The Effects of Cypress Dome Size on Epiphyte Diversity in Southern Florida

by

Jordan Muss

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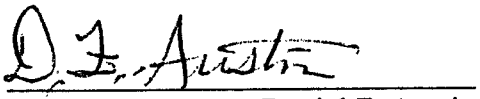
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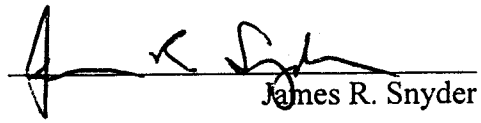
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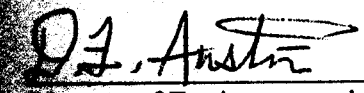
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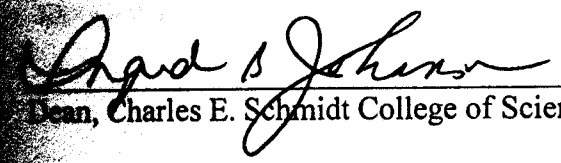
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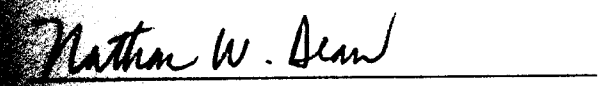
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Abstract

Epiphyte richness and abundance were observed in 18 cypress domes two regions in South Florida that were classified by annual low differences of 4.05 °C. Using the Preston model of island biogeography regression, the following hypotheses were tested:

1. Larger domes have greater epiphyte diversity because they moderate temperature extremes better than smaller domes.
2. The effect of cypress dome size is reduced in subtropical compared to more temperate regions.
3. A measurable temperature gradient exists within cypress domes.

analyses indicated that epiphyte distribution in cypress domes fits the model. In addition to an increase in diversity with area, there were regional that were correlated to temperature, however, these differences as dome size increased. Within the domes, an increase in diversity was to significant differences between dome edge and center temperatures, the occurrence of factors that were influenced by area.

# of Contents

f Figures....vi

f Tables....vii

ion....1

and Methods....5

lysis....9

....11

ytes Observed....11

ionship of Species Diversity to Area....14

erature Analysis....23

ity Analysis within Domes....31

....36

Cited....40

x: A List of Epiphytes Observed....44

Listing of Figures

Figures:

1. Low temperature isotherms in southern Florida for January 1973.....7

2. The abundance of each epiphyte observed across all domes.....15

3. The species-area curve of epiphytes growing in cypress domes in the Big Cypress National Preserve.....16

4. Measures of diversity and evenness plotted against dome area and by isotherm (warm v. cold).....19

5. The relationship between the number of individual epiphytes counted in a dome, and the area of the dome.....20

6. The relationship between each dome's basal area per quadrat and the area of the dome. 21

7. The relationship between quadrat basal area and the distance the quadrat is from the nearest edge.....22

8. Average (±SE) cold season low temperature recorded outside of 6 domes plotted from north to south.....25

9. Temperature differences between each dome's approximate center and edge plotted against its area and relative north-south position.....33

10. Raw species count (S) and species evenness (J') per quadrat plotted against the distance from the nearest dome edge.....34

11. Species diversity (D_s and H') per quadrat plotted against the distance from the nearest dome edge.....35

Listing of Tables

Tables:

1. Individual counts of each epiphyte species observed.....13

2. Area, total counts of epiphyte species (S), calculated z-values, and predicted species counts for each cypress dome.....17

3. Total individual epiphyte counts (n), total counts of epiphyte species (S), calculated measures for diversity and evenness for each cypress dome.....18

4. Linear model analyzing the relationship between temperature and north-south position in the Big Cypress National Preserve.....26

5. Linear model analyzing the effects that temperature and cypress dome area have on the species count of epiphytes in the Big Cypress National Preserve.....27

6. Linear model analyzing the effects that temperature and cypress dome area have on the Shannon diversity index for epiphytes in the Big Cypress National Preserve.....28

7. Linear model analyzing the effects that temperature and cypress dome area have on the Simpson diversity index for epiphytes in the Big Cypress National Preserve.....29

8. Linear model analyzing the effects that temperature and cypress dome area have on the evenness of epiphyte distribution in the Big Cypress National Preserve.....30

9. Paired t-test of the differences between the temperature at the approximate center and at the edge in each cypress dome during the cold season.....32

Introduction

Epiphytes are plants that grow nonparasitically upon another, using the host only for support (Craighead, 1963). I further defined epiphytes as plants that are obligated to live upon a non-soil substrate, thus excluding plants that can, but are not obliged to do so (such as *Boehmeria*, *Ficus*, etc.). Epiphytes are of interest globally because they provide habitats for many plant and animal species, increase nutrient availability for canopy fauna and host trees (Nadkarni, 1994), and are widely used as indicator species of forest and canopy disturbances (Renhorn et al., 1997; Strong, 1997; Esseen and Renhorn, 1998). The life form has attracted attention in Florida as an indicator of air pollution (Benzing and Bermudes, 1991) and because epiphytes comprise a significant portion of the state's threatened and endangered plant species (Coile, 1998). In South Florida's Big Cypress National Preserve, 52 different species of epiphytes, representing 14 families, have been identified (Black and Black, 1980; Muss et. al. 2001). Twenty-nine of these are on the State's threatened and endangered species list, and make up 43% of the threatened and endangered plant species found in the preserve (Coile, 1998). Despite their great diversity and ecological importance, little is known about the biotic and abiotic factors that influence vascular epiphyte communities.

In South Florida, cypress domes are one of the major communities in which epiphytes grow. Cypress domes are the most common and widespread of Florida's swamps (Ewel, 1990). They are circular islands of differing sizes, dominated by cypress trees scattered in a matrix of wet prairies, pine flatwoods, or sawgrass marsh.

ide excellent model systems for testing theories of island

of island biogeography can be traced back to Darwin (MacArthur
), however its modern study did not begin in earnest until a
n the area of West Indian islands and the richness of their
noticed (Darlington, 1957). Shortly thereafter, Preston (1962)
ion between the size of an island and its species richness. This
the number of species on an island at equilibrium (S_E) is exponentially
area (A) of the island by a factor *z* and a constant (c), where *z* must
ge of 0.20 - 0.35. Mathematically, this was written as:

$$S_E = cA^z$$

and Wilson (1967) modified the theory by incorporating the effects
species source has on an island's diversity. In addition, they derived
lated the number of species on an island to the rates of immigration
hat island. The premise behind the MacArthur-Wilson theory, that
increased rates of immigration and decreased rates of extinction, is
rget and rescue effects. The target effect states that species are more
r islands through immigration; an organism has a higher
ing a larger island than a smaller island. The rescue effect explains
rates by assuming that a larger island can support more individuals
maller island. New immigrants of a species are more likely to arrive
d before the species becomes extinct, thus "rescuing" it (Wu &

Venkat, 1991). Therefore, as island area increases, species abundance increases, and the extinction rate decreases.

The MacArthur-Wilson model does not relate species richness to species abundance, and it is difficult to test the immigration and extinction rates of long-lived, nonmotile organisms. Therefore, in this study, I chose to apply the Preston species-area model to examine the relationship between epiphyte diversity and cypress domes. Since the Preston model only predicts a relationship without stating a cause, I also tested temperature as a primary abiotic factor influencing epiphyte diversity (Phillips, 1951; Woodward, 1988; Specht, 1994; Freiberg & Freiberg, 2000).

Specifically, I hypothesized that larger cypress domes would have greater epiphyte diversity because they would moderate temperature extremes better than smaller domes. Moderation of temperature in larger cypress domes is thought to result from standing water within the cypress dome and its canopy, thus providing a higher relative humidity within the dome throughout the year compared to smaller domes. In geographic areas where the overall temperature and humidity conditions were more favorable for epiphytic growth, diversity differences as a result of dome size would be reduced. Therefore, my second hypothesis stated that in a more subtropical climate, cypress domes would have a greater species richness and evenness of epiphytes than domes located in a more temperate climate. Within a more subtropical climate, differences in epiphyte diversity would be less apparent among different cypress dome sizes compared to domes of different sizes located in a more temperate climate. Finally, my third hypothesis theorized that a measurable temperature gradient existed within cypress domes. This gradient would allow for more temperature niches within larger

compared to smaller domes, resulting in greater epiphyte diversity within the larger domes.

Materials and Methods

This study focused on cypress domes in the Big Cypress National Preserve. The preserve protects 260,000 hectares of the historic 312,000 hectare Big Cypress Swamp (MacPherson, 1984). The Big Cypress Swamp is located in southwestern Florida, and is characterized by cypress domes and sloughs, intermixed in a matrix of wet prairies, pine flatwoods, and hammocks (McPherson, 1984).

Monthly temperature readings, recorded prior to 1973, were used to draw isotherms across a map of Florida (Thomas, 1974). These readings determined that historically, January was the coldest month of the year in southern Florida, and that each isotherm for that month varied from its neighbor by 0.6 °C (Figure 1). Using this information, two sets of nine cypress domes were selected; one set was in the coldest isotherm, which had an average monthly low temperature of 16.7 °C, while the other set of nine domes was in the isotherm with an average monthly low temperature of 18.3 °C. (The latter isotherm was the warmest region in the preserve where cypress trees still dominated the landscape.) Each set of domes were represented by three size classes, small (0.20 to 0.35 hectares), medium (0.70 - 1.0 hectares), and large (1.5 – 2.9 hectares). These guidelines were used to provide a distribution of dome sizes for species-area analyses. Domes were initially selected by utilizing USGS land classification data, aerial photographs, and a geographic information system. Due to the nature of cypress growth and dome formation, well established domes with mature trees were deemed to be in a late successional dynamic equilibrium stage that is

characteristic of this type of habitat. After a dome was selected, it was examined in the field to ensure that it had not undergone any severe disturbance.

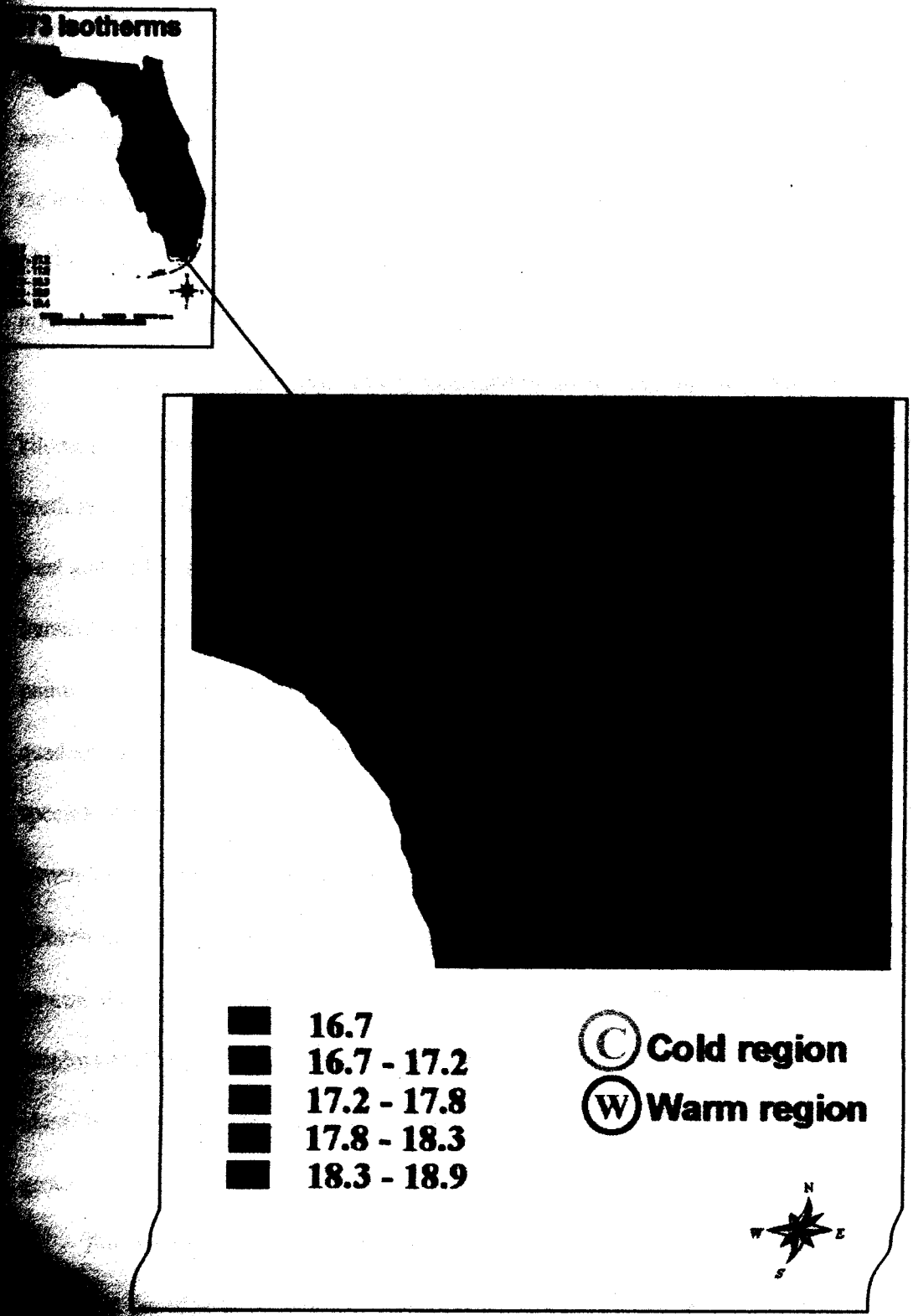


Figure 1. Low temperature isotherms in southern Florida for January 1973 (Thomas, 1974). Big Cypress National boundary denoted by red polygon.

at a point midway between the edge and pond, and ten meters outside the dome in one small, one medium, and one large dome in each temperature zone. The readings taken outside the domes were used to confirm the existence of the north-south isotherms in the study area. They were also used to test a linear model that related temperature to a north-south position (Y) relative to the farthest north dome. This model was formulated as:

$$\textbf{Temperature} = C + \alpha * Y$$

where the constant C and the linear coefficient α relate position to temperature. All temperature readings were taken two meters above the ground.

Data Analysis

A species-area curve was drawn to determine how well the data fit the Preston model, which was then transformed so that z-values could be calculated for each dome as a function of area (A) and species count (S). This formula was expressed as:

$$z = \ln S / \ln A$$

The same sampling size was then examined for each dome to test whether the species-area results were due to large domes having more niches than small domes. This sample size was determined by using the fewest number of quadrats sampled in any of the domes. Monte Carlo simulations were then performed for each dome to determine the average number of species expected using this minimum number of quadrats.

Additionally, comparisons between quadrats and between domes were made by calculating standardized values for diversity using the plant counts. These values measured richness (Simpson's diversity index (D_s) and the Shannon diversity index

(H')) and evenness of distribution (Shannon evenness (J')) of epiphytes (Shannon, 1948; Brower et. al, 1998). The formulas used for calculating these indices were:

$$D_s = 1 - (\Sigma\, n_i(n_i - 1))/N(N-1)$$

$$H' = -\,\Sigma\, p_i \ln p_i$$

$$J' = H'/\ln N$$

The indices were then plotted against the area of the domes and linear regression analysis was used to test the hypothesis that epiphyte diversity was significantly influenced by temperature.

Paired sample t-tests were calculated on each dome to determine whether the temperature at the dome's approximate center was significantly different from its edge temperature. The temperature differences were then plotted against each dome's relative north-south position and its area to test for any obvious patterns. Finally, the diversity within the domes was plotted against the distance that each quadrat was from a dome edge, and analyzed with linear regression.

Results

Epiphytes Observed

More than 17,000 epiphytes were counted in the 18 cypress domes. Of these, 17 distinct species of mature epiphytes were identified, representing 11 genera in six families (Figure 2; Appendix A). Due to ambiguity, the immature plants could only be identified as *Tillandsia* sp. In fact, the most dominant genus in the cypress domes was *Tillandsia*, of which 16,685 individuals were observed (Table 1). Within this genus, 10,881 plants were classified into seven species, of which, *T. fasciculata* represented almost 50% of the genus. Of the remaining six species, *T. usneoides, T. balbisiana, T. paucifolia,* and *T. recurvata* had greater numbers of individuals in regionally warm domes, while *T. setacea* and *T. variabilis* were more abundant in the cold region. With 318 individuals counted, the most common non-*Tillandsia* was the resurrection fern (*Polypodium polypodioides*), followed by the butterfly orchid (*Encyclia tampensis*), of which 59 individuals were observed. The remaining orchids (*Epidendrum nocturnum, E. rigidum,* and *Harrisella filiformis*) were observed only in study domes in the cold region, although both species of *Epidendrum* were seen in non-study domes in the warm region.

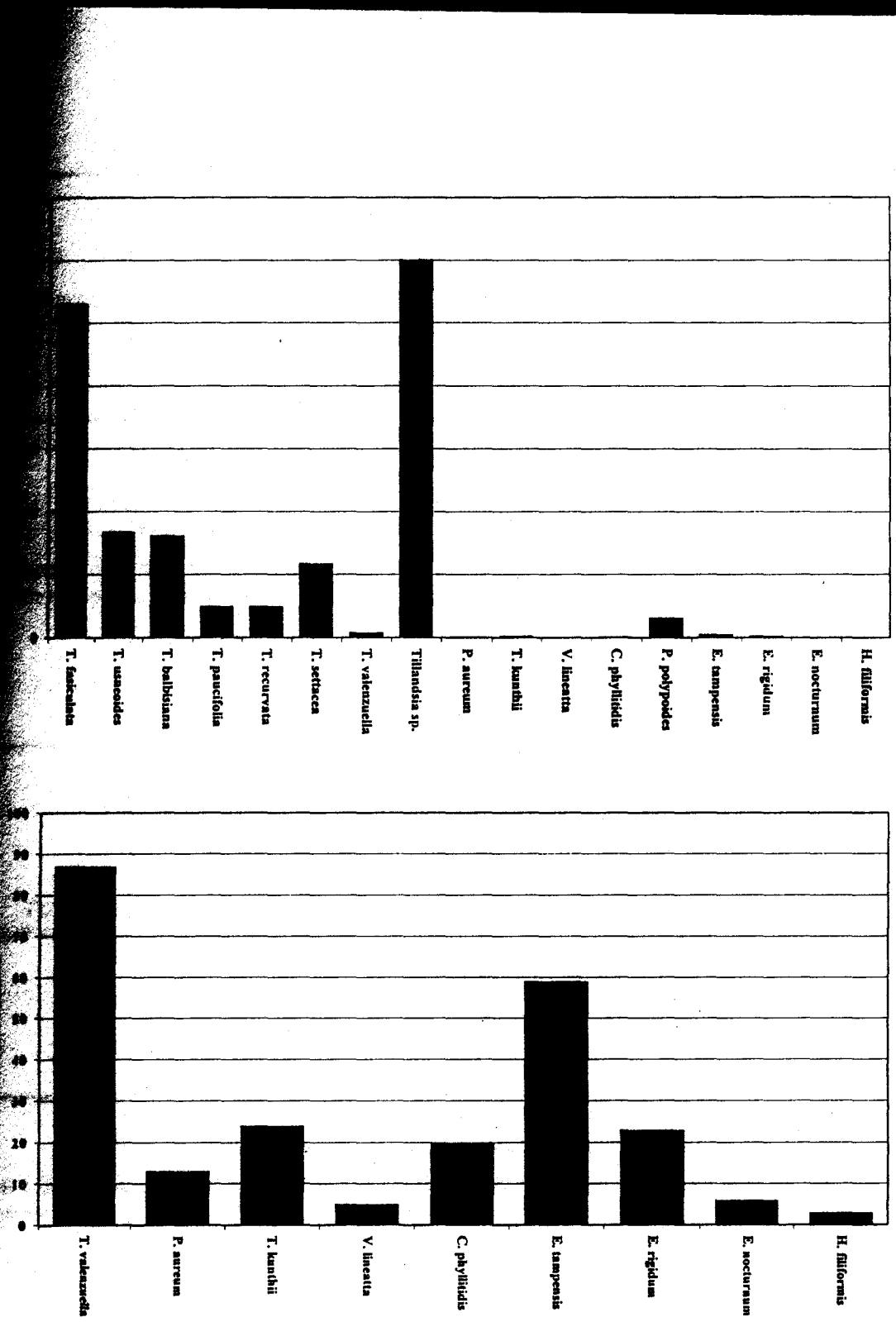


Figure 2. (A) The abundance of each epiphyte observed across all domes. (B) The abundance of epiphytes for which fewer than 100 total individuals were observed in all domes.

Isotherm	Dome	*T. fasiculata*	*T. usneoides*	*T. balbisiana*	*T. paucifolia*	*T. recurvata*	*T. setacea*	*T. variabilis*	*Tillandsia sp.*	*P. aureum*	*T. kunthii*	*V. lineatta*	*C. phyllitidis*	*P. polypodioides*	*E. tampensis*	*E. rigidum*	*E. nocturnum*	*H. filiformis*
Warm (South Region)	B	165	57	85	53	48	0	0	226	0	0	0	0	0	1	0	0	0
	C	80	32	40	52	69	0	0	175	0	0	0	0	0	2	0	0	0
	A	201	176	53	29	0	0	0	208	0	0	0	0	0	0	0	0	0
	D	395	49	152	48	87	4	0	410	0	0	0	0	0	2	0	0	0
	F	324	160	91	29	5	6	0	331	3	0	0	0	0	0	0	0	0
	E	334	105	228	40	53	0	0	634	0	0	0	0	0	0	0	0	0
	I	429	67	77	36	7	87	0	352	0	0	0	0	17	1	0	0	0
	G	395	290	281	63	69	7	0	535	4	0	0	0	0	6	0	0	0
	H	384	186	177	8	68	94	0	314	1	1	0	18	102	10	0	0	0
Cold (North Region)	P	68	11	17	18	1	0	0	105	0	6	0	0	0	2	0	0	0
	Q	201	35	66	8	11	0	0	147	1	0	0	0	0	0	0	0	0
	R	200	5	14	10	1	0	0	168	0	5	0	0	0	1	0	0	0
	K	376	67	96	61	18	1	0	585	0	4	0	0	0	3	0	0	0
	J	480	103	90	25	13	15	2	270	1	4	0	0	0	7	0	0	0
	L	392	68	8	10	18	69	0	297	0	3	0	0	34	10	0	0	0
	M	396	96	56	8	19	206	0	560	0	0	0	0	100	7	0	0	0
	N	206	106	61	4	17	305	22	330	3	0	4	1	28	2	8	0	3
	O	282	65	29	2	5	380	63	357	0	1	1	1	37	5	15	6	0
	Totals:	5308	1678	1621	504	509	1174	87	6004	13	24	5	20	318	59	23	6	3

Table 1. Individual counts of each epiphyte species observed. Domes are classed by isotherm and size. Each dome was assigned a letter designation (a-r) for identification purposes.

Relationship of Species Diversity to Area

The species count and area for each dome were plotted on a log-log graph (Figure 3) as a first step of species-area analysis. Simulations were then performed for each dome to determine the average number of species expected after any five quadrats were sampled. These simulations tested whether the species-area results were merely due to large domes having had more quadrats sampled than small domes. Five quadrats were chosen, because that was the fewest number of quadrats sampled in any dome (domes P and Q). The results of this analysis ($y = 0.17x + 0.35$; $R^2 = 0.45$; $p < 0.002$) was similar to those observed using the complete data set ($y = 0.24x + 0.0061$; $R^2 = 0.58$; $p < 0.0002$). However, the greater slope and R^2 of the complete data set do indicate that the data could be better represented with a larger sampling.

The data were also used to calculate z-values for each dome using Preston's model (Table 2). The calculated z-values ranged between 0.20 and 0.27, with an average $z = 0.24$. When the domes were grouped by isotherm, there was a small divergence in z-values; the warm group had a z-value of 0.23 while the value for the cold group was 0.25. Therefore, diversity was normalized by area to examine regional differences. For this analysis, the Simpson diversity index, Shannon diversity index, and Shannon evenness value were calculated for each dome (Table 3), and plotted against dome area (Figure 4). Both diversity indices increased with dome size, while the measure of evenness decreased with area. In all cases, when plotted by temperature zone, each index was greater for the warmer domes than the colder domes, but these differences converged as the dome size increased.

The total basal area was calculated for each quadrat, to address the argument that the greater diversity in the larger domes was the result of more available colonizing area. The basal areas were plotted against the number of epiphytes per dome (Figure 5) and each dome's area (Figure 6). These results indicated that the number of individual epiphytes increased significantly with basal area and that basal area increased significantly with dome size. When basal area was examined in relation to the distance from the nearest edge (Figure 7), basal area increased moderately as this distance increased.

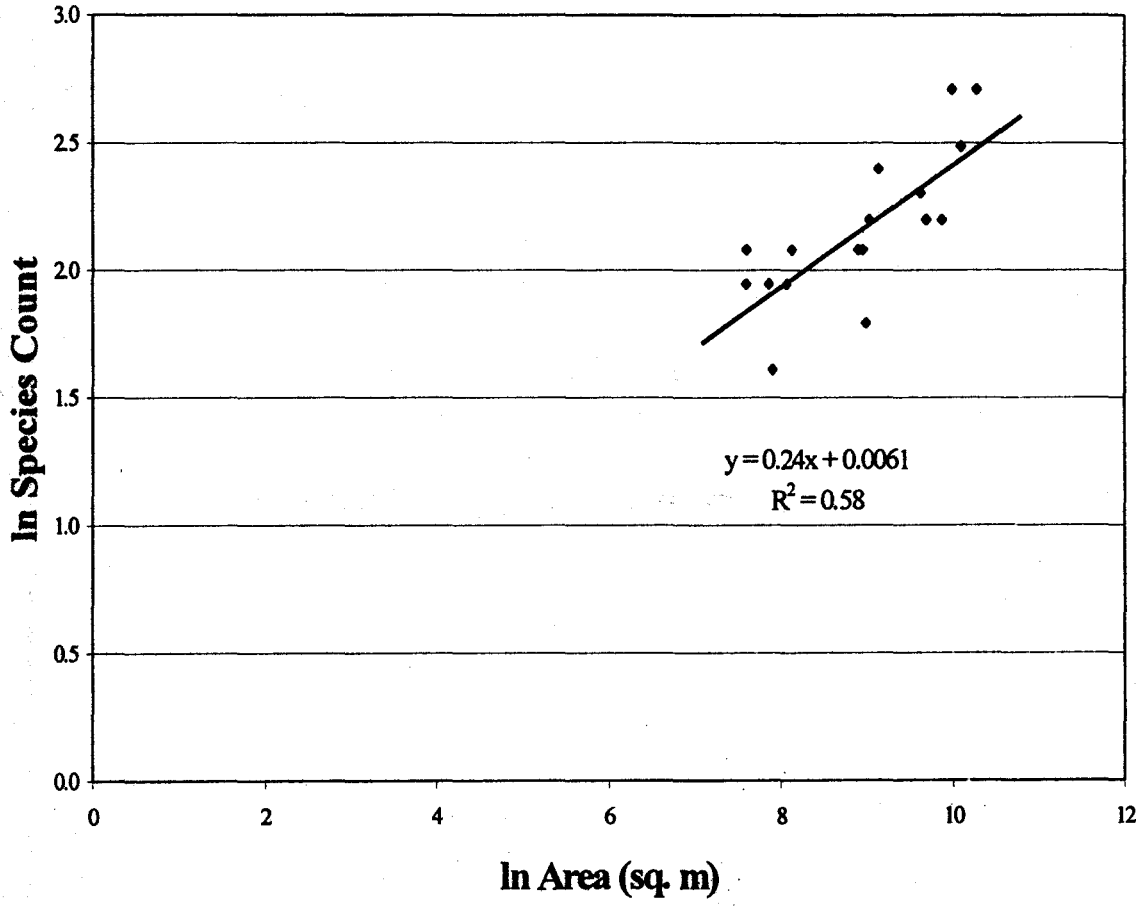


Figure 3. The species-area curve of epiphytes growing in cypress domes in the Big Cypress National Preserve. This indicates that the number of species of epiphytes found in a cypress dome is exponentially related to the area of the dome ($p < 0.0002$).

Isotherm	Dome	Area (m^2)	S	z	Predicted S
Cold (North Region)	P	2,000	8	0.27	6.3
	Q	3,200	7	0.24	7.0
	R	3,400	8	0.26	7.1
	K	8,300	9	0.24	8.8
	J	9,200	11	0.26	9.1
	L	15,100	10	0.24	10.2
	M	19,300	9	0.22	10.8
	N	21,800	15	0.27	11.2
	O	29,000	15	0.26	12.0
			Average:	**0.25**	
			SE:	**0.0057**	
Warm (South Region)	B	2,000	7	0.26	6.3
	C	2,600	7	0.25	6.7
	A	2,700	5	0.20	6.7
	D	7,300	8	0.23	8.6
	F	7,700	8	0.23	8.7
	E	8,000	6	0.20	8.8
	I	16,000	9	0.23	10.4
	G	16,100	9	0.23	10.4
	H	24,100	12	0.25	11.4
			Average:	**0.23**	
			SE:	**0.0064**	
All Domes			**verage :**	**0.24**	
			SE:	**0.0049**	

Table 2. Area, average epiphyte species counts (S) for five quadrats, calculated z-values, and predicted species counts for each cypress dome. Domes are classed by isotherm and size. Each dome was assigned a letter designation (a-r) for identification purposes.

Isotherm	Dome	n	S	Simpson Index	Shannon Diversity Index	Shannon Evenness
Cold (North Region)	P	228	8	0.69	1.42	0.68
	Q	469	7	0.69	1.37	0.70
	R	404	8	0.58	1.06	0.51
	K	1211	9	0.66	1.33	0.60
	J	1010	11	0.68	1.44	0.60
	L	909	10	0.69	1.48	0.64
	M	1448	9	0.75	1.60	0.73
	N	1100	15	0.79	1.78	0.66
	O	1249	15	0.77	1.70	0.63
			Average:	**0.70**	**1.46**	**0.64**
			SE:	**0.020**	**0.072**	**0.022**
Warm (South Region)	B	635	7	0.77	1.62	0.83
	C	450	7	0.77	1.64	0.84
	A	667	5	0.74	1.41	0.88
	D	1147	8	0.73	1.50	0.72
	F	949	8	0.72	1.44	0.69
	E	1394	6	0.70	1.42	0.79
	I	1073	9	0.72	1.52	0.69
	G	1650	9	0.77	1.63	0.74
	H	1363	12	0.82	1.89	0.76
			Average:	**0.75**	**1.56**	**0.77**
			SE:	**0.012**	**0.051**	**0.022**

Table 3. Total individual epiphyte counts (n), total counts of epiphyte species (S), calculated measures for diversity and evenness for each cypress dome. Domes are classed by isotherm and size (from smallest to largest in each region). Each dome was assigned a letter designation (a-r) for identification purposes.

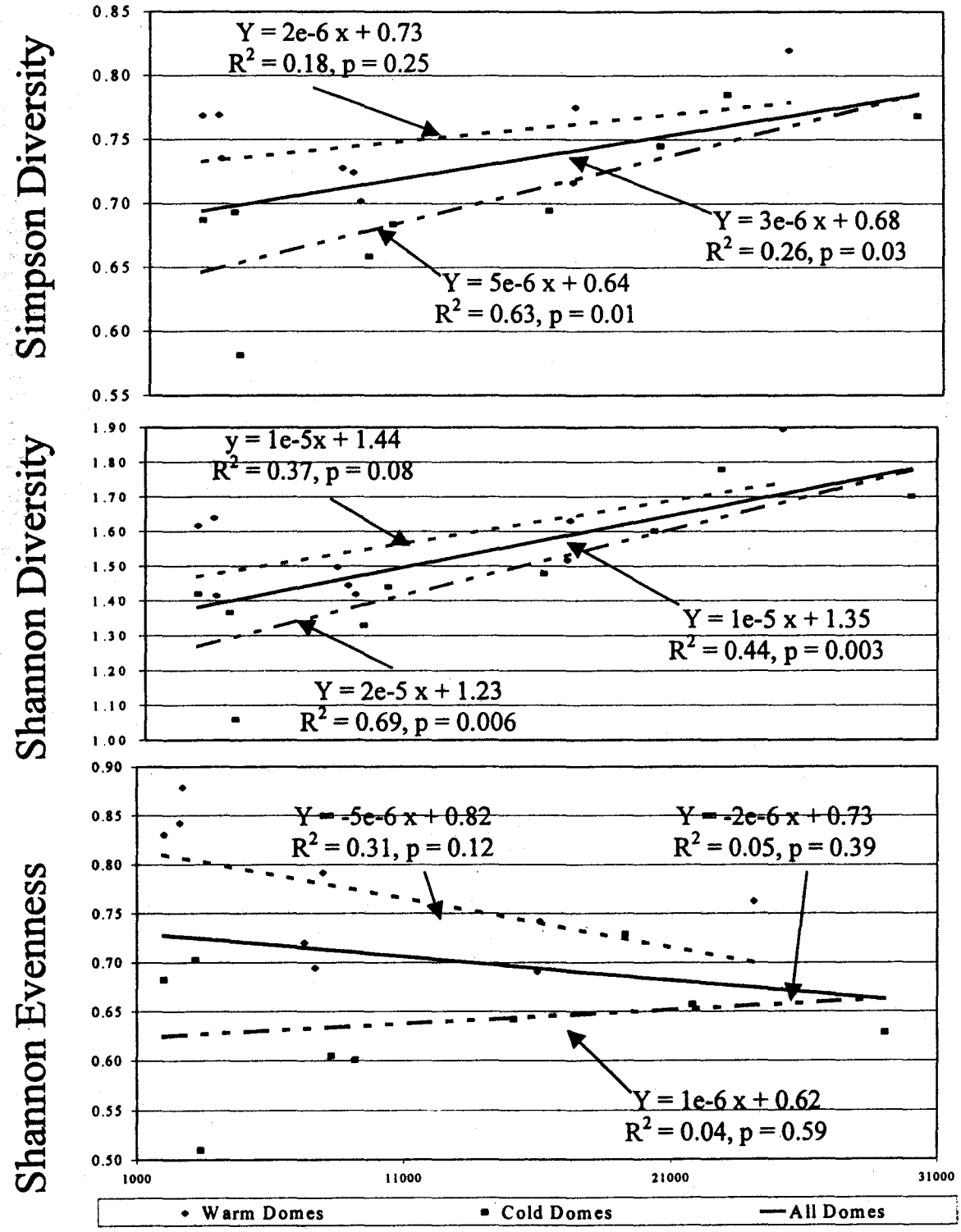


Figure 4. Measures of diversity and evenness plotted against dome area (m^2) and by warm (---) and cold (- - -) isotherm.

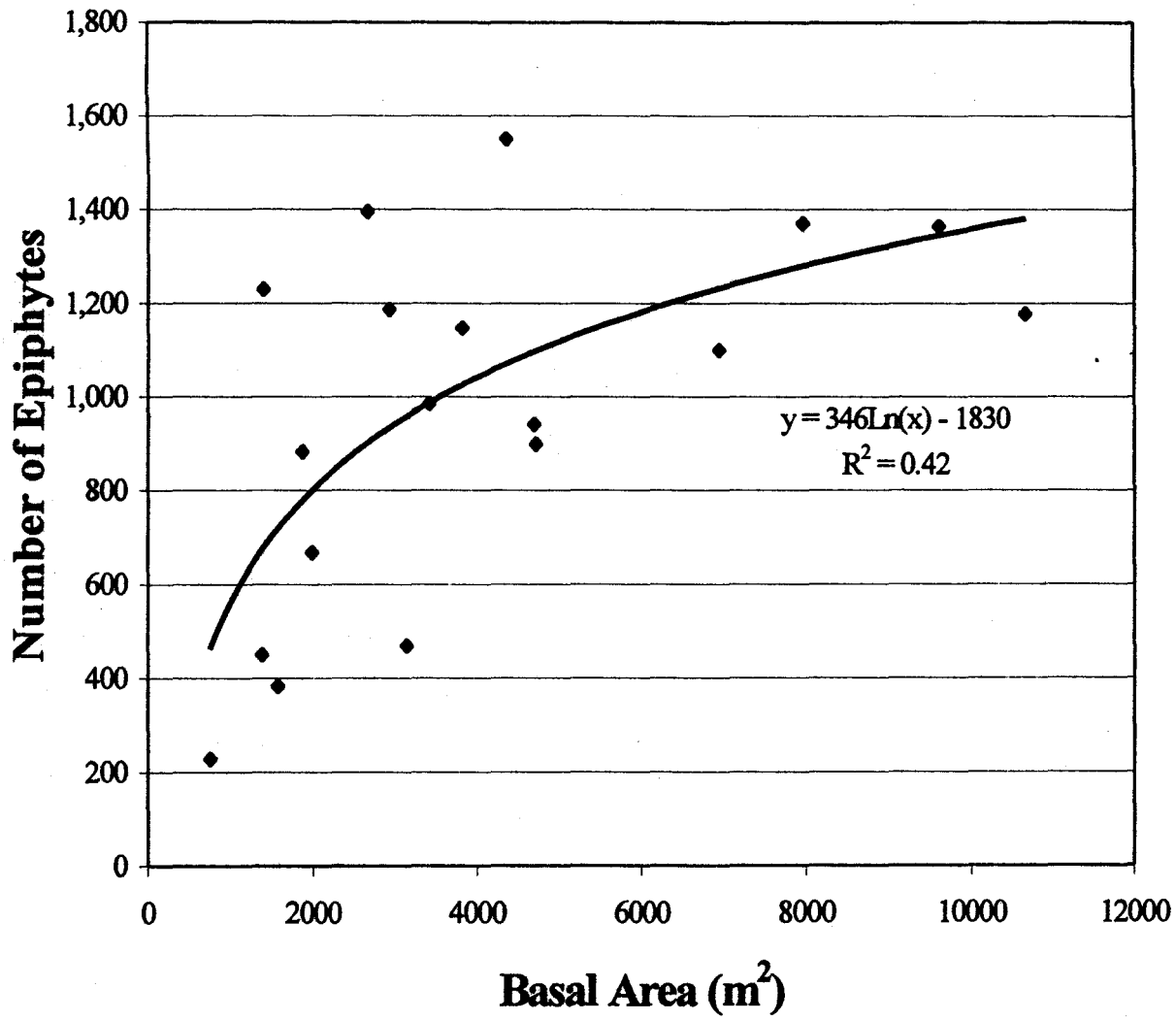


Figure 5. The relationship between the number of individual epiphytes counted in a dome, and the area of the dome ($p < 0.02$).

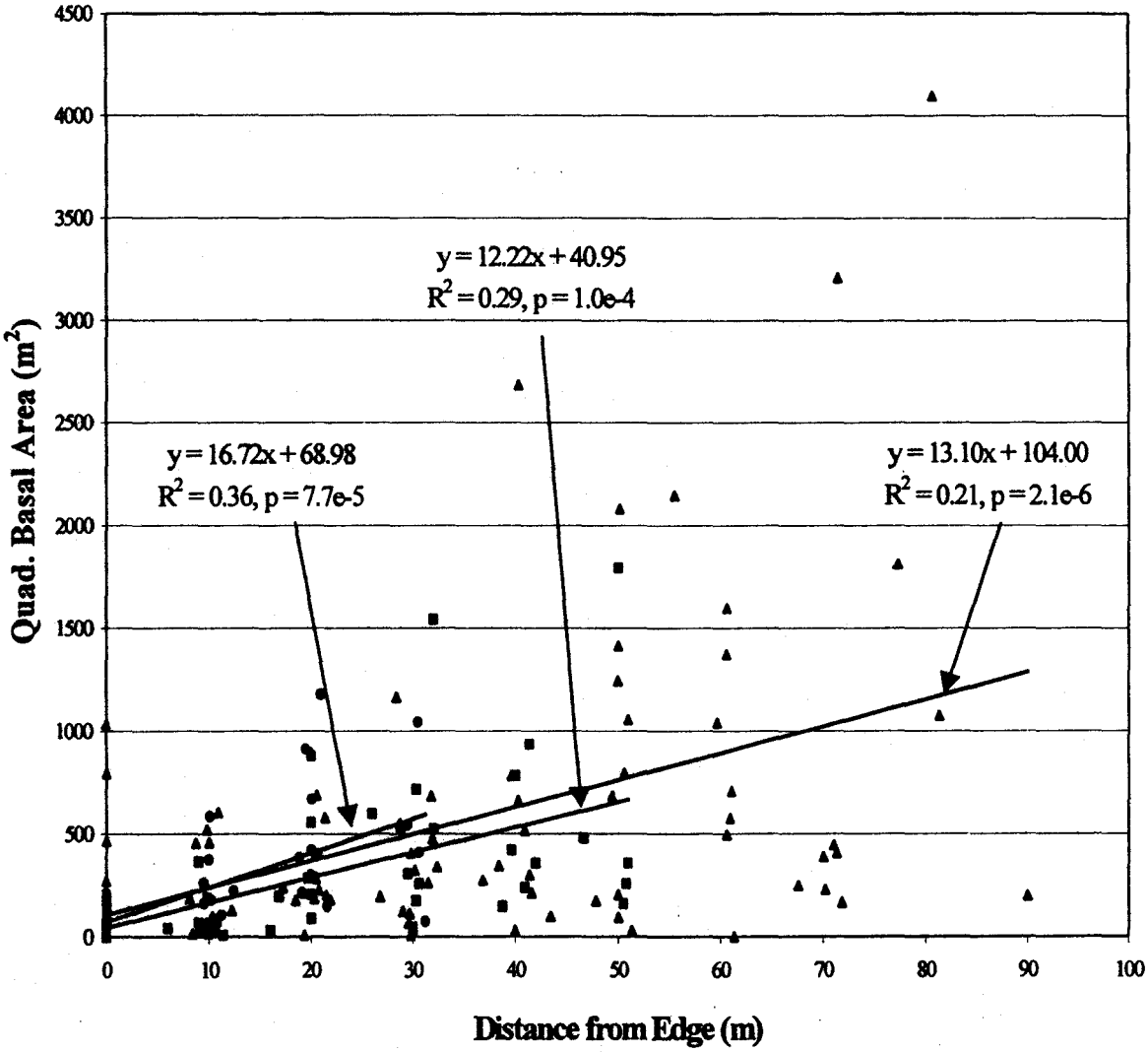


Figure 7. The relationship between quadrat basal area and the distance the quadrat is from the nearest edge ($p < 0.0009$). ● = small domes, ■ = medium domes, ▲ = large domes.

Temperature Analysis

The *a priori* temperature isotherms were confirmed by recording the daily low temperature outside of six of the domes, which spanned the complete 36 Km of the north-south study area, during the cold seasons (December through February) of 1999-2000 and 2000-2001. The average temperatures for each position indicated a maximum variation of 4.05 °C between the coldest and warmest isotherm (Figure 8). The average temperature of the three northern domes was 10.84 °C (±SE 0.24), while the three southern domes averaged 13.90 °C (±SE 0.25). Linear regression was then used to determine the nature and the spacing of the isotherms in the area (Table 4), and to test the model expressed earlier. The resulting model was relative to a point just south of the northern boundary of the preserve and was expressed as:

$$\textbf{Temperature} = 10.46 + Y * 0.11$$

It confirms ($p < 0.05$) that the regional isotherms exist. Moreover, the isotherms appear to be colder and more distinct than indicated by Thomas (1974; Figure 1).

The next step in the analysis of the relationship between temperature and epiphyte diversity in cypress domes, was to use linear regression to examine the correlation of temperature and area with all measures of diversity. Although each dome did not have temperatures recorded for the surrounding environment, the model indicated that temperature and relative position were highly correlated ($R^2 = 0.96$), allowing the use of relative position as a substitute for temperature for the missing recordings. The regression analyses indicate that species counts (Table 5) and diversity (Table 6), as measured using the Shannon diversity index, are significantly correlated

with dome size. In each case, position added a small increase to the models' prediction abilities. Individually, these same measurements were not as accurate at predicting the Simpson index (Table 7), but together had a much higher degree of correlation with that diversity index. Finally, evenness was significantly correlated with position, but not area (Table 8). This was probably the result of a greater presence of rare species in the more tropical region compared to the more temperate region.

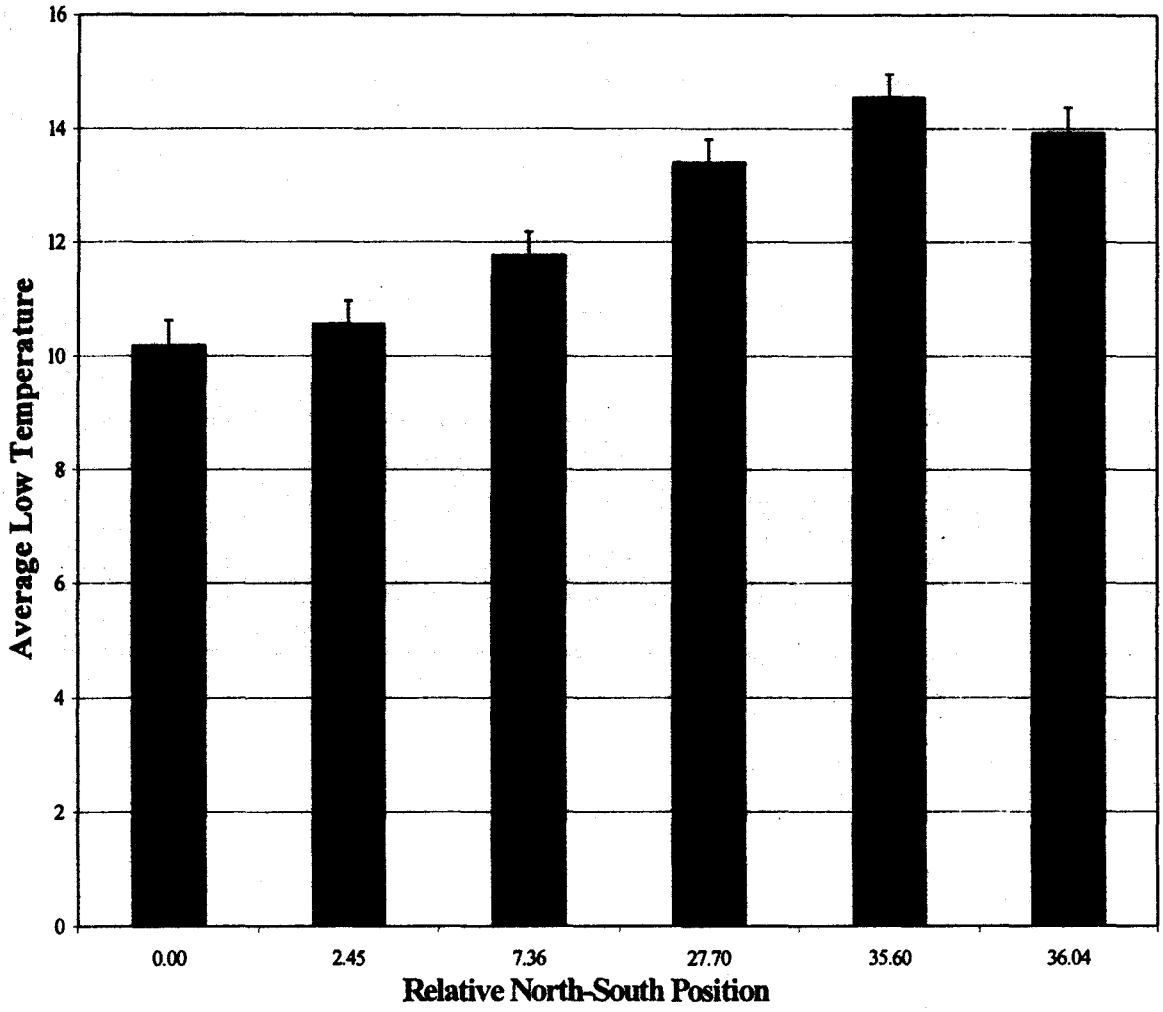


Figure 8. Average (±SE) cold season low temperature (°C) recorded outside of 6 domes plotted from north to south. Distance in kilometers.

Table 4. Linear model analyzing the relationship between temperature and north-south position in the Big Cypress National Preserve ($p < 0.05$, $df = 17$).

a) Model Summary[b]

R Square	Adjusted R Square	Std. Error of the Estimate
0.96	0.95	0.39

a Predictors: (Constant), Relative north-south position
b Dependent Variable: Average minimum temperature over 139 cold days

b) Coefficients[a,b]

	Coefficients	Standardized Coefficients	t	Sig.
(Constant)	10.46		42.66	< 0.001
Position	0.11	0.98	10.35	< 0.001

a Dependent Variable: Average minimum temperature spanning 139 cold days
b Predictor: Relative north-south position

Table 5. Linear model analyzing the effects that temperature and cypress dome area have on the species count of epiphytes in the Big Cypress National Preserve ($p < 0.05$, $df = 17$).

a) Model Summary[f]

Model	R Square	Adjusted R Square	Std. Error of the Estimate
1[a]	0.70	0.68	1.54
2[b]	0.29	0.24	2.38
3[c]	6.4e-5	-0.06	2.82
4[d]	0.79	0.76	1.34
5[e]	0.80	0.75	1.36

a Predictors: (Constant), Area (m^2)
b Predictors: (Constant), Relative north-south position
c Predictors: (Constant), Interaction: Position*Area
d Predictors: (Constant), Area (m^2), and Relative north-south position
e Predictors: (Constant), Area (m2), Relative north-south position, Interaction: Position*Area
f Dependent Variable: Distinct species count (S)

b) Coefficients[a]

Model		Coefficients	Standardized Coefficients	t	Sig.
1	(Constant)	6.08		10.04	< 0.001
	Area (m^2)	2.7e-4	0.84	6.14	< 0.001
2	(Constant)	10.77		12.30	< 0.001
	Relative n-s	-9.2e-5	-0.54	-2.55	0.021
3	(Constant)	9.07		10.44	< 0.001
	Interaction	-1.1e-10	-0.008	-0.032	0.98
4	(Constant)	7.40		9.90	< 0.001
	Area (m^2)	2.4e-4	0.74	5.97	< 0.001
	Relative n-s	-5.3e-5	-0.31	-2.49	0.025
5	(Constant)	7.14		8.16	< 0.001
	Area (m^2)	2.62e-4	0.81	4.87	< 0.001
	Relative n-s	-3.68e-5	-0.21	-1.07	0.30
	Interaction	-1.70e-9	-0.13	-0.63	0.54

a Dependent Variable: Distinct species count (S)

Table 6. Linear model analyzing the effects that temperature and cypress dome area have on the diversity (Shannon Diversity index) of epiphytes in the Big Cypress National Preserve ($p < 0.05$, $df = 17$).

a) Model Summary[f]

Model	R Square	Adjusted R Square	Std. Error of the Estimate
1[a]	0.44	0.41	0.14
2[b]	0.02	-0.04	0.19
3[c]	0.15	0.09	0.18
4[d]	0.58	0.52	0.13
5[e]	0.60	0.51	0.13

a Predictors: (Constant), Area (m^2)
b Predictors: (Constant), Relative north-south position
c Predictors: (Constant), Interaction: Position*Area
d Predictors: (Constant), Area (m^2), and Relative north-south position
e Predictors: (Constant), Area (m2), Relative north-south position, Interaction: Position*Area
f Dependent Variable: Shannon Diversity index (H')

b) Coefficients[a]

Model		Coefficients	Standardized Coefficients	t	Sig.
1	(Constant)	1.35		23.73	< 0.001
	Area (m^2)	1.5e-5	0.666	3.57	0.003
2	(Constant)	1.48		20.99	< 0.001
	Relative n-s	1.7e-6	0.15	0.59	0.56
3	(Constant)	1.46		26.35	< 0.001
	Interaction	3.6e-10	0.38	1.65	0.12
4	(Constant)	1.24		16.99	< 0.001
	Area (m^2)	1.7e-5	0.78	4.45	< 0.001
	Relative n-s	4.6e-6	0.39	2.19	0.045
5	(Constant)	1.20		14.30	< 0.001
	Area (m^2)	2.0e-5	0.92	3.94	0.001
	Relative n-s	6.8e-6	0.58	2.07	0.058
	Interaction	-2.3e-10	-0.25	-0.88	0.39

a Dependent Variable: Shannon Diversity index (H')

Table 7. Linear model analyzing the effects that temperature and cypress dome area have on the diversity (Simpson's index) of epiphytes in the Big Cypress National Preserve ($p < 0.05$, $df = 17$).

a) Model Summary[f]

Model	R Square	Adjusted R Square	Std. Error of the Estimate
1[a]	0.26	0.22	0.049
2[b]	0.12	0.06	0.054
3[c]	0.16	0.11	0.052
4[d]	0.54	0.47	0.040
5[e]	0.59	0.50	0.039

a Predictors: (Constant), Area (m^2)
b Predictors: (Constant), Relative north-south position
c Predictors: (Constant), Interaction: Position*Area
d Predictors: (Constant), Area (m^2), and Relative north-south position
e Predictors: (Constant), Area (m2), Relative north-south position, Interaction: Position*Area
f Dependent Variable: Simpson's index (D_s)

b) Coefficients[a]

Model		Coefficients	Standardized Coefficients	t	Sig.
1	(Constant)	0.69		35.67	< 0.001
	Area (m^2)	3.4e-6	0.51	2.39	0.029
2	(Constant)	0.70		35.56	< 0.001
	Relative n-s	1.2e-6	0.34	1.45	0.17
3	(Constant)	0.71		43.84	0.0
	Interaction	1.1e-10	0.40	1.75	0.099
4	(Constant)	0.64		28.47	< 0.001
	Area (m^2)	4.5e-6	0.68	3.69	0.002
	Relative n-s	1.9e-6	0.55	2.97	0.01
5	(Constant)	0.62		24.85	< 0.001
	Area (m^2)	5.8e-6	0.88	3.74	0.002
	Relative n-s	2.9e-6	0.84	2.96	0.010
	Interaction	-1.0e-10	-0.37	-1.33	0.21

a Dependent Variable: Simpson's index

Table 8. Linear model analyzing the effects that temperature and cypress dome area have on the evenness (Shannon's measure of evenness) of epiphyte distribution in the Big Cypress National Preserve ($p < 0.05$, df = 17).

a) Model Summary[f]

Model	R Square	Adjusted R Square	Std. Error of the Estimate
1[a]	0.047	-0.013	0.094
2[b]	0.51	0.48	0.068
3[c]	0.078	0.02	0.093
4[d]	0.51	0.45	0.070
5[e]	0.58	0.49	0.067

a Predictors: (Constant), Area (m^2)
b Predictors: (Constant), Relative north-south position
c Predictors: (Constant), Interaction: Position*Area
d Predictors: (Constant), Area (m^2), and Relative north-south position
e Predictors: (Constant), Area (m2), Relative north-south position, Interaction: Position*Area
f Dependent Variable: Species evenness (J')

b) Coefficients[a]

Model		Coefficients	Standardized Coefficients	t	Sig.
1	(Constant)	0.73		19.70	< 0.001
	Area (m^2)	-2.4e-6	-0.22	-0.89	0.39
2	(Constant)	0.63		25.21	< 0.001
	Relative n-s	4.2e-6	0.72	4.10	0.001
3	(Constant)	0.68		23.90	< 0.001
	Interaction	1.3e-10	0.28	1.16	0.26
4	(Constant)	0.63		16.04	< 0.001
	Area (m^2)	2.2e-8	0.002	.010	0.99
	Relative n-s	4.2e-6	0.72	3.780	1.8e-3
5	(Constant)	0.60		13.83	< 0.001
	Area (m^2)	2.5e-6	0.23	0.96	0.36
	Relative n-s	6.1e-6	1.04	3.63	0.003
	Interaction	-2.0e-10	-0.42	-1.47	0.16

a Dependent Variable: Species evenness (J')

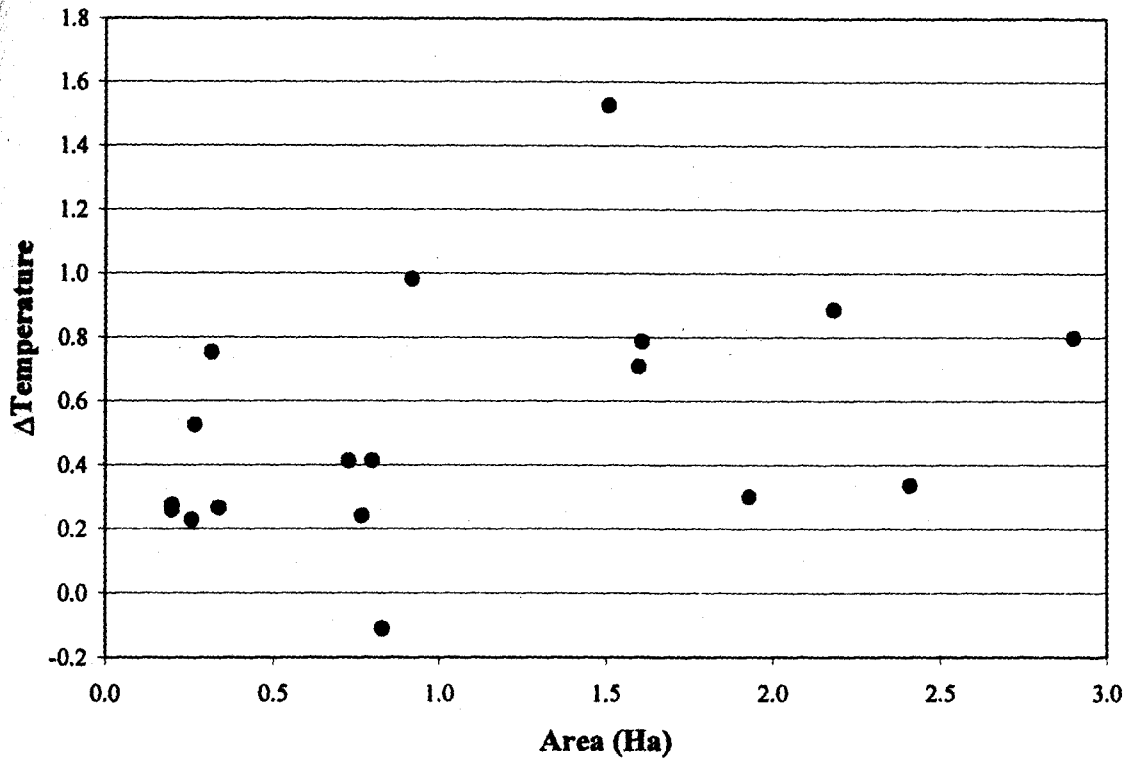
The final analysis examined the effects of temperature on epiphyte diversity within the domes. Paired sample t-tests were calculated for each dome to determine if the temperature at the dome's approximate center was significantly different from its edge temperature (Table 9). In all cases, the temperature at the center of a dome was significantly different from the edge temperature ($p < 0.05$). These differences were then plotted against each dome's area and its relative north-south position to examine for correlations (Figure 9). No discernible patterns were evident, therefore the relationship between quadrat diversity and quadrat position within a dome was analyzed (see below).

Diversity Analysis within Domes

The raw species counts and the three measures of diversity used in earlier analyses were calculated for each quadrat sampled. Each measure was plotted against the distance from the quadrat to the nearest dome edge (Figures 10 & 11). All of the measures increased as distance from the edge increased, but Species counts, Simpson's diversity, and Shannon diversity increased more significantly than did evenness. In addition the graphs clearly indicate that these increases were not merely a factor of dome size.

Isotherm	Dome	df	Mean ΔTemperature	Std. Error	Sig. (2-tailed)
Cold (North Region)	P	145	0.30	0.033	< 0.001
	Q	67	0.78	0.064	< 0.001
	R	67	0.26	0.058	< 0.001
	K	67	-0.11	0.033	0.001
	J	90	0.69	0.049	< 0.001
	L	64	1.52	0.083	< 0.001
	M	9	0.27	0.10	0.025
	N	145	0.85	0.045	< 0.001
	O	67	0.80	0.058	< 0.001
Warm (South Region)	B	55	0.36	0.039	< 0.001
	C	127	0.21	0.026	< 0.001
	A	69	0.56	0.051	< 0.001
	D	141	0.39	0.037	< 0.001
	F	52	0.35	0.061	< 0.001
	E	55	0.55	0.056	< 0.001
	I	66	0.77	0.068	< 0.001
	G	141	0.78	0.048	< 0.001
	H	70	0.37	0.056	< 0.001

Table 9. Paired t-test ($p < 0.05$) of the differences between the temperature at the approximate center and at the edge in each cypress dome during the cold season. Domes are classed by isotherm and size (from smallest to largest in each region). Each dome was assigned a letter designation (a-r) for identification purposes. Domes j and m had missing recording days due to battery failures in key loggers. Domes b, c, e, and f have missing data; they were started after the first cold season had begun, and their memories were filled to capacity 14 days before their last download. In January of the second cold season data from the warm domes was downloaded 3 days before data was downloaded from the cold domes. Data missing from the remaining domes is a result from being started after the first cold season had begun.



B)

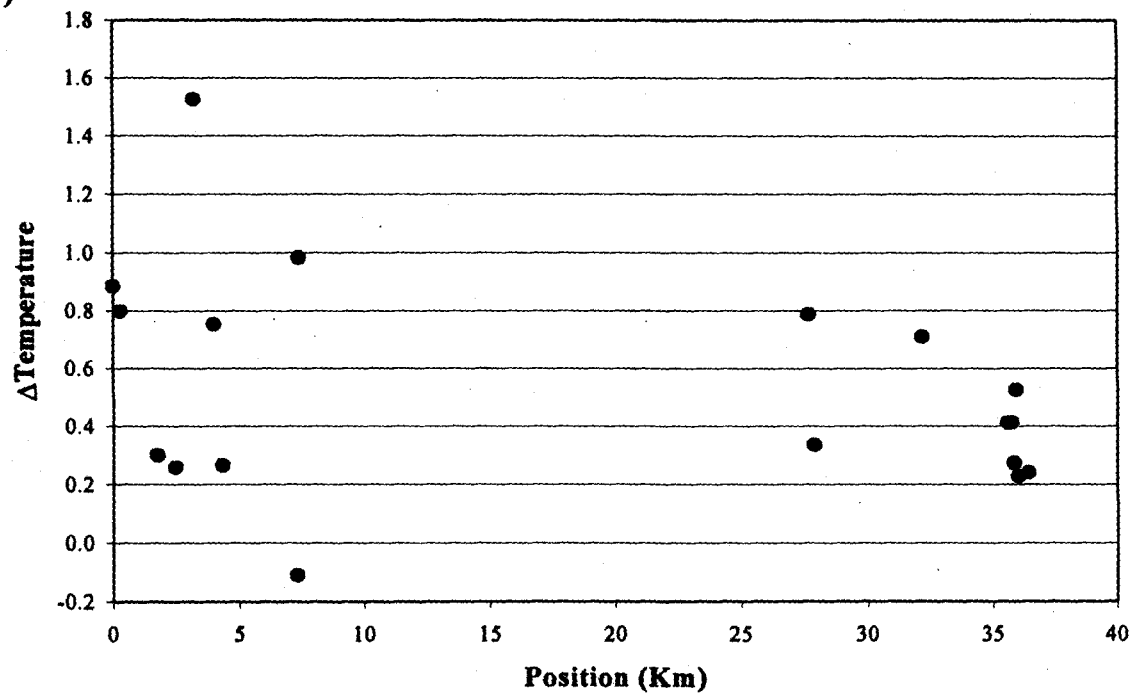


Figure 9. Temperature differences between each dome's approximate center and edge plotted against its area (A) and relative north-south position (B).

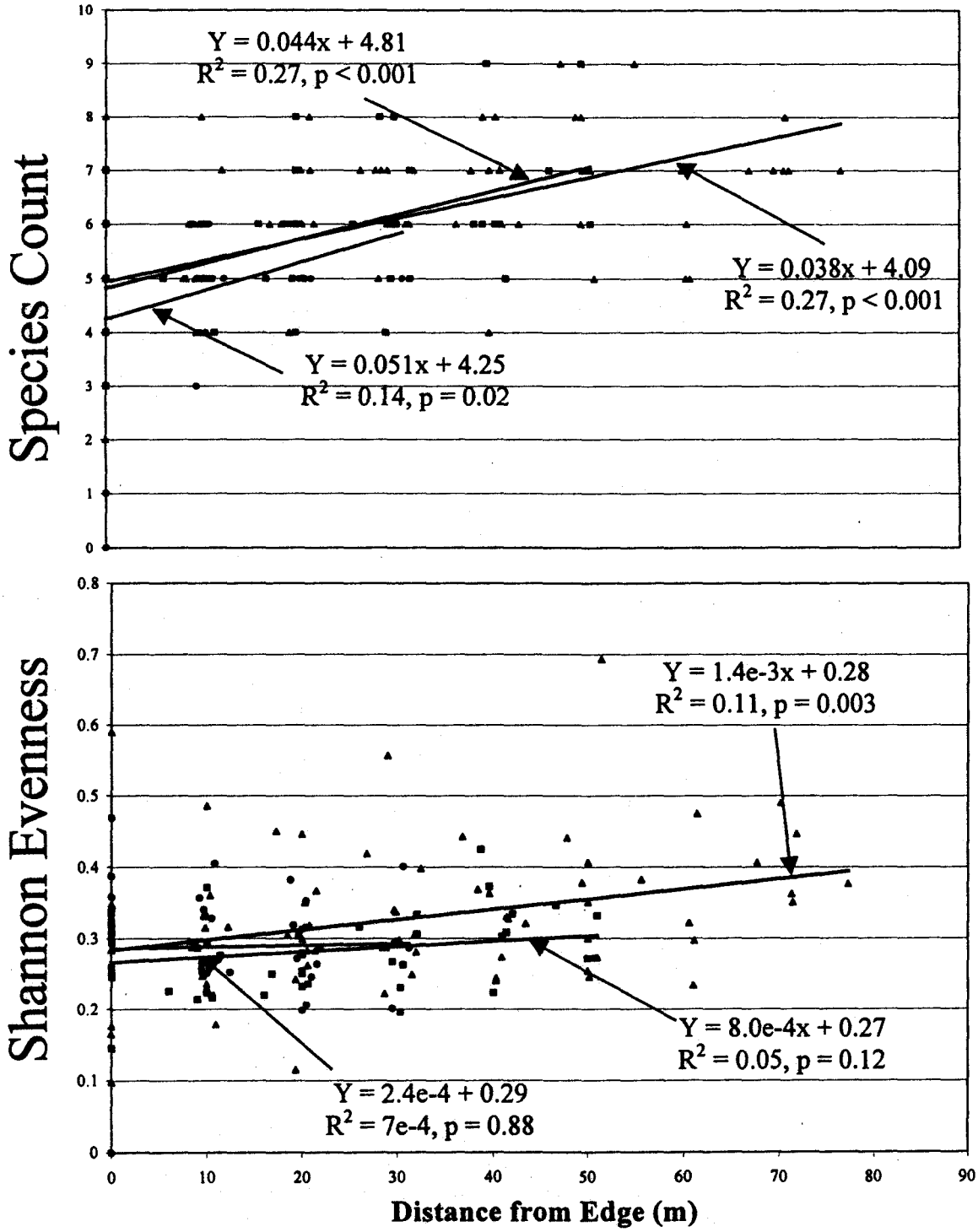


Figure 10. Raw species count (S) and species evenness (as measured using Shannon's measure of evenness (J')) per quadrat plotted against the distance (in meters) from the nearest dome edge. ● = small domes, ■ = medium domes, ▲ = large domes.

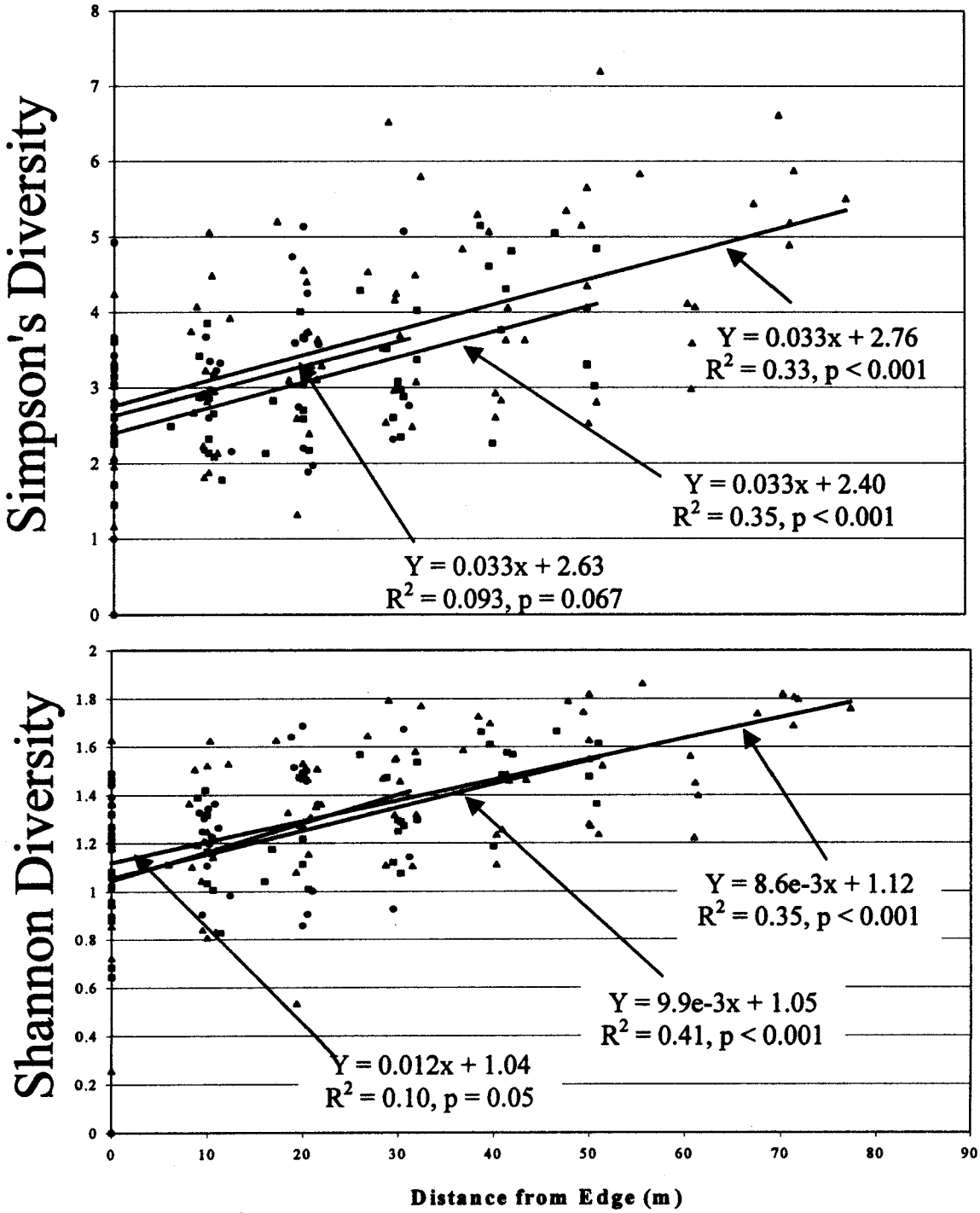


Figure 11. Species diversity (as measured using Simpson's diversity index (D_s) and Shannon's diversity index (H')) per quadrat plotted against the distance (in meters) from the nearest dome edge. ● = small domes, ■ = medium domes, ▲ = large domes.

Discussion

This study showed that epiphyte diversity in cypress domes adheres to the species-area relationship as expressed by Preston (1962); specifically, larger domes have more species of epiphytes than smaller domes. While the positive correlation between basal area and dome size might be a factor, it likely indicates that the larger domes provide conditions that allow larger tree growth. In turn, these larger trees provide more area for epiphytes to colonize, thus the larger domes have more epiphytes.

When the dome areas and measures of diversity were analyzed using linear regression, species diversity (as measured using the Shannon diversity index) increased with area, however, epiphyte evenness was not significantly affected. The data exhibited a greater diversity as well as a greater across dome temperature difference for larger domes compared to smaller domes in the same region. Although it does not prove cause and effect, it does lend support to my first hypothesis—that larger domes have greater diversity because they moderate temperature extremes better than smaller domes.

The hypothesis regarding epiphyte diversity in subtropical versus more temperate domes, was addressed using the Shannon diversity index. Linear regression supported this hypothesis with respect to richness and evenness. The size of cypress dome had less of an impact on epiphyte diversity and evenness in the southern compared to the northern region. This was likely the result of the diminished difference in temperature across domes in the more subtropical climate as compared to the

northern domes. Finally, the analysis showed that the differences in diversity in the regions converged as dome size increased. Since the larger domes have the greatest across dome temperature differences, the domes in the cold region were likely able to produce more subtropical temperature niches, allowing for greater epiphyte diversity, thus explaining the convergence.

The final hypothesis, that a measurable temperature gradient existed within cypress domes, was substantiated by the significant differences in the temperature at the domes' edges compared to that at their approximate centers. In 17 of 18 cases, the center of the dome was warmer than the edge. Due to mitigating factors, such as pond surface area and volume and the complexity of convective systems (which is hypothetically how domes function), it was not possible to establish an accurate model of temperature across a dome. Further study of cypress dome microclimate dynamics would be necessary to develop an accurate model.

An increase in diversity, but not evenness, from the edge to the center within each dome was observed. This increase in diversity but not evenness indicated factors occurring within domes that increase with area. For instance, in small domes the *Tillandsia* species dominated to such a degree that evenness appeared high, however as domes increased in size, rarer epiphytes became more prevalent and caused evenness to decrease. Further research is required to determine whether these factors are niche-based, climate-oriented, or an interaction of the two.

Ultimately, it was shown that epiphyte diversity in cypress domes adhered to the species-area model. My findings lend credence to the Preston (1962) model by addressing some of the controversy that has been raised. One such objection focused on

the idea that prior studies have largely been ornithological, therefore restricting the model exclusively to bird habitats (Gilbert, 1980; Margules et al., 1982; Zimmerman & Bierregaard, 1986). Since my study dealt with perennials, it increased the range of organisms that fit the model, thus lending further support to it. Others have objected that oceanic islands are significantly different from continental habitat islands and reserves (Margules et al., 1982; Wright & Hubbell, 1983; Mader, 1984; Zimmerman & Bierregaard, 1986), and that islands created by human-made barriers to dispersal are not actually described by this model. However, human-made borders and barriers may affect natural systems active in preserves in such a way that they need much more time to reach equilibrium than critics have allowed; after all, these systems originally took thousands of years to develop. This does not mean that the species-area model can not be used as a tool for the creation and analysis of preserves. Although the model should not be used as the primary tool, it does provide a good starting point since it offers order and mathematical backing to the logical assumption that larger areas will harbor more species than smaller areas.

There have been objections as to how the species-area model is used (Zimmerman & Bierregaard, 1986), however, the model only answers the question as to whether or not area and species number are related, not why they are related. Only after a relationship is determined, can a cause be addressed. In this study, the model was used to establish a relationship between epiphyte diversity and cypress dome size and correlative reasons for this relationship were examined. In this case, climate appeared to be a significant factor in explaining the relationship between dome area and epiphyte diversity. Even across the relatively short distances examined in this study, dome size

was found to greatly affect epiphyte diversity. These climatic differences were muted as dome size increased, presumably the result of temperature buffering capabilities of larger domes. This accentuates the importance of habitat size on diversity in conjunction with other regional factors.

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Appendix A

A list of the epiphytes found growing in cypress domes in the Big Cypress National Preserve.

Ferns and Fern Allies

POLYPODIACEAE - Polypody Fern Family	
Campyloneurum phyllitidis (L.) C. Presl	Long Strap Fern
Phlebodium aureum (L.) J. Sm.	Golden Polypody
Pleopeltis polypodioides (L.) E.G. Andrews & Windham var. *michauxiana* (Weath.) E.G. Andrews & Windham	Resurrection Fern
PSILOTACEAE - Psilotum Family	
Psilotum nudum (L.) P. Beauv.	Whisk Fern
THELYPTERIDACEAE - Marsh Fern Family	
Thelypteris kunthii (Desv.) C.V. Morton	Widespread Maiden Fern
VITTARIACEAE - Shoestring Fern Family	
Vittaria lineata (L.) Sm.	Shoestring Fern

Monocotyledons

BROMELIACEAE - Pineapple Family	
Tillandsia balbisiana Schult. & Schult. f.	Northern Needleleaf
Tillandsia fasciculata Sw. var. *densispica* Mez.	Cardinal Air Plant
Tillandsia paucifolia Baker	Potbelly Airplant
Tillandsia recurvata (L.) L.	Ball Moss
Tillandsia setacea Sw.	Southern Needleleaf
Tillandsia usneoides (L.) L.	Spanish Moss
Tillandsia variabilis Schtdl.	Leatherleaf Air Plant
Tillandsia sp.	
ORCHIDACEAE - Orchid Family	
Cyrtopodium punctatum (L.) Lindl.	Cowhorn Orchid
Encyclia tampensis (Lindl.) Small	Florida Butterfly Orchid

Epidendrum nocturnum Jacq.	Night-Scented Orchid
Epidendrum rigidum Jacq.	Rigid Epidendrum
Harrisella filiformis (Sw.) Cogn.	Needleroot Airplant Orchid