

AN ABSTRACT OF THE THESIS OF

Minh D. Le for the degree of Master of Science in Geography presented on Sep 27, 1999.

Title: Distribution Patterns of Reptiles and Amphibians in Puerto Rico

Abstract approved: _____

Gordon E. Matzke

This study examined the question of whether a big island can be divided into many smaller islands with the same pattern of area-species curve as that of the complete island. To address this question, this study used data on the number and distribution of amphibians and reptiles on Puerto Rico and landbridge islands of the Puerto Rican Bank, which were fragmented from the big island about 10,000 years ago. In Puerto Rico, the data show correlations between the number of species and area available at different elevation levels and between species and area after removing effects of elevation. These patterns are different from the patterns of correlation between area and the number of reptiles and amphibians on 29 islands on the Puerto Rican Bank. The area-species curves of the elevationally and areally subdivided "islands" on Puerto Rico tend to have steeper slopes than the curves of the

Puerto Rican Bank islands. Analyses of area and the number of those species on fragmented habitat islands at different elevations also indicated correlation between them. However, patterns of correlation seem not to be the same at each altitude. The slope of the area-species curve seems to decrease with increasing elevation levels. Other patterns of species distribution of Puerto Rico's herpetofauna are: there are linear relationships between the number of species and elevation, the number of species and distance from the coast, and the number of species and the species range areas. Multiple regression analyses of three variables: area, precipitation, and elevation, suggested that variation of species distribution in Puerto Rico is partly caused by interactions among these variables. Elevation plays an especially important role in explaining reptile and amphibian distribution. The rainfall variable had the least effect on determining herpetofauna diversity. The study results suggest that area-species correlation is a consequence of habitat heterogeneity on the island.

**Distribution Patterns of Reptiles and Amphibians
in Puerto Rico**

by

Minh D. Le

A THESIS

submitted to

Oregon State University

in partial fulfillment of

the requirement for the

degree of

Master of Science

Presented Sep 27, 1999

Commencement June, 2000

Master of Sciences thesis of Minh D. Le presented on Sep 27, 1999

APPROVED:

Major Professor, representing Geography

Chairman of Department of Geosciences

Dean of the Graduate School

I understand that my thesis will become part of the department collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Minh D. Le, Author

Acknowledgments

First of all, I would like to thank Dr. Ross Kiester for his help in all aspects throughout the process of doing this thesis. He inspired me with his ideas about island biogeography and patterns of species distribution in the West Indies. I have greatly benefited from conversations with him. In addition, his assistance as well as encouragement become an integral part of this thesis. I also wish to thank Dr. Gordon Matzke for the suggestions and encouragement in the course of conducting this research as well as throughout my education in the Department. Dr. A. Jon Kimerling has helped me a lot from the beginning when the thesis was only an idea. He was always willing to provide assistance in spatial analyses and map and image processing. Dr. Chris Daly guided me in making the rainfall maps and patiently discussed problems with me.

A number of individuals provided support in the completion of this research. Mark Meyer assisted me with many aspects in the process of undertaking the thesis. He was the lead person in building the database that made this research possible. Eileen Helmer kindly let me use unpublished data. Tim Worley helped me improve the writing of the thesis draft. I also would like to thank Linh Nguyen, Vinh Nguyen, and Matthew Gregory for their help and discussion of the problems I faced. I wish to thank Mr. David Hulse and WWF fellowship for funding my study at Oregon State University.

Finally, my special thanks go to my wife Tran Ngoc Hoa. Without her support and encouragement, I could have never finished this work. She helped me overcome very tough times in the process of doing this research. I also wish to thank my parents for their support and sacrifices that have made my education possible.

TABLE OF CONTENTS

1.0	Introduction	1
2.0	Database	7
3.0	Methods of Data Analysis	11
4.0	Results	17
5.0	Discussion	29
6.0	Conclusion	36
	Literature Cited	37
	Appendices	
	Appendix 1: Maps of Puerto Rico	40
	Appendix 2: Summary Statistics	44

LIST OF FIGURES

FIGURE 1.	The area-species curve of the West Indian herpetofauna (after MacArthur and Wilson, 1967).....	2
FIGURE 2.	Paleogeography map of the Puerto Rican Island Shelf.....	5
FIGURE 3.	Distribution of <i>Anolis cristatellus</i> in Puerto Rico	8
FIGURE 4.	Number of amphibian and reptile species per hexagon.....	9
FIGURE 5.	Fragmentation of Puerto Rico at 500m.	12
FIGURE 6.	Subdivision by distance from the coast.	14
FIGURE 7.	The area-species curves of Puerto Rican Bank's islands and vertically subdivided islands in Puerto Rico.....	18
FIGURE 8.	Correlation between amphibian and reptile diversity and elevation in Puerto Rico.....	19
FIGURE 9.	The area-species curves of fragmented island habitats at 60m altitude....	20
FIGURE 10.	The area-species curves of fragmented island habitats at 750m altitude...	21
FIGURE 11.	The area-species curve based on the hexagon grid... ..	22
FIGURE 12.	Correlation between number of species and distance from the coast.	23
FIGURE 13.	The area-species curve with increasing distance from the coast.....	24
FIGURE 14.	Relation between Puerto Rican herpetofauna and rainfall.	25
FIGURE 15.	Residuals plotted with fitted values between species diversity and the combination of the three variables of area, elevation, and rainfall.....	26
FIGURE 16.	Residuals plotted with fitted values between species diversity and elevation and rainfall.....	27
FIGURE 17.	Relation between the number of reptiles and amphibians and their range areas.....	28

Distribution Patterns of Reptiles and Amphibians in Puerto Rico

1.0 Introduction

Patterns of species distribution on islands are always of interest to biogeographers and ecologists. This interest goes back to Wallace's book, *Island Life* (1880), with his ideas about the importance of islands in studying distribution of species. MacArthur and Wilson (1967) in their influential book about the theory of island biogeography tried to quantify the relationship between island area and the number of resident species. Their theoretical formation stated that this relationship could be described by the equation $S=CA^z$, where S is the number of species on an island, A is area of the island, and C and z are constants and depend on the taxon. MacArthur and Wilson (1967) drew an area-species curve for herpetofauna of the West Indies (Figure 1).

According to the theory, the ecological processes of extinction and colonization are major factors determining species diversity on islands. This idea builds on the concept of species equilibrium in which the species richness on an island is a result of the equilibrium of the two processes of extinction and colonization. Extinction and colonization processes, in turn, were believed to be strongly dependent on island area and distance from source areas, respectively.

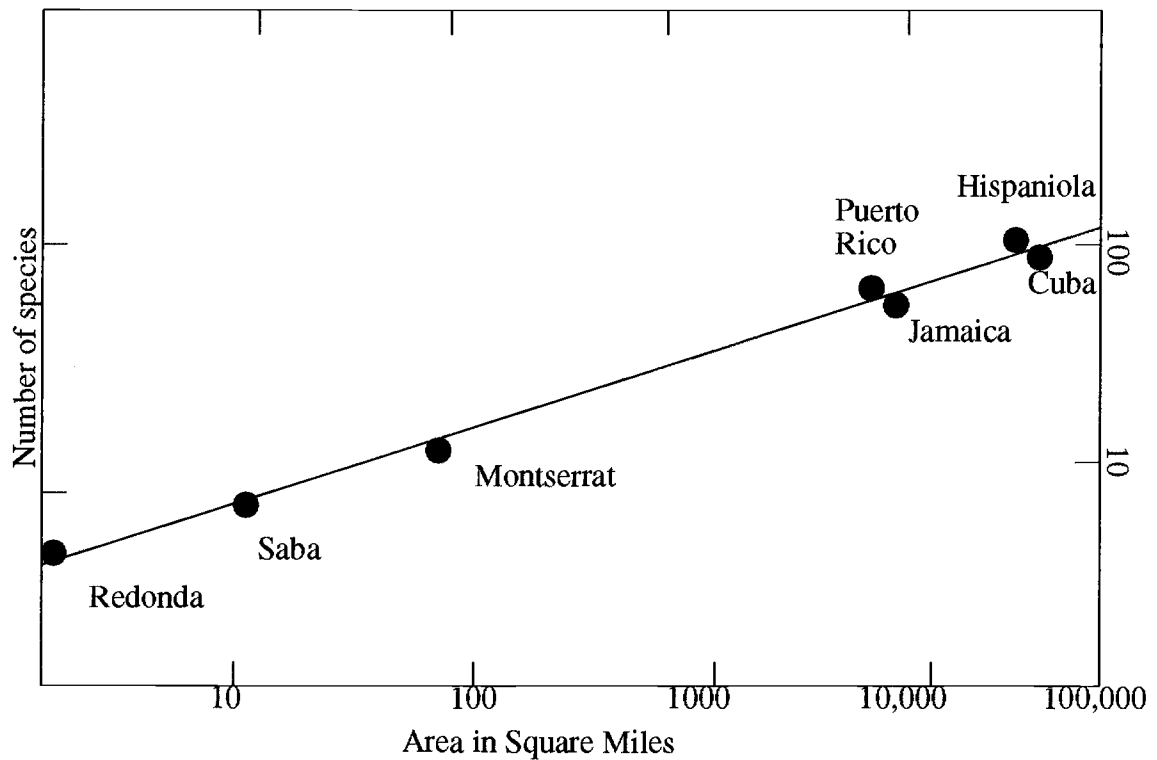


FIGURE 1. The area-species curve of the West Indian herpetofauna (after MacArthur and Wilson, 1967).

MacArthur and Wilson's theory has inspired many subsequent studies conducted in order to test the theory. These works showed that the relationship held, and that the z value normally fell within the range from 0.20 to 0.35 as also indicated by the theory (Losos, 1998). In reality, it is not so simple. The number of species on an island is the product of many factors, such as habitat diversity, climate, and elevation, which are positively correlated with island area (Hedges, 1996). In fact, MacArthur and Wilson (1967) also admitted that area seldom has direct effect on a species occurrence, and that the lack of good data on diversity of habitat led to their use of area as an explanatory variable.

Using the equilibrium theory of island biogeography to explain the correlation between the number of species and area of islands deemphasizes the importance of habitat diversity, and proposes an "area-per se hypothesis" (Connor and McCoy, 1979). The theory also has been criticized for ignoring important aspects of the biology of species, for considering all species equally in the stochastic processes of colonization and extinction, and for not considering the historical factors (Williamson, 1981).

Rand (1969) and Losos (1998) noted in their studies on more than 100 islands in the West Indies that the effect of island area on the number of anole species existed only among land-bridge islands (islands which were once connected to big land masses). The generally limited success of these species in overwater colonization of oceanic islands makes it rare for these islands to have more than two species of anoles. According to Rand (1969), this pattern is probably a result of fluctuation of sea level during the Pleistocene period when land-bridge islands received their fauna through overland colonization. These two distinct processes are probably major causes producing the pattern of varying species richness between oceanic and landbridge islands.

Losos (1998) also indicated that the species-area relationship among Greater Antilles anoles primarily is a result of evolutionary factors. To understand the patterns of species distribution on islands, he suggested that ecological, evolutionary, and historical factors affect species distribution and need to be simultaneously examined. Thus, the species-area

relationship is produced by the integration of many factors. Other authors [Abele (1974), Harman (1972), and Dexter (1972)] also demonstrated a positive correlation between species number and number of habitats (Connor and McCoy, 1979). Therefore, there is a need to test the correlation between the number of species on an island and the island's area. This study will test both the "habitat-diversity hypothesis" and the "area-per se hypothesis" by using other variables such as rainfall and elevation.

Roughgarden (1989) showed that the pattern of species distribution in the cays of Bahamas and Puerto Rico, which were united in a few large banks in the last ice age, about 10,000 years ago, seems to be the result of extinction alone. These islets today, which used to be hill tops during the low sea level period, thus, contain remnant special subsets of the larger fauna that experienced the sea level rise. Losos (1998) also wrote, "The cause of this nesting of species probably is a result of habitat specializations. Islands lose habitats in a predictable pattern as they get smaller, which would result in a deterministic pattern of species disappearance". Figure 2 shows a Paleogeography map of Puerto Rico during the Pleistocene. The island at that time was twice as big as it is today. Subsequent sea level rise has created many smaller cays now in existence.

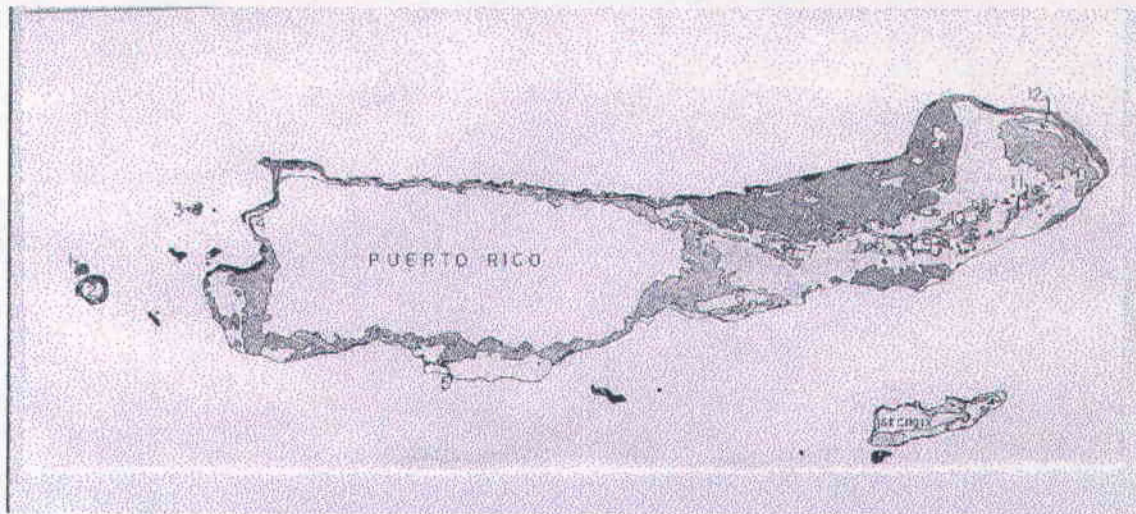


FIGURE 2. Paleogeography map of the Puerto Rican Island Shelf. Largest outline indicates land configuration at maximum sea-level lowering during the Pleistocene. Black areas indicate additional area submerged at 14,000 B. P., cross-hatching presents areas submerged between 14,000 and 10,000 B. P., stippling represents those submerged between 10,000 and 8000 B. P., and the diagonal lines the area submerged between 8000 and 6000 B. P. (Heatwole and MacKenzie, 1966).

The studies above also raise this question: How do species react to the shrinking of island area as sea level rises? In other words, if the structure of the community of species on an island is already in the form predicted by the species-area curve because of species' "habitat specialization", is the species- area curve produced by subsequent interactions among species still worth examining? MacArthur (1972) in his study of bird diversity in New Guinea pointed out that the number of species on the mountain, also viewed as a habitat island by itself, were somewhat correlated with the elevation of the mountain. This pattern

is probably due to the combination of area, habitat diversity, and elevation effects. A mountain range contains a number of vegetation zones separated by altitude. The number of species decreases with increasing altitude in the mountain range as a result of the smaller area available and less diverse habitats at higher elevations. Based on this point of view, an island can be divided into a number of smaller islands corresponding to certain elevation levels. These smaller islands will have distinct characteristics of area, habitat diversity, and number of species.

The questions above are tested using Puerto Rican herpetofauna since the data for reptiles and amphibians are well documented by Schwartz and Henderson (1991). Detailed data on the island's elevation and precipitation, which are rare for other islands in the West Indies, are also available. Therefore, to address the relationship between area and the number of species on the island, this study focuses on the distribution of Puerto Rican herpetofauna. The island is subdivided by elevation, area, precipitation regions, and distance from the coast in this study. The relationship between area and the number of amphibians and reptiles on 29 landbridge islands within the Puerto Rican Bank (including the Virgin Islands) is also tested. This relationship is then compared to the patterns of correlation between area and the number of species on the islands produced by the above subdivisions in Puerto Rico.

1.0 Database

All data about the number of reptiles and amphibians, and their distribution in Puerto Rico, were compiled from Schwartz and Henderson (1991). The data are in the form of point locality records, which the authors put together from a large number of sources including field notes and computer printouts from collections. The data are quite complete, but these point locality data were recorded on small scale maps. The size of the points is quite big compared to map scale, therefore, the original spatial accuracy of points is subject to considerable error.

These data were digitized by using the software ARC/INFO (ESRI, 1996). In the process of entering the data to the computer, all the points were checked carefully to make sure that errors were not introduced through this process. The final data set used in this study included the 1039 point localities belonging to a total of 55 amphibian and reptile species after all points falling outside Puerto Rico were removed. The data show that some species in Puerto Rico are widely distributed around the island (Figure 3). The distribution of all amphibians and reptiles on the island is displayed on the species richness map (Figure 4).

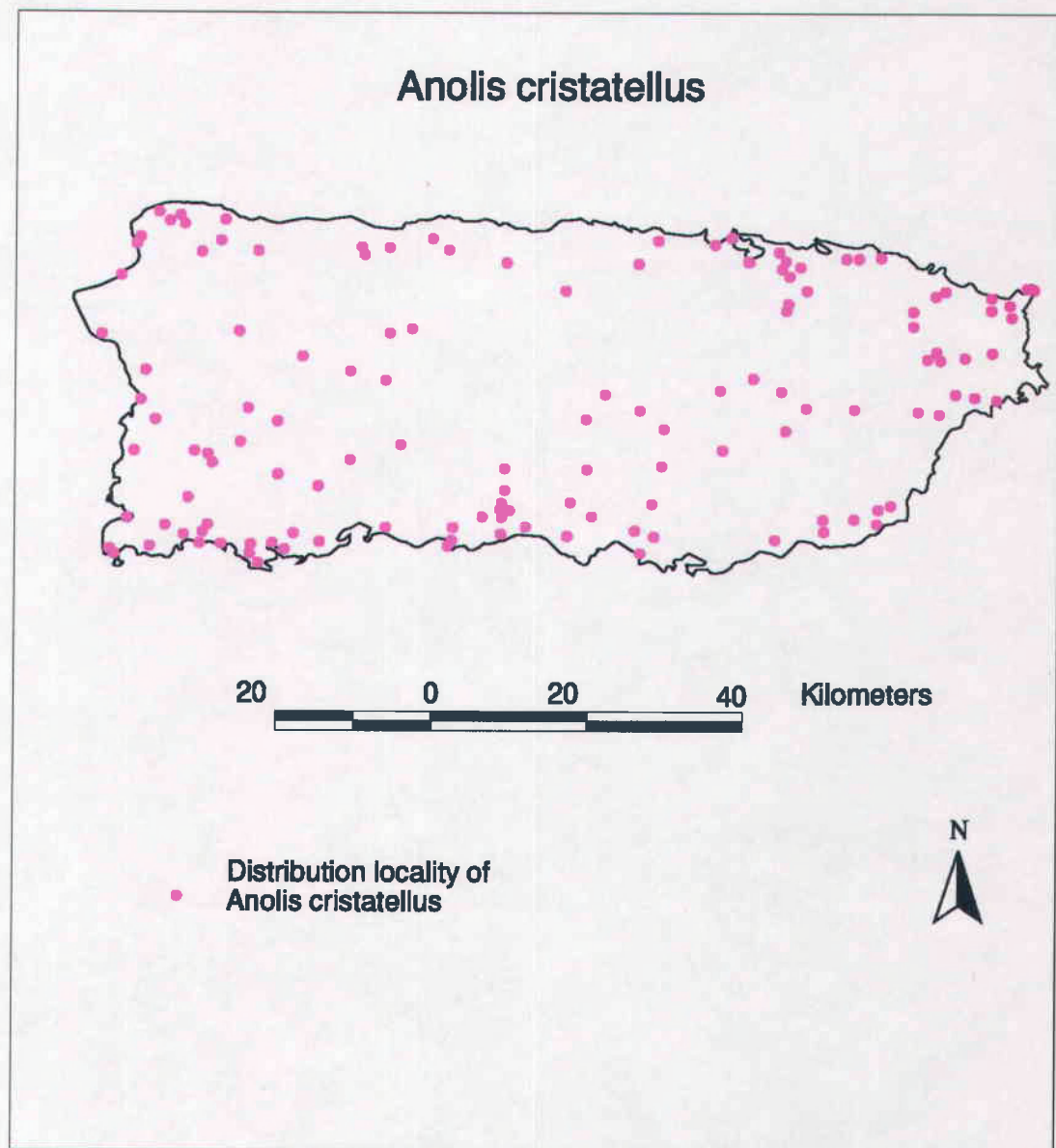


FIGURE 3. Distribution of *Anolis cristatellus* in Puerto Rico. This is one of the most widely distributed species of the herpetofauna in Puerto Rico.

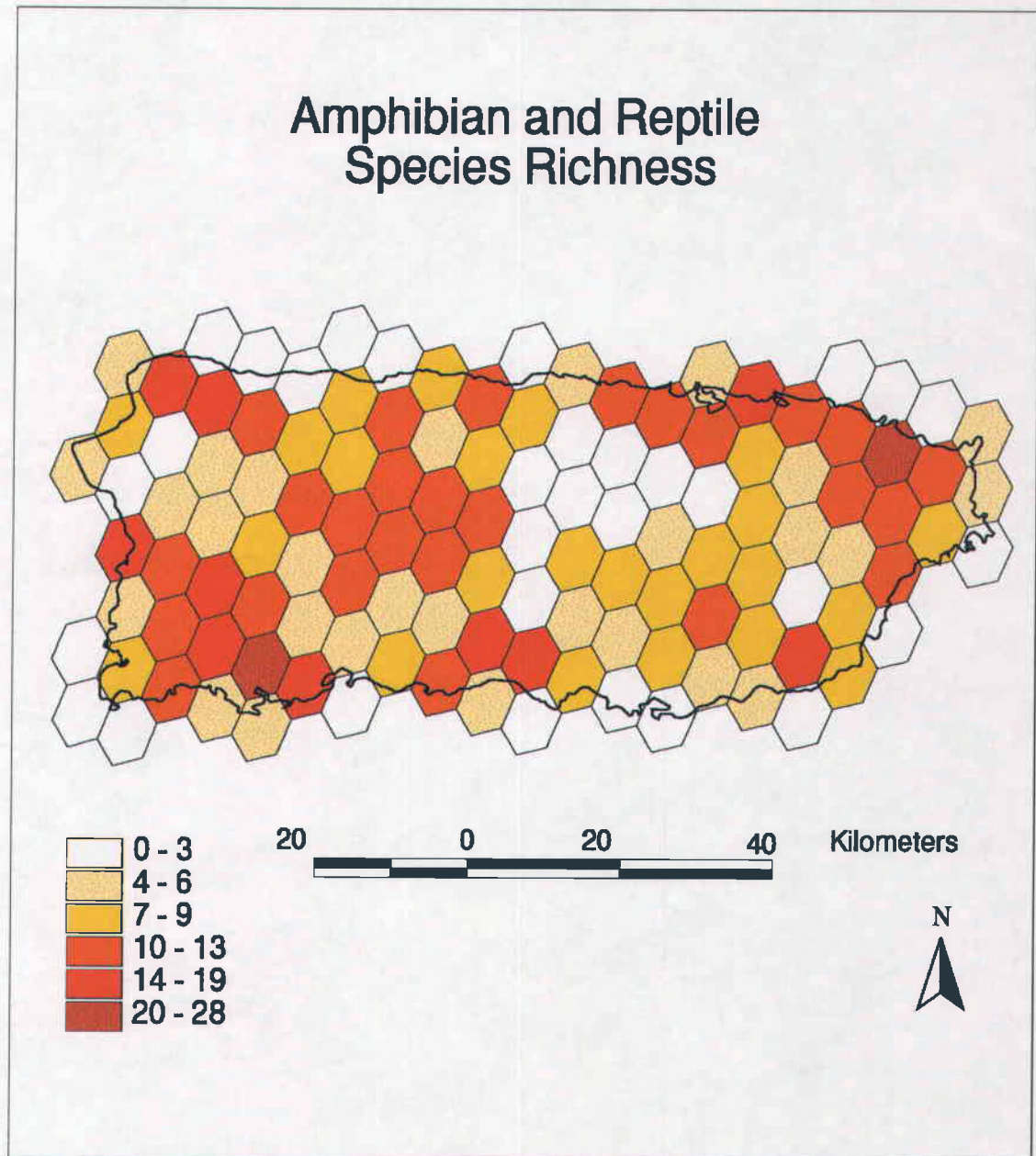


FIGURE 4. Number of amphibian and reptile species per hexagon. Data are compiled from distribution point localities for the 55 species in Puerto Rico.

The number of herpetofauna species on the 29 islands of the Puerto Rican Bank and data about the islands' areas were compiled from Rand (1969) and Maclean (1977). This data set included islands with areas ranging from 0.324 km² (Dog Island) to 8891.643 km² (Puerto Rico). Elevation and area data for Puerto Rico were acquired from USGS's DEM (Digital Elevation Model from United States Geological Survey). This DEM is in the 3-arc second format (compiled from 1:250,000 scale topographic maps), with integer elevation data value ranging from 1m to 1338m. The whole island, thus, is covered by a total of 1,062,684 pixels, which have a spatial resolution of about 90 meters. The map used for digitizing species point localities was clipped from the Digital Chart of the World (ESRI, 1992), which was compiled from 1:1000,000 scale aeronautical charts.

Precipitation data for Puerto Rico were acquired from the USDA's International Institute of Tropical Forestry in Puerto Rico (Figuerola, unpubl. map) in the form of an unpublished map from the USDA Forest Service. The data are in the form of an ARC/INFO grid with a scale of about 1:225,000 with floating point rainfall data values ranging from 762mm to 5317mm. The precipitation map includes total of 868,996 pixels having a spatial resolution of about 100 meters.

2.0 Methods of Data Analysis

The digitized point locality data from Schwartz and Henderson (1991) were overlaid on the DEM, using their latitudes and longitudes, to get the elevation value (m) for each point locality. These localities' elevation values were then compared to elevation values of that at the longitudes and latitudes on 1:20,000 topographic maps of Puerto Rico (USGS, 1967). The root mean square error between elevation values from these two sources showed fair consistency (RMS=17.78m). Elevation range for each species was also determined based on these data. Correlation between precipitation and the number of species was accomplished in the same manner as that of elevation. Species point data were overlaid on the precipitation map to get the rainfall value (mm) for each point. These values and the number of species were plotted together in order to find the correlation.

The first method to subdivide the island used elevation data (subdivision method 1). The island of Puerto Rico was divided vertically into 44 smaller islands by raising elevation levels based on the elevation range of the species distribution. Areas available at each elevation level were determined from the DEM. The number of species at each elevation level was counted and a species-area curve for these 44 small islands was drawn. This curve was compared to the species-area curve drawn for 29 islands in the Puerto Rican Bank. Since Puerto Rico has been fragmented by the effect of hypothetical elevation rise (Figure 5), the fragmented island habitats at nine elevation levels were also analyzed. Areas of the frag-

mented island habitats were calculated and the number of species, which fall into these islands, was counted. Species-area curves based on these island habitats were then drawn for the nine elevation levels.

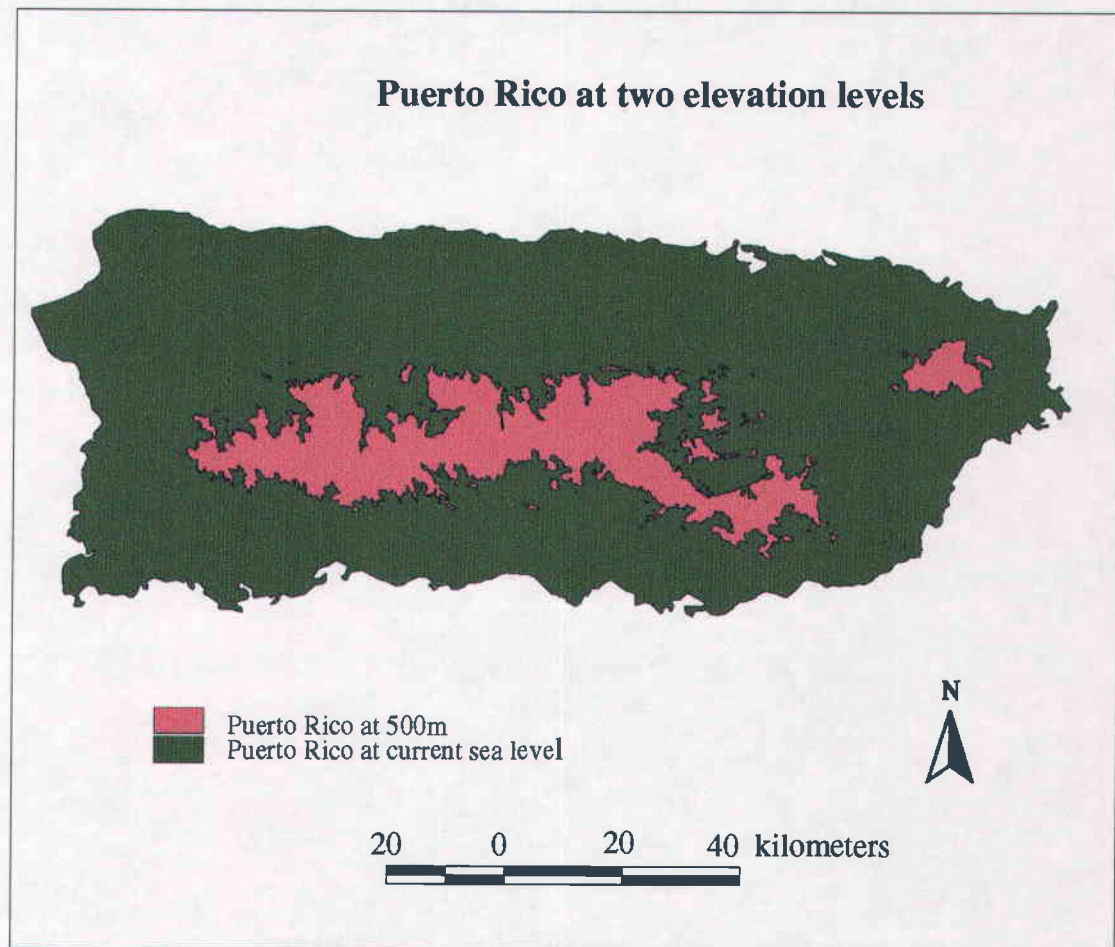


FIGURE 5. Fragmentation of Puerto Rico at 500m.

The second method involved subdividing the island into a number of polygons in order to separate the effect of area from the effect of elevation (the subdivision method 2). A hexagon grid consisting of 122 hexagons (see Figure 4) was overlaid on Puerto Rico to divide the island into small, relatively equal areas. The area of each hexagon is about 96 km² in the middle of the island. In the coastal areas, these hexagons were clipped to smaller polygons due to the shape of Puerto Rico. There is a total number of 136 polygons covering the whole island.

A simulation program (see Appendix 2) was used to select a number from 1 to 40 polygons. For each number from 1 to 40 polygons, this program used 100 different ways to choose the polygons. It selected one polygon using one-hundred different computations and then took the average of the area of these polygons as well as the average number of species that fall within these hexagons. The simulation program continued its selection procedure with 2, 3, and 4 and so on up to 40 polygons. The mean area and the mean number of species were then plotted together. This process was conducted without replacement of polygons to generate a random permutation set of polygons.

The third method of island subdivision used the distance from the coast (subdivision method 3). The assumption is that species migrating to the island will first colonize the coastal areas. These species advance to the middle of the island after adapting to the new environment. Therefore, the reduction of area with increasing distance from the coast may have an

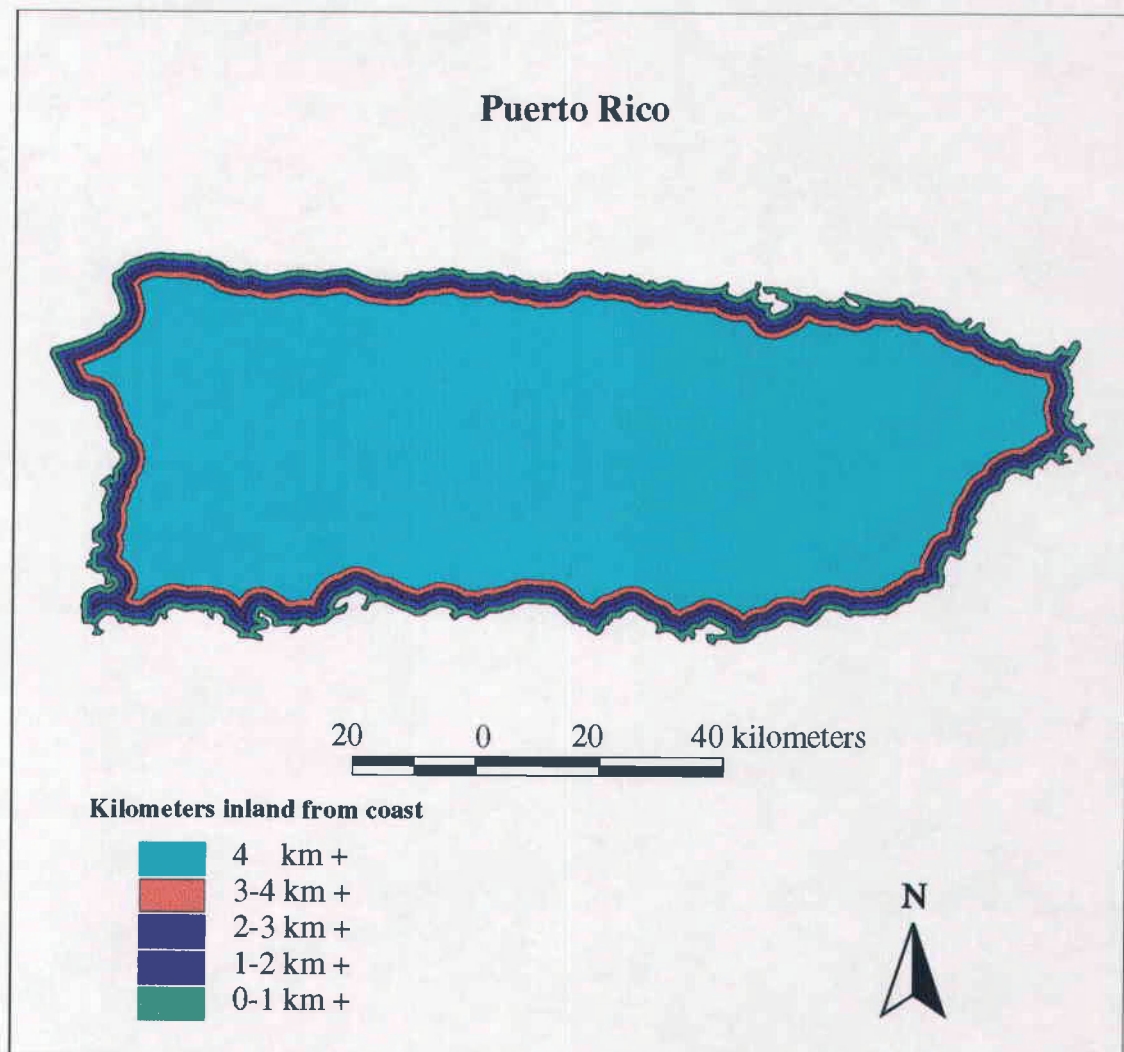


FIGURE 6. Subdivision by distance from the coast. Each polygon stands for one kilometer increment from the coast (0 km polygon is present day Puerto Rican coastline).

influence on the species diversity. Twenty-six polygons were established to define how the species number changes with increasing distance from the coast. Each polygon was created based on a 1 kilometer increment (Figure 6). The first polygon was formed by a line one kilometer inland from the coast, the second by the line two kilometers from the coast, and

so on. The area of each polygon was calculated, and the number of species resident in each polygon was determined. Finally, the area, the distance from the coast, and the number of species were plotted together.

Range areas of amphibian and reptile species in Puerto Rico were determined by using the convex polygon method (Rose, 1982). Range areas of species could not be calculated by this method if the number of their distribution locations was lower than three. The range areas and the number of species were plotted together.

Hedges (1996) indicated that, in general, amphibian and reptile species richness closely correlate with both topography and precipitation. Nevertheless, the number of species decreased with higher altitude and increased with higher rainfall. He also pointed out that rainfall is an important factor for amphibian distribution, and that high elevation is not required. However, it is difficult to separate the effects of elevation, area, and precipitation on species diversity since they are interrelated. The regions with higher rainfall are also located at high altitude, and, thus, have smaller areas.

To do a multiple regression analysis between species number and elevation, area, and precipitation, the island was divided into nine elevation and eleven precipitation classes based on elevation and precipitation values to produce 83 classes of polygons. Each polygon class, therefore, has the same elevation and precipitation values. The area of each polygon class then was determined, and the number of species distributed in each class was counted.

This study only used precipitation, area, and elevation data. Data about vegetation are much more difficult to quantify and there is little correlation between these species, especially amphibians, with any particular kind of vegetation (Hedges, 1996).

3.0 Results

The analysis of the correlation between area and the number of amphibians and reptiles on 29 islands of the Puerto Rican Bank indicated a strong relationship ($r^2=0.71$, $F_{1,27}=66.68$, $P<0.001$). There is also a strong relationship between area and number of species among subdivided islands of the first method ($r^2=0.97$, $F_{1,42}=1263$, $P<0.001$). These two curves were put together in Figure 7. Two regression fitting lines indicate the numbers of species per area unit, i.e per km^2 , on the Puerto Rican Bank's islands are higher than the numbers of species on the subdivision method 1's islands in Puerto Rico. In addition, the correlation between elevation and number of species is very high, with the species diversity decreasing with increasing elevation ($r^2=0.99$, $F_{1,42}=3051$, $P<0.001$) (Figure 8).

A separate analysis conducted on fragmented island habitats at nine distinct elevation levels showed correlations between the species number and area. However, these curves are not identical at different altitudes. The area-species curves at the elevation levels of 60m and 750m are displayed in Figure 9 and 10. While regression correlation of area and species of 10 island habitats at 60m ($r^2=0.83$, $F_{1,8}=40.48$, $P<0.001$) can be achieved only after log transformation of both the x and y axis, the regression correlation between these two variables of nine island habitats at 750m ($r^2=0.99$, $F_{1,7}=3630$, $P<0.001$) is apparent without any transformation.

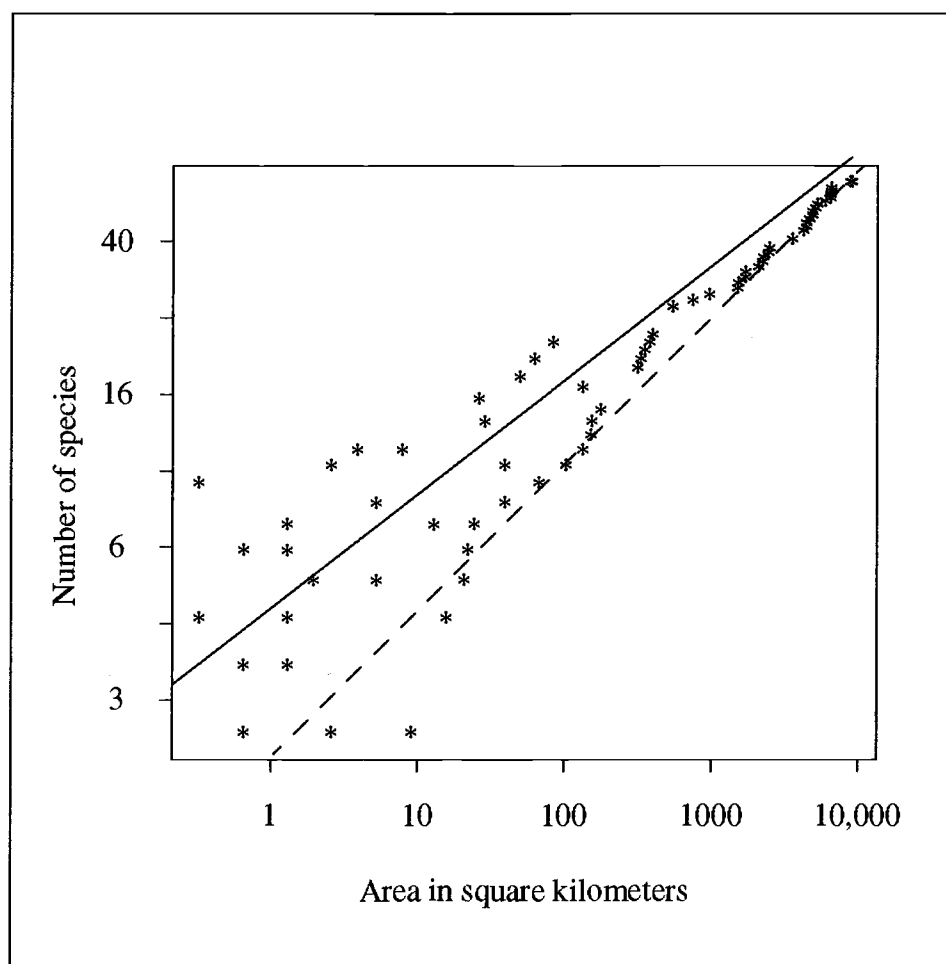


FIGURE 7. The area-species curves of Puerto Rican Bank's islands and vertically subdivided islands in Puerto Rico. (The green dots correlate to Puerto Rico, and black dots to the Puerto Rican Bank's islands. The broken line is the regression fit for Puerto Rico and the continuous line is regression fit for the Bank's islands. There is strong correlation between area and number of species in this model).

Hexagons generated via the subdivision method 2 were used to model the area-species curve without elevation effects. The mean areas of 1 to 40 polygons, which were chosen by 100 different computations without replacement, and the mean numbers of species, which are located within these hexagons, were plotted together in Figure 11. There is a strong

correlation between mean areas of the hexagons and the mean numbers of species ($r^2=0.94$, $F_{1,38}=596.8$, $P<0.001$).

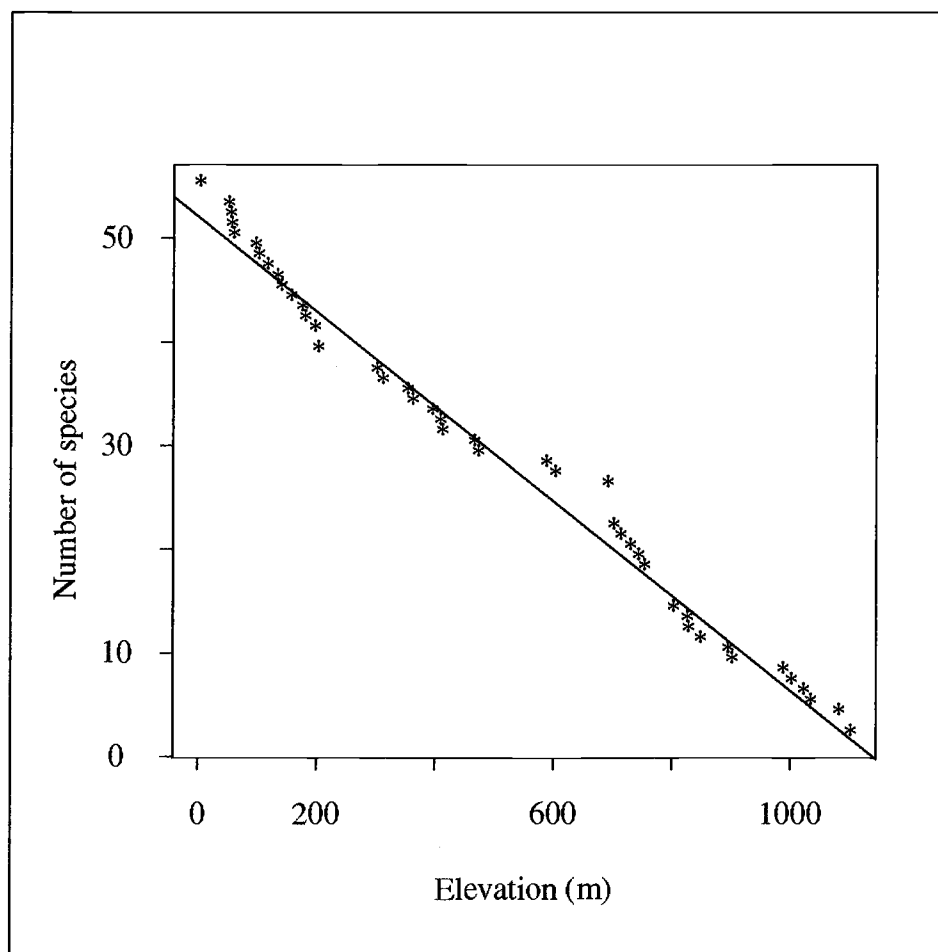


FIGURE 8. Correlation between amphibian and reptile diversity and elevation in Puerto Rico. The line is the regression fit. The figure shows the strong relationship between these two variables.

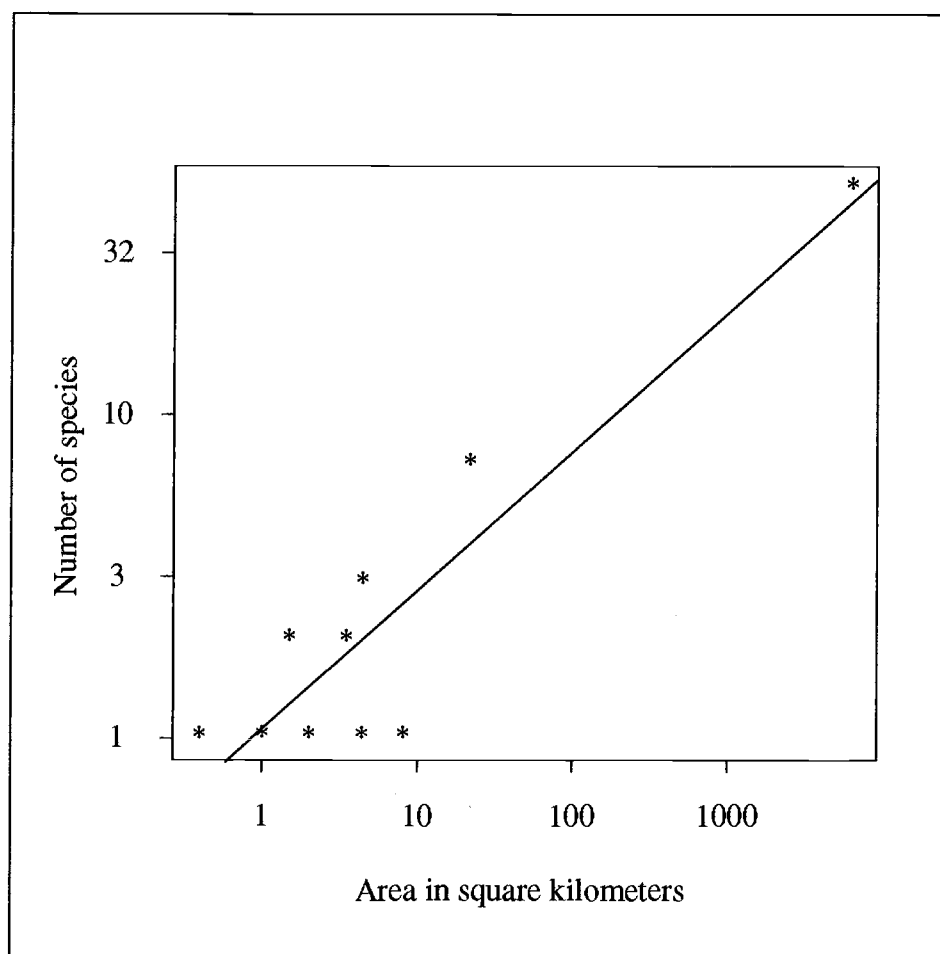


FIGURE 9. The area-species curves of fragmented island habitats at 60m altitude. The line is the regression fit. The linear relationship between area and the number of species exists in the log transformed scale.

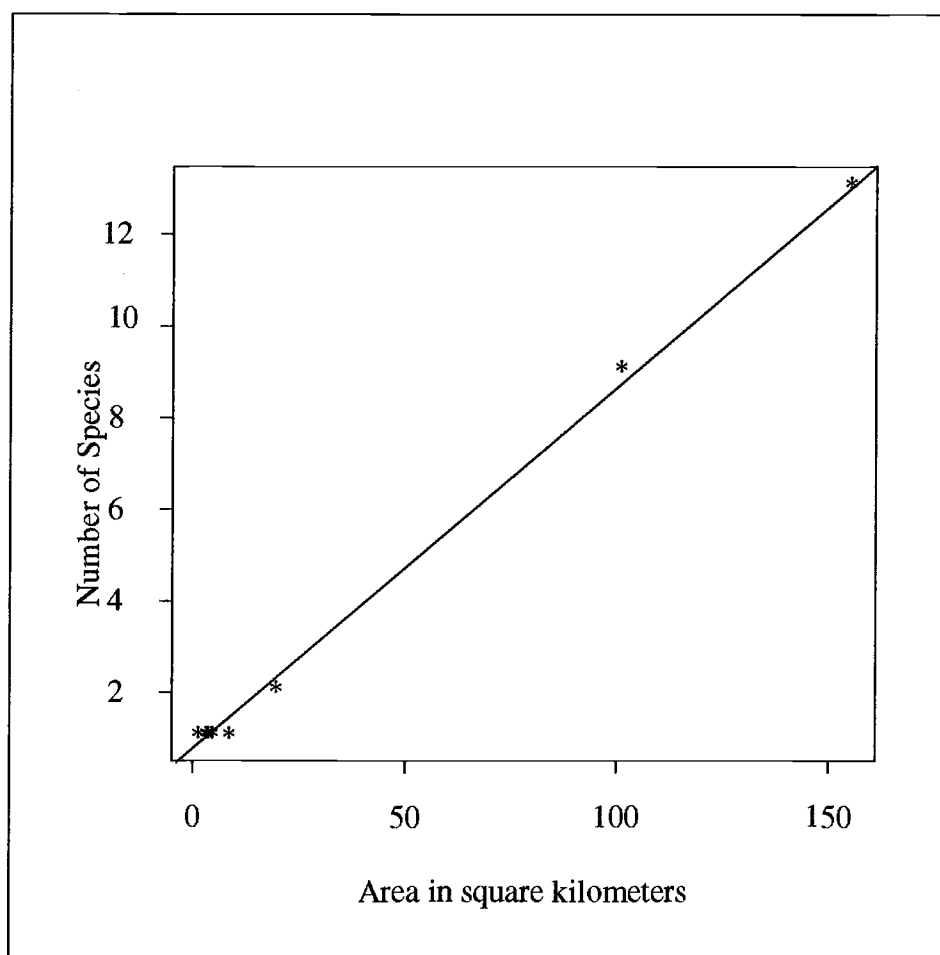


FIGURE 10. The area-species curves of fragmented island habitats at 750m altitude. The line is the regression fit. The linear relationship between area and the number of species in this case exists in the normal data scale.

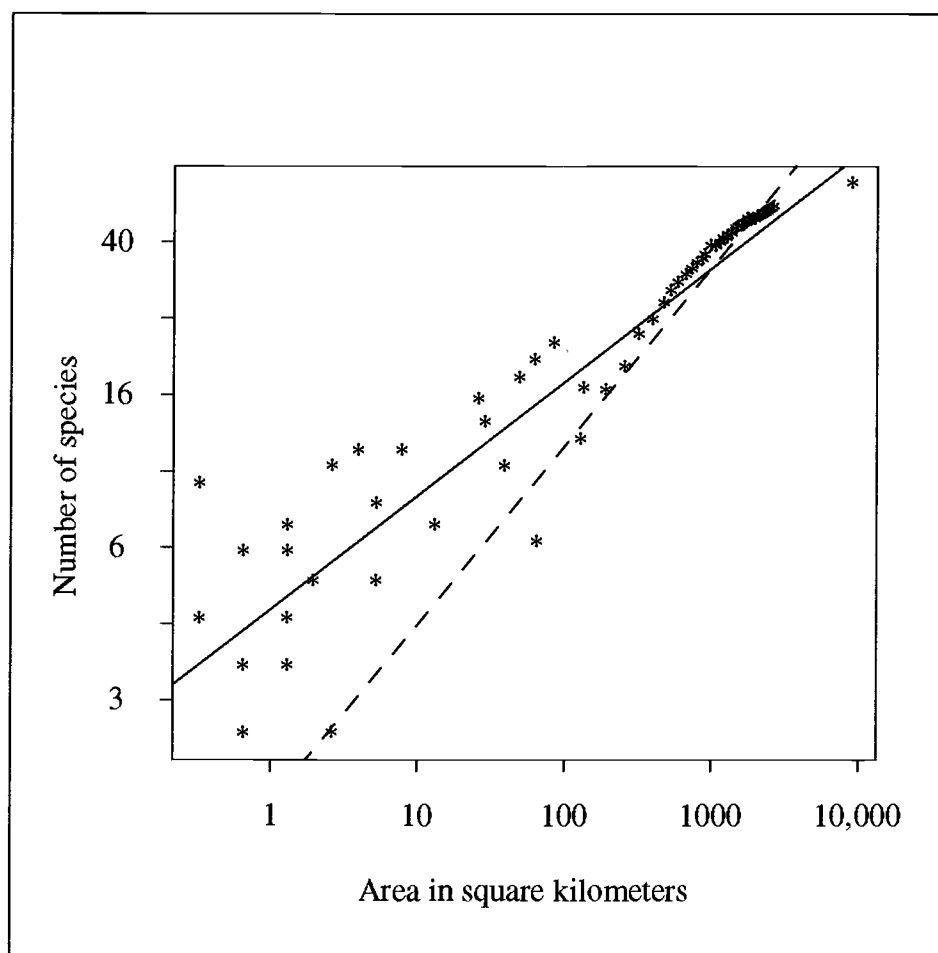


FIGURE 11. The area-species curve based on the hexagon grid. The broken line is the regression fit. There is strong correlation between area and the number of species. (The green dots belong to Puerto Rico's hexagon grid, the black dots belong to landbridge islands within the Puerto Rican Bank. The continuous line is the regression fit for the landbridge islands).

Finally, the subdivision method 3 based on distance from the coast, there is also a strong correlation between species and area ($r^2=0.92$, $F_{1,25}=280.6$, $P<0.001$). This linear relationship, however, is different from the other two curves above in that it exists on normal data scales without any transformation (Figure 12). A separate analysis on the correlation between the number of species and the distance from the coast also indicated a strong rela-

tionship of these two variables ($r^2=0.93$, $F_{1,25}=347.4$, $P<0.001$) with lower species diversity associated with increasing distance from the coast (Figure13).

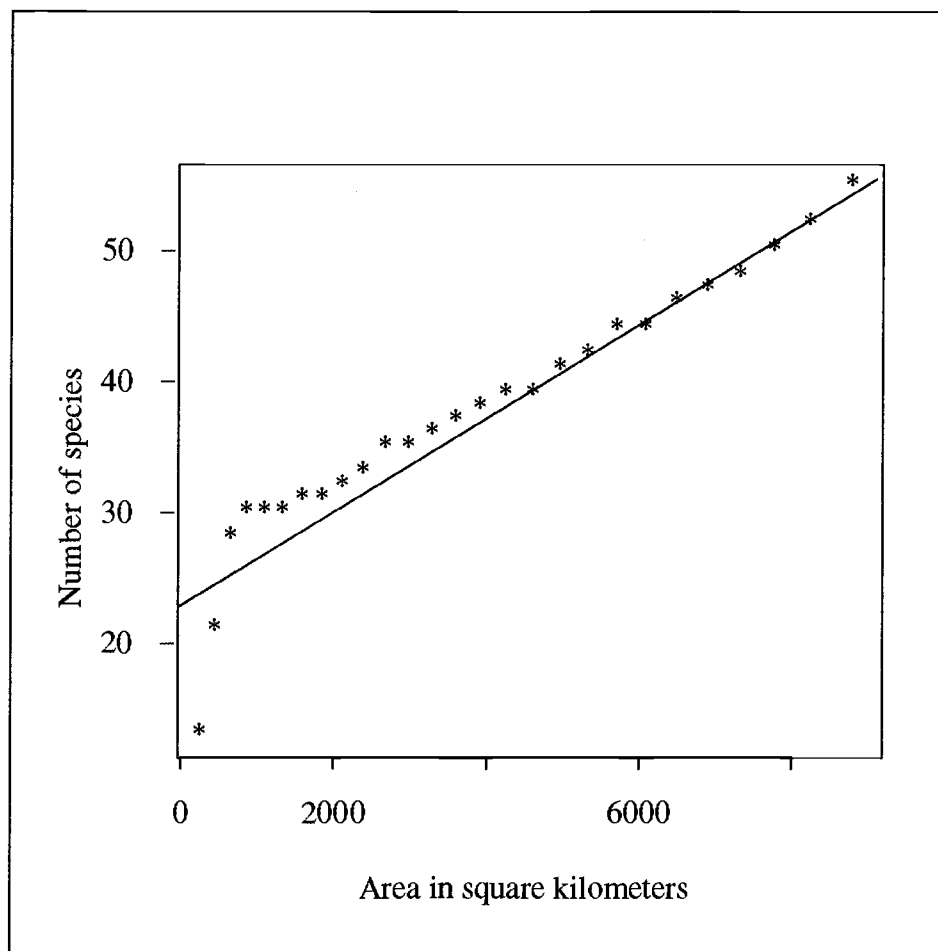


FIGURE 12. Correlation between number of species and distance from the coast. The line is the regression fit. There is strong correlation between the two variables.

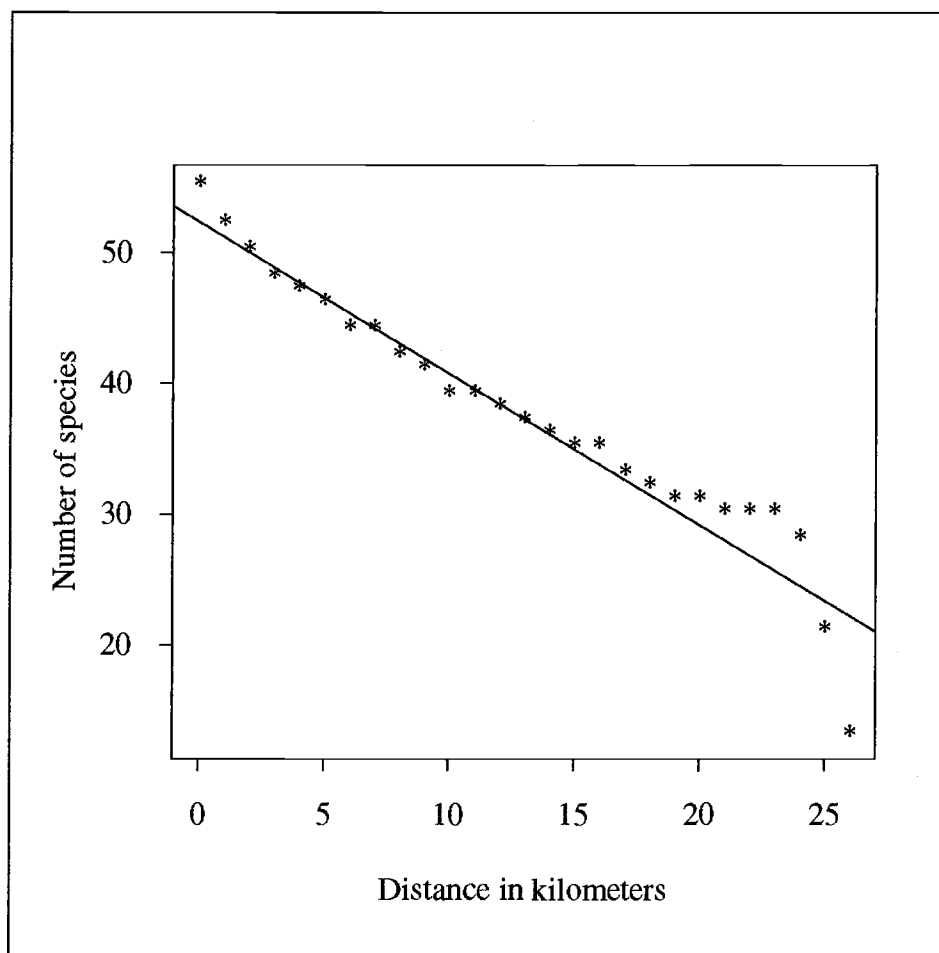


FIGURE 13. The area-species curve with increasing distance from the coast. The line is the regression fit. There is strong correlation between area and the number of species.

The number of species and rainfall are plotted together in Figure 14. There is no clear pattern of correlation between these two variables. The amphibian and reptile diversity seems to increase in the rainfall range from 700mm to 2000mm, but decreases in the range from 2000mm to 3500mm, and remains constant between 3500mm and 5000mm.

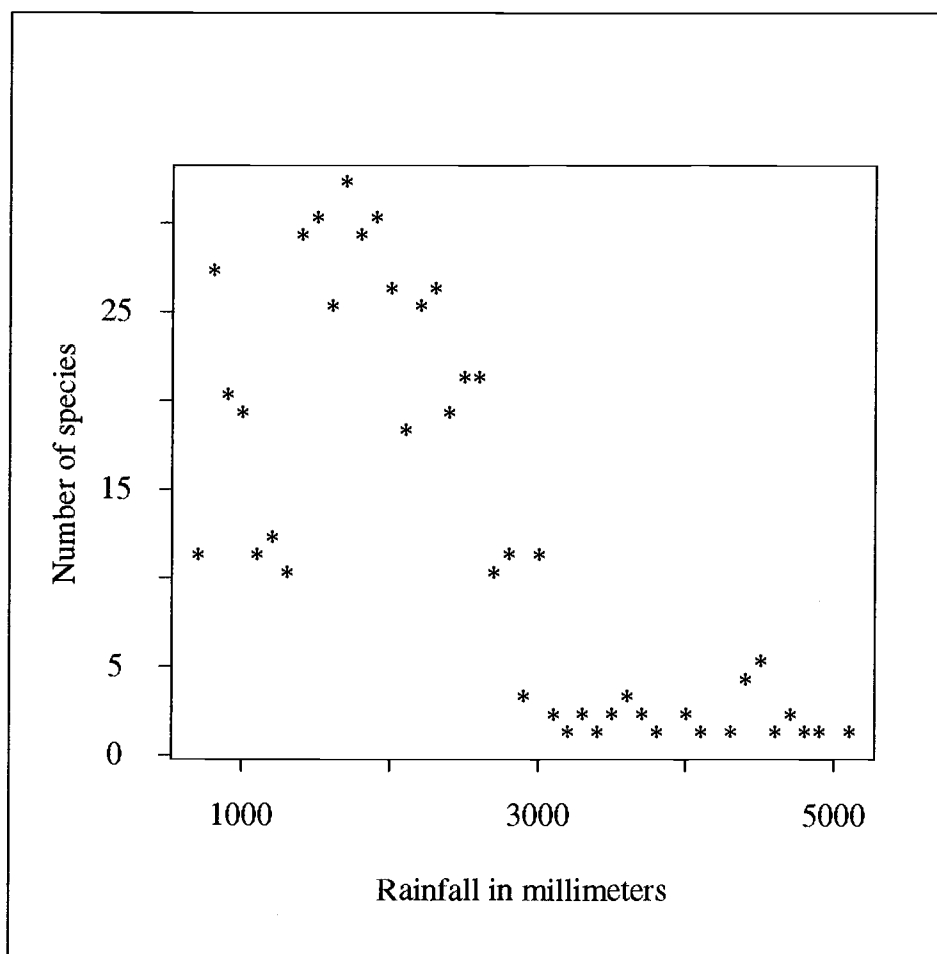


FIGURE 14. Relation between Puerto Rican herpetofauna and rainfall. There is no apparent relationship between the number of species and rainfall.

The multiple regression analysis between species diversity and the combination of the three variables, area, rainfall, and elevation indicated a weak relationship among them ($r^2=0.52$, $F_{7,75}=11.46$, $P<0.001$) (Figure 15). In this model, the area term contributes the least to the multiple regression fit. The simpler model between species diversity and elevation and rainfall seems to retain almost all the explanatory power of the more complicated model ($r^2=0.49$, $F_{3,79}=25.46$, $P<0.001$) (Figure 16).

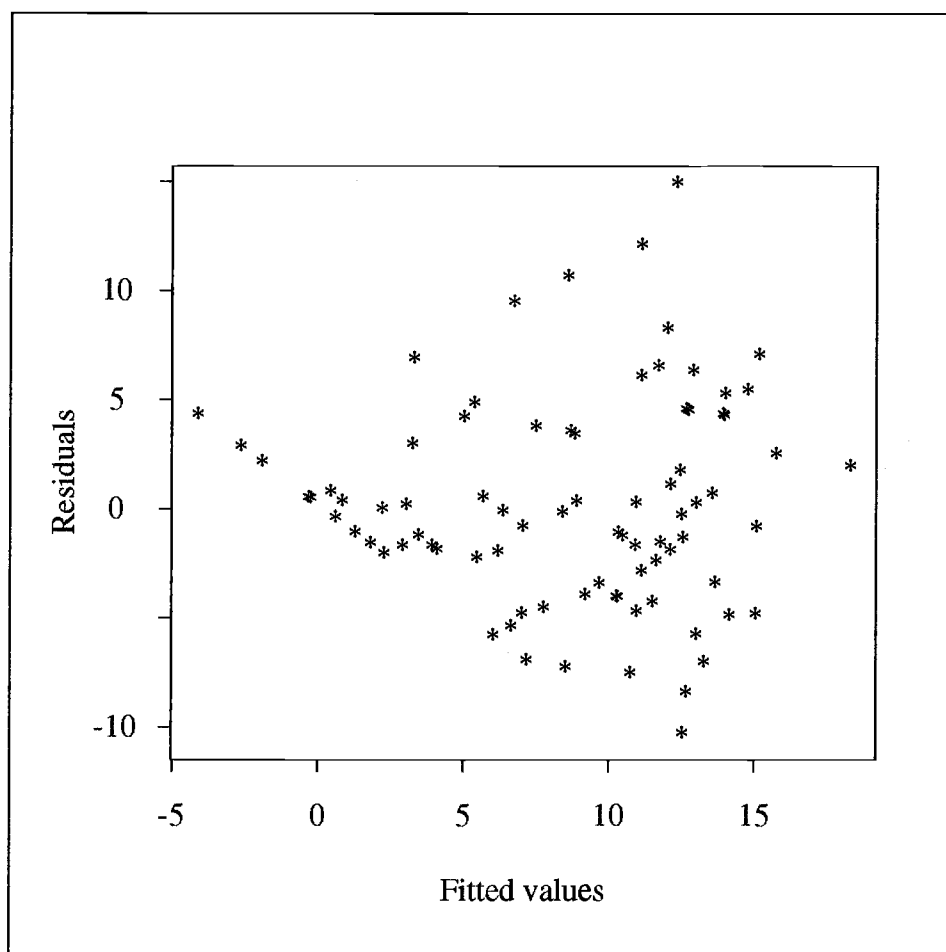


FIGURE 15. Residuals plotted with fitted values between species diversity and the combination of the 3 variables of area, elevation, and rainfall.

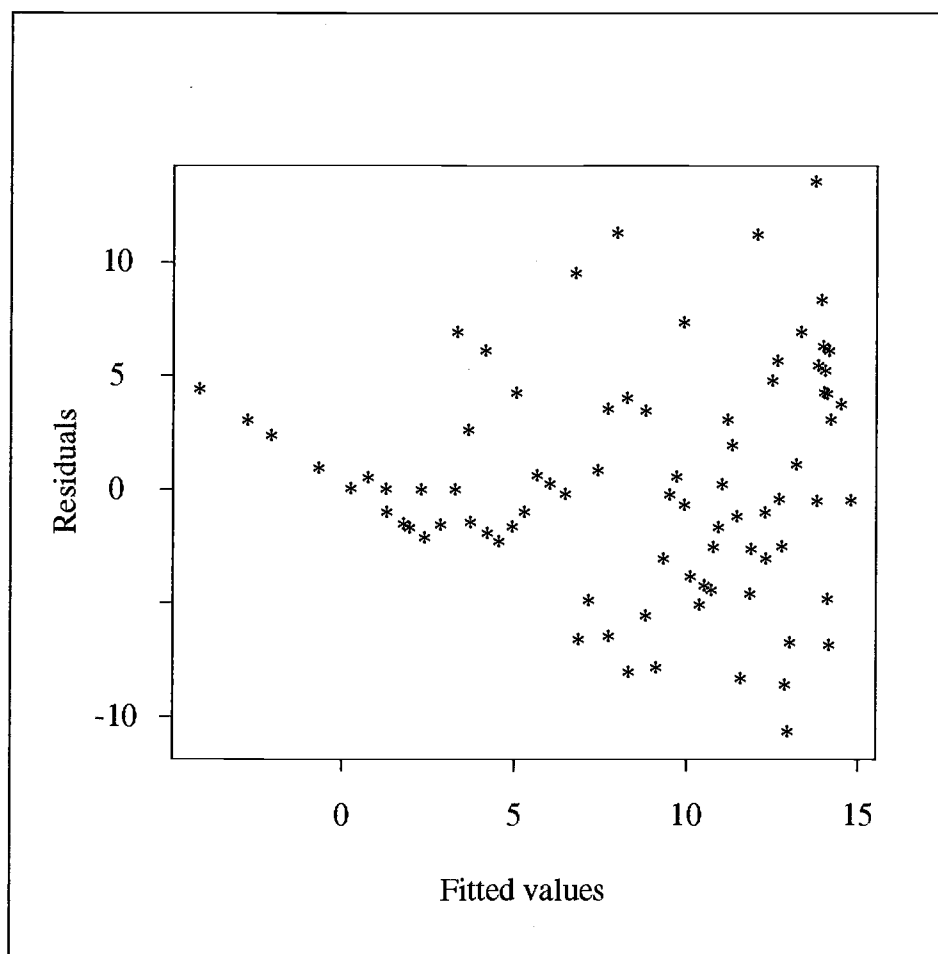


FIGURE 16. Residuals plotted with fitted values between species diversity and elevation and rainfall.

Finally, the analysis on range area and the number of reptiles and amphibians suggested a strong correlation between them ($r^2=0.97$, $F_{1,53}=1963$, $P<0.001$) (Figure 17). There are six species, which have their range areas equal to 0 because they are only distributed at one or two locations. These species are *Caiman crocodilus*, *Cyclura nubila*, *Eleutherodactylus unicolor*, *Hyla cinera*, *Hemidactylus mabouia*, and *Osteopilus septentrionalis*. Total area

of all species ranges is about 182405 km², about 21 times larger than the area of Puerto Rico.

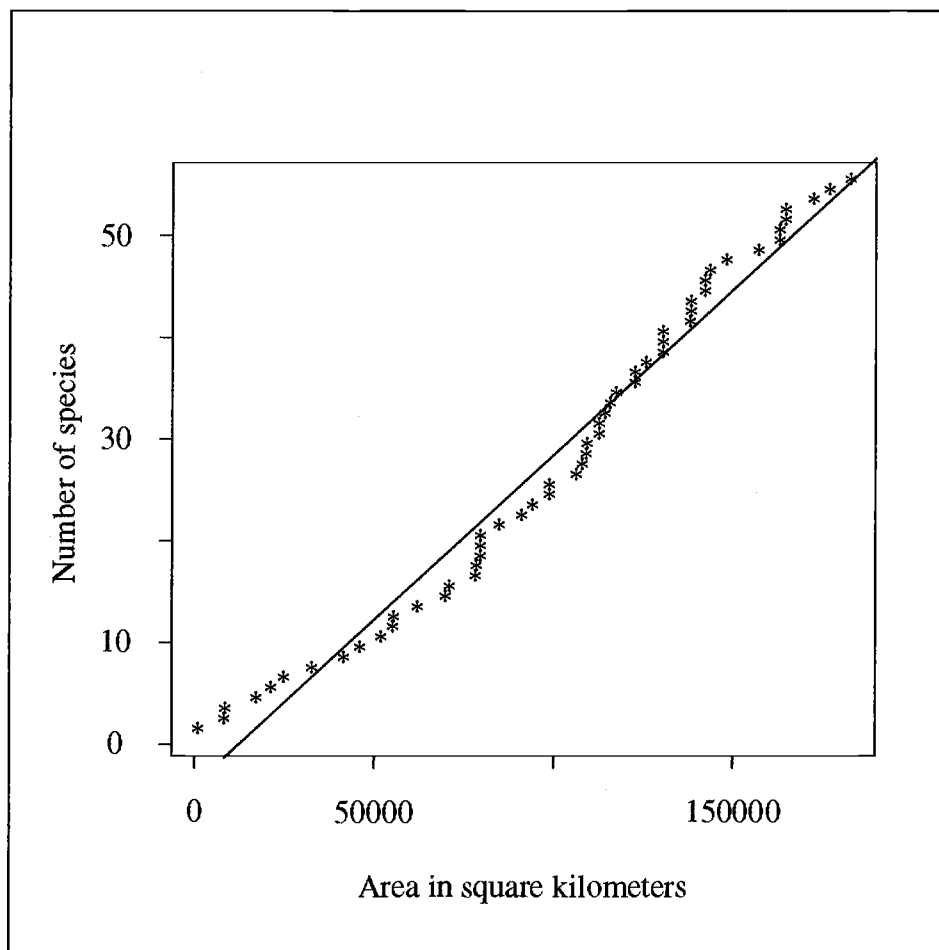


FIGURE 17. Relation between the number of reptiles and amphibians and their range areas. The line is the regression fit. There is a strong correlation between range areas and number of species.

4.0 Discussion

A strong relationship is evident between the number of amphibian and reptile species and the area of the Puerto Rican Bank islands (Figure 5). This pattern, however, is different from the pattern of species area curves drawn for subdivided islands according to the first and second methods of subdivision (Figure 7 and 11). Although the curve for Puerto Rican Bank's islands has lower slope, 0.3 compared to 0.4-0.46 for the Puerto Rican subdivided islands, its intercept is higher. Since the intercept is equal to the log of constant C in MacArthur and Wilson's (1967) model the C value is higher in the Puerto Rican Bank's islands. This is different from general patterns, in which more isolated islands have lower C values (MacArthur and Wilson, 1967).

The number of species on the Puerto Rican Bank islands seems greater than on the subdivided islands on Puerto Rico, according to the first and the second methods of subdivision, although in Figure 9 at the end of the regression lines the number of species on Puerto Rico seems higher than on the landbridge islands. A separate analysis on fragmented island habitats at 60m and 500m altitude also gave the same result. Thus, to some extent, the Puerto Rican Bank islands individually contain more species per area unit, i.e. per km^2 , than subdivided islands of Puerto Rico do. However, this does not mean that the total number of amphibian and reptile species on all of the islands on Puerto Rican Bank is greater than the

number of the species on Puerto Rico. This pattern probably results from the interactions among species when an island's area becomes smaller as a result of sea level rise.

The interactions among species may include the contraction of species' range area to avoid extinction, so that the islands can support more species than before. In other words, the species density changes as a result of island area shrinking. This result is similar to supersaturated island faunas reported by Diamond (1972) and Terborgh (1974) for bird faunas in the southwest Pacific and Neotropics, and Soule' and Sloan (1966) for lizard faunas on islands in the Gulf of California (Wilcox, 1978). Thus, there seems to be no evidence of fauna relaxation on these landbridge islands as indicated by earlier studies (Richman et. al., 1988).

Another hypothesis for high density of species on the landbridge islands within the Puerto Rican Bank is that more species can colonize these islands subsequently from the larger island such as Puerto Rico. This can be tested by comparing the similarities of fauna among these islands. Heatwole and MacKenzie (1966) noted that "[i]slands which have been separated a long time have lower faunal similarities with each other and have higher degree of endemism". This pattern probably indicates that the fragmented islands develop their own fauna (i.e. by speciation from the remnant fauna subsets). In addition, Rand (1969) pointed out that on the satellite islands of the Greater Antilles extinction, rather than colonization, has played an important role in producing area-pattern patterns. Thus, colonizations from

other islands are probably rare since it is harder to colonize the islands overwater, and competition on the islands is also high (Williams, 1969).

In the first two methods of subdividing the island, the species curves seem to have higher slope than the normal range of the area-species curve proposed by MacArthur and Wilson (1967). These curve slope values vary from 0.4 to 0.46, while the slope of the Puerto Rican Bank's islands lies within the normal range ($z=0.3$). This pattern is different from the pattern indicated by MacArthur and Wilson (1967) as they noted that the z value for non-isolated sample area within islands was usually smaller than among different islands, falling between 0.12 to 0.17. However, it seems consistent with Hamilton and Armstrong's (1965) observations, in which they found a decreased slope with isolation (Connor and McCoy 1979).

High values of the slope in the log/log model of species area curve in Puerto Rico probably result from topographical characteristics of the island. In fact, Puerto Rico has very complex topography, and this probably breaks the island up into a large number of heterogeneous habitats, which, in turn, result in higher z values (MacArthur and Wilson, 1967).

From the result above, it can be expected that at a higher elevation the z value becomes smaller since the habitat heterogeneity is lower at higher elevations. At the 500m elevation, the z value of the area-species curve among fragmented islands habitats decreases to 0.28, while this value at the 60m elevation is 0.43. However, at higher elevations the pattern of

this relationship no longer exists. At the 750m elevation, the regression relationship between area and reptile and amphibian diversity is seen only in the normal scale, but not in the logarithmic scale as at lower elevation levels. This pattern may result from growing simplicity of habitat diversity at high elevation. These patterns, therefore, demonstrate that the area-species correlation is most likely a result of environmental heterogeneity as suggested by Williamson (1981, 1988).

The significant correlation between the number of amphibians and reptiles among vertically subdivided islands in this analysis probably indicates a high degree of habitat heterogeneity among different elevation levels in Puerto Rico. This is likely also a major cause of the strong correlation between elevation and reptile and amphibian diversity on the island. Elevation accounts for 99 percent of species variation, which is the highest number among other factors.

Rainfall has no clear relationship with the herpetofauna diversity, even though amphibians may strongly correlate with this variable as indicated by Hedges (1996). On Puerto Rico, the highest number of these species occurs in the area with mean annual rainfall ranging from 1400 to 2000mm. The relationship between the number of amphibians and reptiles and rainfall is probably a result of weak correlation between rainfall and elevation (correlation index equal to 0.459). This demonstrates that elevation is a more influential factor in determining the number of species on the island. A separate multiple regression analysis

also indicates that elevation is more important than area in predicting reptile and amphibian species richness. This may be because elevation has stronger effects on habitat diversity.

The correlation between the number of species and area and distance from the coast on Puerto Rico probably results from combination of several factors. The middle area of the island, which is the greatest distance from the coast, is also the highest area of the island. Thus, the fact that the number of amphibian and reptile species decreases with increasing distance from the coast is not only a result of reduction of area and longer distance for species dispersal, but also an effect of higher elevation. This explains an abrupt change in the number of species in the two inner most polygons. Due to high correlation between the area of these polygons and the distance from the coast, these curves are almost identical. That means we can use either these polygon's area or distance from the coast to present the correlation.

In the analysis of species range, the strong correlation between the number of reptiles and amphibians and their range area probably indicates that most species are widely distributed around the island. Only six species have isolated geographic ranges. Losos (1998) suggested that the difference in geographical ranges of species is a cause of the relationship between island area and number of species. In larger islands such as Cuba or Hispaniola, more species tend to have limited ranges, which probably results from increasing number of species capable of coexisting in sympatry. From this he concluded that, among larger islands

of the Greater Antilles, evolutionary factors played a major role in determining the number of species. Thus, the finer subdivision of habitat and additional habitat utilizations among species on the large islands in the West Indies are possibly an additional cause of the correlation between island area and the number of species in the region. However, the question of whether a higher degree of habitat diversity, or an increasing number of sympatric species on the large island, has more effect on the area-species relationship will need further study.

In considering the effects of sea level fluctuations over time in Puerto Rico, it is possible that at the last glacial minimum, about 120,000 years ago, the sea level was as much as 70m higher than the position of the sea on the island land mass today (Kimber, 1988). Many low lying landbridge islands on Puerto Rican Bank must have been submerged at that time. These changes could have caused the variations of lowland and mangrove forests on the island today. This changes would probably have little effect on distribution of reptiles and amphibians if we look at the current distribution. Only two species in Puerto Rico now have limited a range of distribution under 70m.

At the lowest sea level during the Pleistocene, the sea level was 87 fathoms (about 160m) below the present sea level (Heatwole and MacKenzie, 1966). During this period, amphibians and reptiles probably were distributed all over the Puerto Rican Bank. The subsequent sea level rise produced the current distribution patterns of reptiles and amphibians in Puerto

Rico and the landbridge islands. In these islands, as mentioned above, extinction alone seems to account for species richness.

In recent studies on landbridge islands, some authors believed that the theory of island biogeography of MacArthur and Wilson (1967) could be used to explain the patterns of species on these islands (Richman et al. 1988, Case 1975). These workers found that the extinction rate was negatively correlated with the island area, which is consistent with the theory. This results in fewer species on the small islands. However, the results from this study indicate the opposite is true.

Finally, with regard to z values of the species area curves in Puerto Rico, high values probably indicate a high degree of environmental heterogeneity on the island. However, in general, the z value of the species area curves probably is higher on the islands than on the continent due to an increased immigration rate among continental habitat islands. This pattern overall can lead to a lower number of species on the continent than on the island as indicated by Peter et al. (1996), when they tried to project the number of mammal species for the earth based on data about continents.

5.0 Conclusion

The fact that the area-species curve on a big island is different from that of isolated islands has been examined using data on reptiles and amphibians of Puerto Rico and the Puerto Rican Bank's islands. It is shown that the small isolated islands can contain more species than one big island. During the process of fragmentation, and with the effect of area packing, these species probably experienced the contraction of their geographical ranges to avoid extinction. This leads to higher density of species on the Puerto Rican Bank's islands. However, this pattern may be not true in the other island banks in the West Indies. Results of this study also show that elevation has strongest correlation, and rainfall almost has no correlation, with amphibian and reptile diversity on Puerto Rico. Furthermore, it is possible to conclude from this study that environmental heterogeneity plays a primary role in determining the correlation between species and area on Puerto Rico. However, the correlation between area and species among different islands can also result from an increasing number of sympatric species on the large islands. Finally, the question regarding which factor has stronger effects on the area-species curve needs further study.

Literature Cited

- Barbara, R. 1982. Lizard Home Ranges: Methodology and Functions. In *Journal of Herpetology*. Vol 16, No 3. 253-269.
- Case, T. J. 1975. Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. In *Ecology*, Vol 56 pp. 3-18
- Connor, E. F. and McCoy, E. D. 1979. The statistics and biology of the species-area relationship. *American Naturalist*, 113, 791-833.
- Environmental Systems Research Institute (ESRI). 1992. The Digital Chart of the World for use with ARC/INFO.
- Figueroa, J. C. Unpublished rainfall map from USDA International Institute of Tropical Forestry.
- Heatwole, H. and MacKenzie F. 1967. Herpetography of Puerto Rico. IV. Paleogeography, faunal similarity and endemism. *Evolution*, 21, 429-38.
- Hedges, S. B. 1996. Distribution Patterns of Amphibians in the West Indies. In *Monogr. Mus. Nat. Hist. Univ. Kansas* No9.
- Kimber, C. T. 1988. *Martinique Revisited*. Texas A&M University Press.
- Losos, J. B. 1998. Ecological and evolutionary determinants of the species-area relationship in Caribbean anoline lizards. In *Evolution on Island*, ed. Grant P. Oxford University Press. Oxford. New York. Tokyo.
- MacArthur, R. H., and Wilson, E. O. 1967. *The theory of Island Biogeography*. Princeton University Press. Princeton, New Jersey.
- MacArthur, R. H. 1972. *Geographical Ecology*. Princeton University Press, Princeton, New Jersey.
- Maclean, W. P. 1977. Island lists of West Indian amphibians and reptiles. *Smithsonian Herpetological information service*. No. 40.
- Rand, A. S. April 30, 1969. Competitive exclusion among anoles (*Sauria iguanidae* on small islands in the West Indies). In *Breviora* No. 319.

Richman, D. A., Case T. J., and Schwaner, T. D. May, 1988. Natural and unnatural extinction rates of reptiles on islands. In *The American Naturalist*, Vol. 131, No. 5. pp 611-630.

Roughgarden, J. 1989. The structure and assembly of communities. In *Perspectives in Ecological Theory*, eds. Roughgarden J., May R. M., and Levin S. A. Princeton University Press. Princeton, New Jersey.

Schwartz, A. and Henderson R. W. 1991. *Amphibians and Reptiles of the West Indies*. University of Florida Press, Gainesville.

Wallace, A. R. 1880. *Island Life*, London, Macmillan.

Wilcox, B. A. Mar, 3 1978. Supersaturated Island Faunas: A species-age relationship for lizards on Post-Pleistocene land-bridge islands. In *Science*, Vol. 199. pp 996-998.

Williams, E. E. December, 1969. The ecology of colonizations as seen in the zoogeography of anoline lizards on small islands. In *The Quarterly Review of Biology*. Vol 44, No. 4. 345-389.

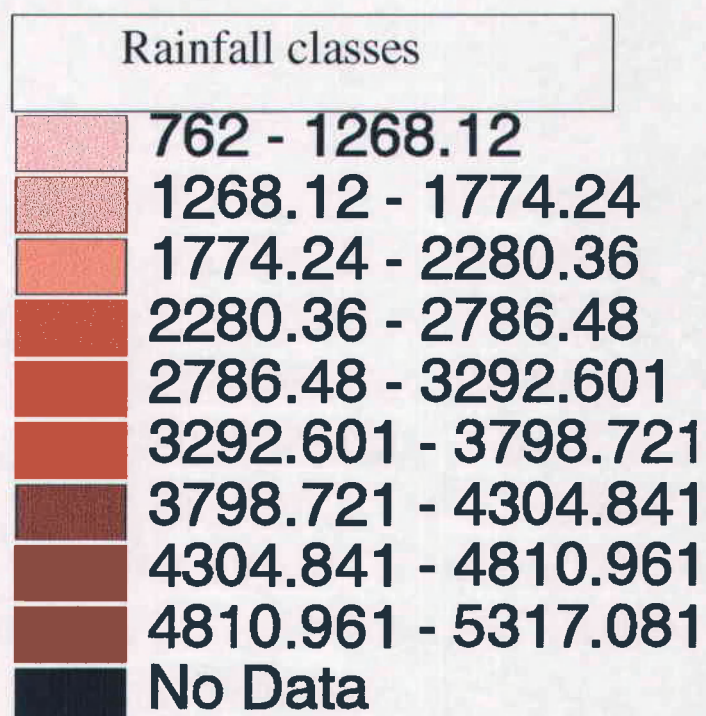
Williamson, M. 1981. *Island population*. Oxford University Press, Oxford, England.

Williamson, M. 1988. Relationship of species number to area, distance and other variables. In *Analytical Biogeography*. New York, NY: Chapman and Hall.

Appendices

Appendix 1: Maps of Puerto Rico

Annual rainfall in Puerto Rico (mm)

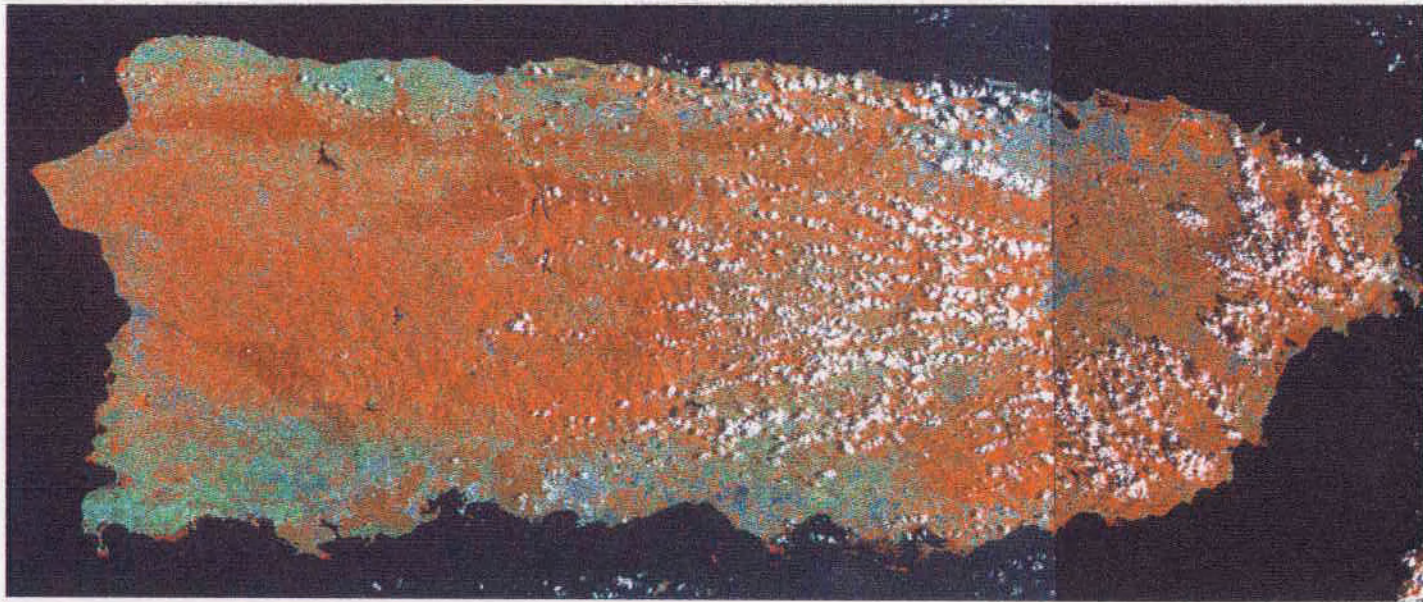


The Color Relief Shaded Map of Puerto Rico

(each color stands for about 150m interval)



Landsat Images of Puerto Rico (in color infrared: color composit band 4, 5, 6)
acquiring date: west scence - 19/Aug/1991, east scence 7/Feb/1991



Appendix 2
Summary Statistics

Summary of multiple regression analyses

Call: lm(formula = Species ~ Area + Meanpre + Meanele + Area * Meanpre + Area * Meanele + Meanpre * Meanele + Area * Meanele * Meanpre, data = multi)

Residuals:

Min	1Q	Median	3Q	Max
-10.49	-2.852	-0.3805	3.264	14.72

Coefficients:

	Value	Std. Error	t value	Pr(> t)
(Intercept)	13.2541	3.3781	3.9235	0.0002
Area	0.0000	0.0000	0.4045	0.6870
Meanpre	-0.0004	0.0017	-0.2676	0.7898
Meanele	-0.0265	0.0084	-3.1652	0.0022
Area:Meanpre	0.0000	0.0000	0.1508	0.8806
Area:Meanele	0.0000	0.0000	0.0982	0.9220
Meanpre:Meanele	0.0000	0.0000	1.6154	0.1104
Area:Meanele:Meanpre	0.0000	0.0000	-0.1506	0.8807

Residual standard error: 4.988 on 75 degrees of freedom

Multiple R-Squared: 0.5168

F-statistic: 11.46 on 7 and 75 degrees of freedom, the p-value is 8.48e-10

Correlation of Coefficients:

(Intercept)	Area	Meanpre	Meanele	Area:Meanpre
	Area	-0.6980		
	Meanpre	-0.8964	0.5942	
	Meanele	-0.8002	0.7000	0.7616
	Area:Meanpre	0.6666	-0.9264	-0.6926
	Area:Meanele	0.5127	-0.8072	-0.5215
	Meanpre:Meanele	0.7368	-0.6466	-0.8129
	Area:Meanele:Meanpre	-0.5078	0.7611	0.5643
	Area:Meanele		Meanpre:Meanele	
	Area		Area	
	Meanpre		Meanpre	
	Meanele		Meanele	
	Area:Meanpre		Area:Meanpre	
	Area:Meanele		Area:Meanele	
	Meanpre:Meanele		Meanpre:Meanele	0.7621
	Area:Meanele:Meanpre		Area:Meanele:Meanpre	-0.9583
				-0.8273

Call: lm(formula = Species ~ Meanpre + Meanele + Meanpre * Meanele, data = multi)

Residuals:

Min	1Q	Median	3Q	Max
-10.93	-2.773	-0.4563	3.409	13.29

Coefficients:

	Value	Std. Error	t value	Pr(> t)
(Intercept)	14.2461	2.3782	5.9903	0.0000
Meanpre	0.0002	0.0012	0.1379	0.8906
Meanele	-0.0270	0.0050	-5.3588	0.0000
Meanpre:Meanele	0.0000	0.0000	2.6426	0.0099

Residual standard error: 4.985 on 79 degrees of freedom

Multiple R-Squared: 0.4916

F-statistic: 25.46 on 3 and 79 degrees of freedom, the p-value is 1.266e-11

Correlation of Coefficients:

	(Intercept)	Meanpre	Meanele
Meanpre	-0.9239		
Meanele	-0.7697	0.6837	
Meanpre:Meanele	0.7510	-0.7785	-0.9341

Simulation program (in Splus)

```

meanarea <- rep(0, 40)
meanrich <- rep(0, 40)

for (k in 1:40)
{
totrich <- rep(0, 100)
totarea <- rep(0, 100)

for (j in 1:100)
{
x <- rep(F, 55)
area <- 0
y <- sample(136, k, replace = F)
for (i in y)
{
x <- x | procur[i,]
area <- area + prhex$area[i]
}
totarea[j] <- sum(area)
totrich[j] <- sum(as.numeric(x))
}

```

```
meanarea[k] <- mean(totarea)
meanrich[k] <- mean(totrich)
}
```