaces (Zartman 2003). To epiphylls the forest is a sea of uninhabitable area with habitable leaves interspersed as islands of habitat. Epiphylls are dispersed by wind and water, and have no known herbivores or pathogens. The fact that their dispersal, colonization, survival and reproduction rely more heavily on chance than species interactions, like most plants and animals, makes epiphylls a good model community to test the effects of stochastic factors. *Geonoma spp.* provides a good substrate on which to observe patterns of epiphyll community composition because of the abundance of epiphylls, epiphyll diversity, and clearly defined and separated leaves that serve as convenient local communities (Figure 2) (Hooker 2002, Zuchowski 2005). For purposes here, the collection of leaves on one *Geonoma spp.* plant makes up a single metacommunity (Figure 1).

METHODS

Study Site and Sampling Criteria

To control potentially compounding environmental variables that may affect epiphyll communities, I sampled plants that were located, within a 200 meter radius, under approximately identical light conditions, and at the same elevation. I sampled the oldest two photosynthetically active leaves on each plant, because the UNT makes predictions about stable communities, not those going through succession. Older leaves were more likely to have older communities of epiphylls and thus more equilibrated communities. The oldest two leaves are the two leaves closest to the base of the tree.

I used palms from the Cerro Chomongo (1725 m) behind the Estación Biológica Monteverde, Monteverde, Costa Rica. The sample size included 42 leaves from 21 plants.

Data Collection

Local community species richness and diversity: Local community species richness of each leaf was calculated by subsampling an area of 20 cm^2 from one leaflet (Figure 2). I sampled the leaflet closest to the tip of the leaf that had a width between 1.6 and 3.2 cm at the base of the leaflet. The 20 cm^2 grid was located four centimeters from the base of the leaflet. I checked the 480 crosshairs of the grid for epiphyll presence and determined their morphospecies.

Prediction 1: Higher levels of community connectivity should lead to greater local community species richness. I measured the distance from the sampled leaves to their closest neighboring leaves. Specifically, I measured from the base of the sampled leaf blade to the base of the nearest leaf blade (See Figure 1).

Prediction 2: Increased local community area should increase local community richness. I made two measure of local community area. I measured both the length of the leaf blade, and also the "area" of the leaflet that was sampled to check for even finer scale effects (Figure 2). Leaf length is an approximation for area of the local community. This seems reasonable because most *Geonoma spp.* leaves have similar widths. Leaflet area is a measure of the microcommunity from which the diversity was sampled. It is an approximation, using the length of the leaflet multiplied by its width at the point of attachment, because *Geonoma spp.* leaflets are sigmoid shaped, this is most certainly an overestimate, but it is consistently so.

Prediction 3: Greater j and J should both independently lead to increases in local community species richness. J and j are the number of individuals in the local and metacommunities, respectively. It is difficult and time consuming both to determine individuals of epiphylls as well as count them on a plant that must support thousands. Instead, area was used as a proxy for number of individuals. Area of the epiphylls was estimated for each leaf on the plant. I used a scale of 1 unit = 5 cm^2 and took squares of 1, 5, and 10 units to help visually approximate the area of epiphylls on the leaves in the field.

Prediction 4: The area of the metacommunity should lead to an increase in species richness. To approximate metacommunity area, I measured both the plant height from the base of the tree to the apical meristem and counted the number of leaves on the plant (Figure 1).

Prediction 5: Dominance of a community should be negatively correlated with species richness, local and metacommunity area, and immigration. I analyzed the slopes of the Dominance-Diversity Curves produced by the species compositions and abundances of the 42 leaves sampled during the experiment. Only the effects of species richness and community size were tested because rates of immigration were too difficult to obtain in such a short term study.

RESULTS

I sampled 42 leaves from 21 plants of *Geonoma spp.* I found 27 morphospecies of epiphylls. The local community richness ranged from 2 to 14 species per 20 cm^2 ($\bar{x}$ = 8.4, S.D. = 2.6). The results of the specific tests of each of the predictions of the UNT are as follows:

Prediction 1: Nearest neighbor distance, a measure of the connectance of the metacommunity, does not correlate significantly with species richness of the local community (R^2 = 0.06, P = 0.12, N = 42). In fact, nearest neighbor distance produced a positive trend (the opposite of that expected) when plotted against species richness (Figure 3a). This result could be contributed to the close correlation between connectedness and metacommunity size (R^2 = 0.23, P < 0.0001, N = 42 and R^2 = 0.20, P = 0.0003, N =42 for plant height and number of leaves respectively). Both plant height and number of leaves are shown to have significant or marginally significant positive effects on the local community species richness, and could be producing this same trend for connectivity.

Prediction 2: The area of the local community positively correlates with local community species richness. Both leaf length and leaflet area are marginally significant and significant predictors of the species richness of a local community respectively (R^2 = 0.08, P = 0.06, N = 42 and R^2 = 0.10, P = 0.03, N = 42 respectively) (Figure 3b, c).

Prediction 3: The estimates of local and metacommunity size (j and J) do not significantly predict the species richness of the local community of epiphylls (R^2 = 0.04, P = 0.23, N = 42, and R^2 = 0.01, P = 0.62, N = 42 respectively) (Figure 3d, e).

Prediction 4: The number of leaves on a plant (a measure of the size of the metacommunity) significantly positively correlates with local community species richness (R^2 = 0.14, P = 0.01, N = 42) (See Figure 3f). Plant height showed no significant effect on local community species richness (R^2 = 0.05, P = 0.15, N = 42).
Prediction 5: The Dominance-Diversity Curves, shown together in Figure 4, seem to fit a family of curves. These curves all have different slopes, which serve as measures of dominance of the community. All the slopes are negative; a slope that is more negative has greater dominance. The UNT predicts that dominance will decrease with species richness, immigration and community size. Species richness is highly correlated with the dominance of the epiphyll communities (R^2 = 0.41, $P < 0.0001$, N = 42; Figure 5a). But, community size was unable to explain variation in dominance (R^2 = 0.04, p-value = 0.23, N = 42, R^2 = 0.03, P = 0.28, N = 42; Figure 5b, c).

DISCUSSION

In this investigation of epiphyll communities, I tested five predictions of Hubbell's Unified Neutral Theory. I found support for only two of the five predictions tested. Species richness of local communities was significantly explained by measures of the size of the local and metacommunities. However, measures of connectivity, and total population were insufficient in explaining local community species richness.

The nearest neighbor distance produces a nonsignificant positive trend with species richness, the opposite trend as expected from the UNT. My measure of community connectivity may not be a good measure of the actual connectivity of the metacommunity. When inspected, the distance of the nearest neighbor on a *Geonoma spp.* plant correlates closely with plant height and number of leaves, two factors which were shown to produce positive trends with species richness.

The UNT predicts that Dominance-Diversity Curves of communities of differing diversity will follow a family of curves that differ in slope. The differences in slope of the graphs are predicted to be a function of different rates of immigration and local community size. The Dominance-Diversity Curves of epiphyll communities on *Geonoma spp.* do belong to a family of curves with different slopes. The slope of these lines, or the community dominance, can be predicted by the species richness of a community, a result consistent with the UNT. However, local and metacommunity size were unable to predict the dominance (slope of the Dominance-Diversity curve) of a community, a result inconsistent with the UNT.

The role of a stochastic model is to try to explain a community with the least amount of knowledge possible (Hubbell 2005). The Unified Neutral Theory proposes that a small number of factors will be able to predict community richness. In this examination of 42 local communities, it seems that the information was not enough. Only the leaf length and community size helped to predict 10% and 14% of the variation in local community species richness, respectively (not necessarily independent of one another). These two significant factors can account for at most 24% of the variation in species richness. It seems the Unified Neutral Theory of ecology does not provide enough parameters to sufficiently predict the dominance or diversity of the epiphyll community as it is organized on islands of palm leaves.

This evidence corroborates findings of many other studies (Chave 2004, Harpole and Tilman 2006, Assaf 2005). The failure of Unified Neutral Theory to predict the dominance and diversity of local communities could be due to the role of many disregarded factors in community composition. The basic assumptions of competitive equivalence and constant population size could be wrong. Also mechanisms such as density dependent selection, dispersal limitations, and epiphyll species interactions could be important in these epiphyll communities.

ACKNOWLEDGMENTS

I appreciate the help of Karen Masters, Alan Masters, Maria Jost and Oliver Hyman. Thanks also to Ellen Frondorf for collaborating in epiphyll identification and Kevin Loope for his ever-patient manner in helping with the infinitely enjoyable task of making Microsoft Word© diagrams.

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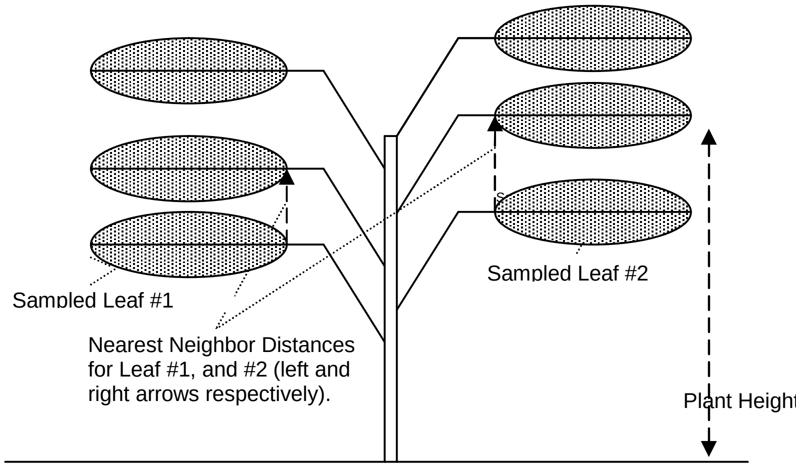

Figure 1: Representation of one metacommunity. The epiphylls of each leaf is a local community. The epiphylls on all leaves of a *Geonoma spp.* palm are the metacommunity. The manner of collection of data taken from each metacommunity is shown here. Plant height was taken from the base of the plant to the apical meristem. The nearest neighbor distances were measured from the base of the leaf blade sampled to the nearest leaf blade base. Also, the number of unfolded leaves was counted for each plant, here 6 leaves.

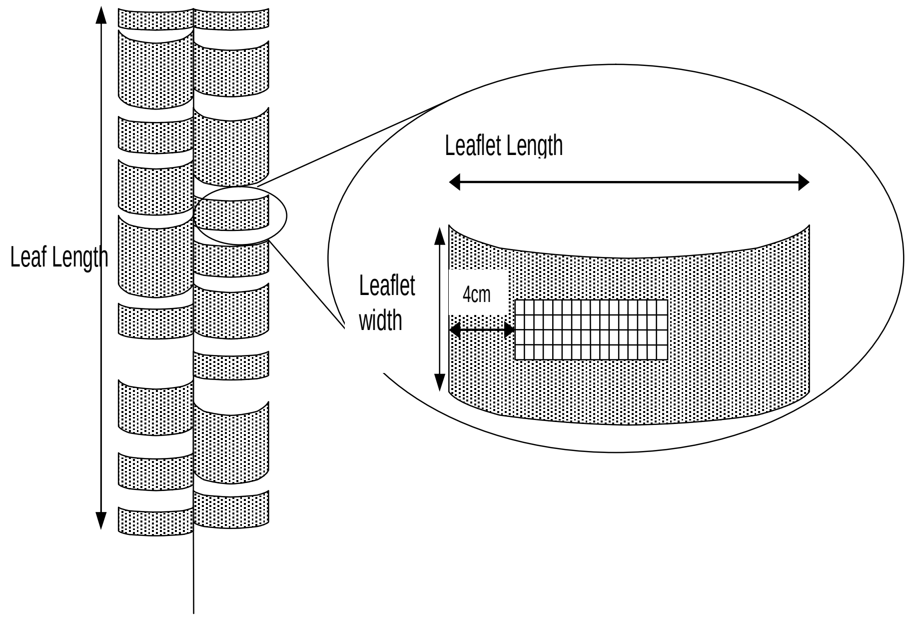

Figure 2: The local community and the sampling system. One local community is defined as one leaf blade in this experiment. The leaves of *Geonoma spp.* are split irregularly as is shown. To determine the diversity of a leaf, I examined an area of constant size. The leaflet I chose to sample from the leaf was the one closest to the top of the leaf with a width ranging between 1.6 and 3.2 cm. The large oval is an enlargement of the sampled leaflet. A grid was placed four centimeters from the base of the leaflet. This grid was $20cm^2$ and contained 480 crosshairs. At each crosshair the presence and morphospecies of epiphyll was recorded.

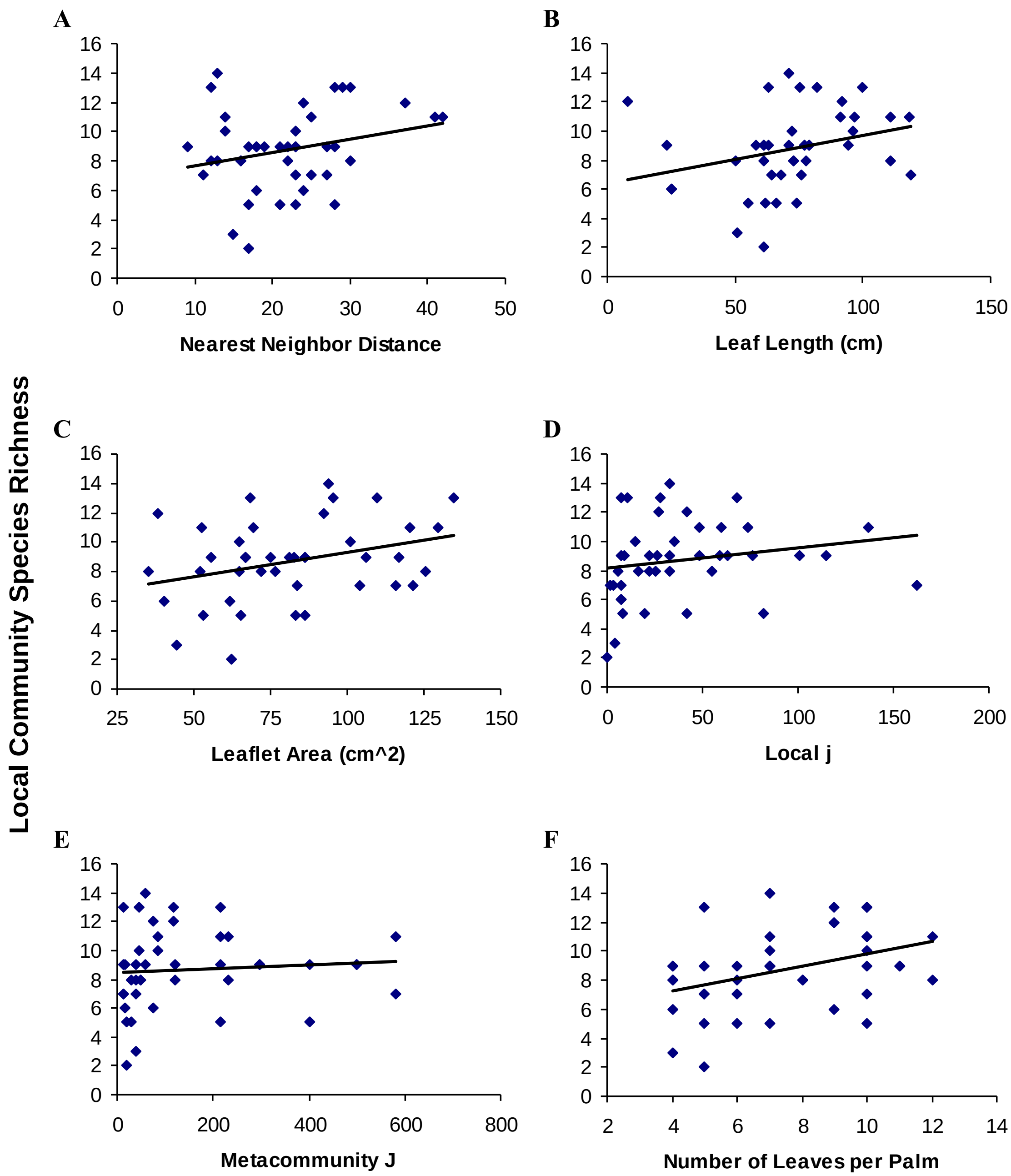

Figure 3: The effect of six different parameters on local community species richness. All parameters, except for nearest neighbor distance are predicted by the UNT to correlate positively with local community species richness. (A) Local community species richness as predicted by nearest neighbor distance, a measure of connectivity, predicted to be a negative trend by the UNT but here is a positive trend ($R^2 = 0.06$, $P = 0.12$, $N = 42$). (B) Local community species richness as predicted by the size of the local community. This trend is marginally significant and shows that greater community area could be effective

as slowing community drift to increase diversity (R^2 = 0.08, P = 0.06, N = 42). (C) The area of the leaflet chosen to sample significantly correlates with local community species richness, again supporting the second prediction of the UNT (R^2 = 0.10, P = 0.03, N = 42). (D) The population size of the local community, J does not significantly explain the variation in local community species richness (R^2 = 0.04, P = 0.23, N = 42). (E) The estimation of total population size for the metacommunity, total J, also does not significantly explain the variation in local community species richness (R^2 = 0.0063, P = 0.6175, N = 42). (F) Number of leaves on the plant (number of islands in the metacommunity) significantly correlates with local community species richness (R^2 = 0.14, P = 0.01, N = 42). Metacommunity size could also be an important factor in slowing community drift for the epiphyll communities.

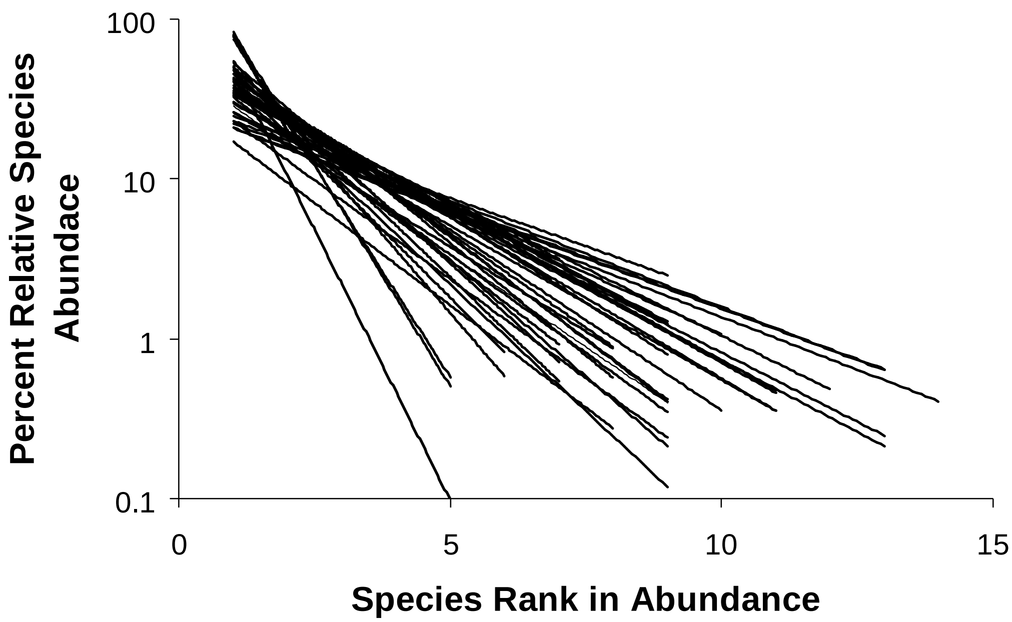

Figure 4: The Dominance-Diversity Curves of all the epiphyll communities sampled. Each line represents one of the 42 communities leaves sampled in the experiment. The x-axis, species rank in abundance, is the rank of abundance of each species in that community. The rank 1 species is the most abundant species in the community. The y-axis is percent relative species abundance. This is the species' percent of the total individuals in the community, represented on a log 10-scale. The slope of the trendline is proportional to dominance of the community. The point at which the trendline stops on the x-axis signifies the number of species in that community.

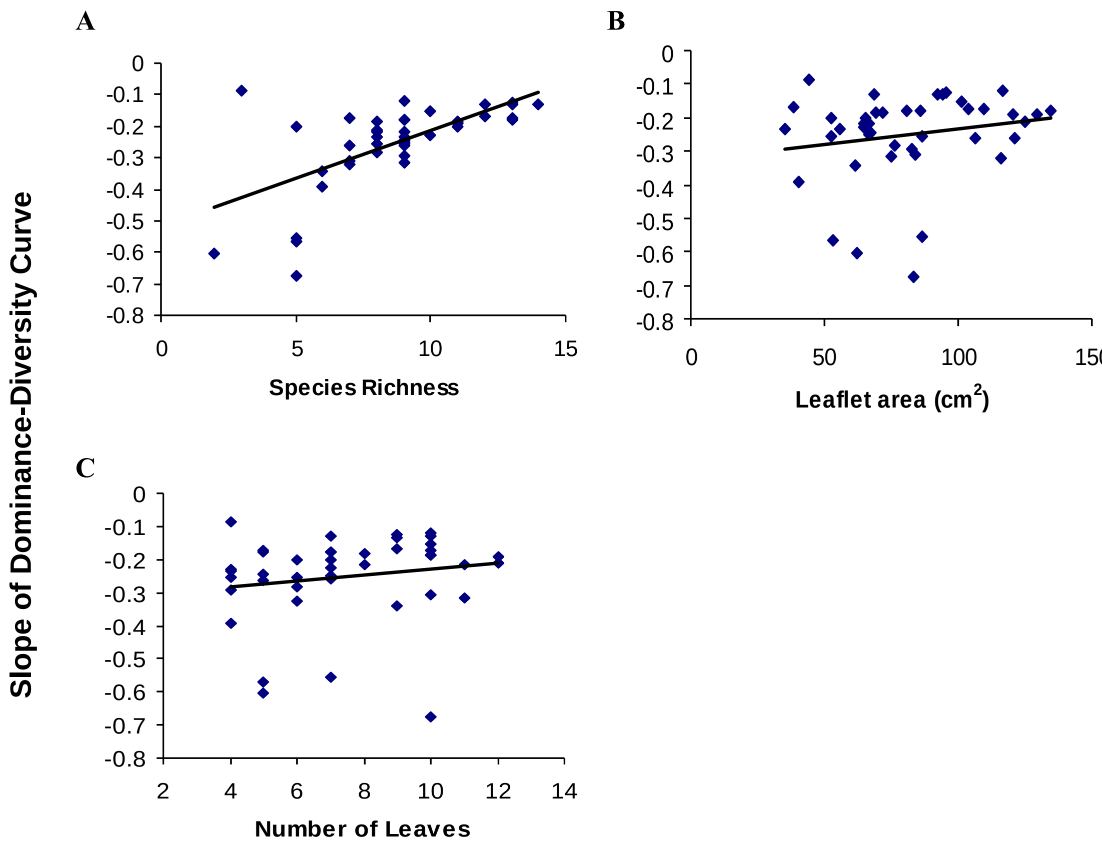

Figure 5: The relationship between dominance, (as determined by the slopes of the dominance-diversity curves) species richness and community size (a measure of community size). Note that the slopes of the dominance-diversity curves are all negative. A more negative slope corresponds to a community of greater levels of dominance. (A) This regression is a summary of Figure 4. The slopes of each of the lines represented there are plotted against species richness, where each of the lines stops on the x-axis of Figure 4 ($R^2 = 0.41$, $P < 0.0001$, $N = 42$). Communities of epiphylls with fewer species present have significantly greater dominance than those with high species richness. (B) and (C) Both graphs show dominance as predicted by community size. Leaflet area, and number of leaves were chosen because they were the only parameters that significantly affected the species richness. Neither is able to significantly predict the dominance of a community as was predicted by the UNT ($R^2 = 0.04$, p-value = 0.23, $N = 42$ and $R^2 = 0.03$, $P = 0.28$, $N = 42$ for B and C respectively).