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INSULAR BIOGEOGRAPHY IN CONTINENTAL REGIONS. I. THE NORTHERN ANDES OF SOUTH AMERICA

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INTRODUCTION

Biogeographers often assume that, among continental biota, those found on high mountains are insular because mountain tops are as isolated from one another as true islands. The empirical evidence available to test the validity of this postulate is, however, very scanty. In order to discover whether high mountain biota have insular patterns of distribution, I studied species numbers and endemism among the birds living in “islands” of páramo vegetation in the Andes of Venezuela, Colombia, and northern Ecuador.

The region and fauna selected for analysis are especially well suited for an investigation of insularity in a continental area. First, páramo vegetation occurs above tree line on high mountains isolated from one another by different types of vegetation, especially wet montane forest (cloud forest) at lower altitudes. Thus factors of geographical isolation, such as distance between páramo islands, can be measured easily, and compared to similar factors in archipelagos. Second, the relatively uniform páramo vegetation (consisting of dense tussocks of Gramineae of the genera *Festuca*, *Stipa*, *Calamagrostis*, and *Deyeuxia*, and of shrubby or aborescent Compositae of the genus *Espeletia*) minimizes potential variance in species diversity (see MacArthur and Wilson 1967, p. 19). Third, the comparatively well-known history of the avifauna inhabiting the páramo vegetation (Chapman 1917, 1926; Vuilleumier 1969b) indicates a major, unidirectional faunal flow from southern centers of origin toward the north. Factors of distance of a given páramo island to a source area can therefore easily be quantified. Finally, the inventory of the fauna is relatively complete (Chapman 1917, 1926; de Schauensee 1948–1951, 1964; Phelps and Phelps 1958, 1963), and I have personally visited selected páramo islands in Ecuador, Colombia, and Venezuela, and gained field experience with 65% of the bird species considered in this paper.

THE PÁRAMO ISLANDS

The lower limit of páramo vegetation depends upon exposure and the climatic regime, especially rainfall, and often differs on two sides of a mountain. The base altitude decided upon for a given island is a com-

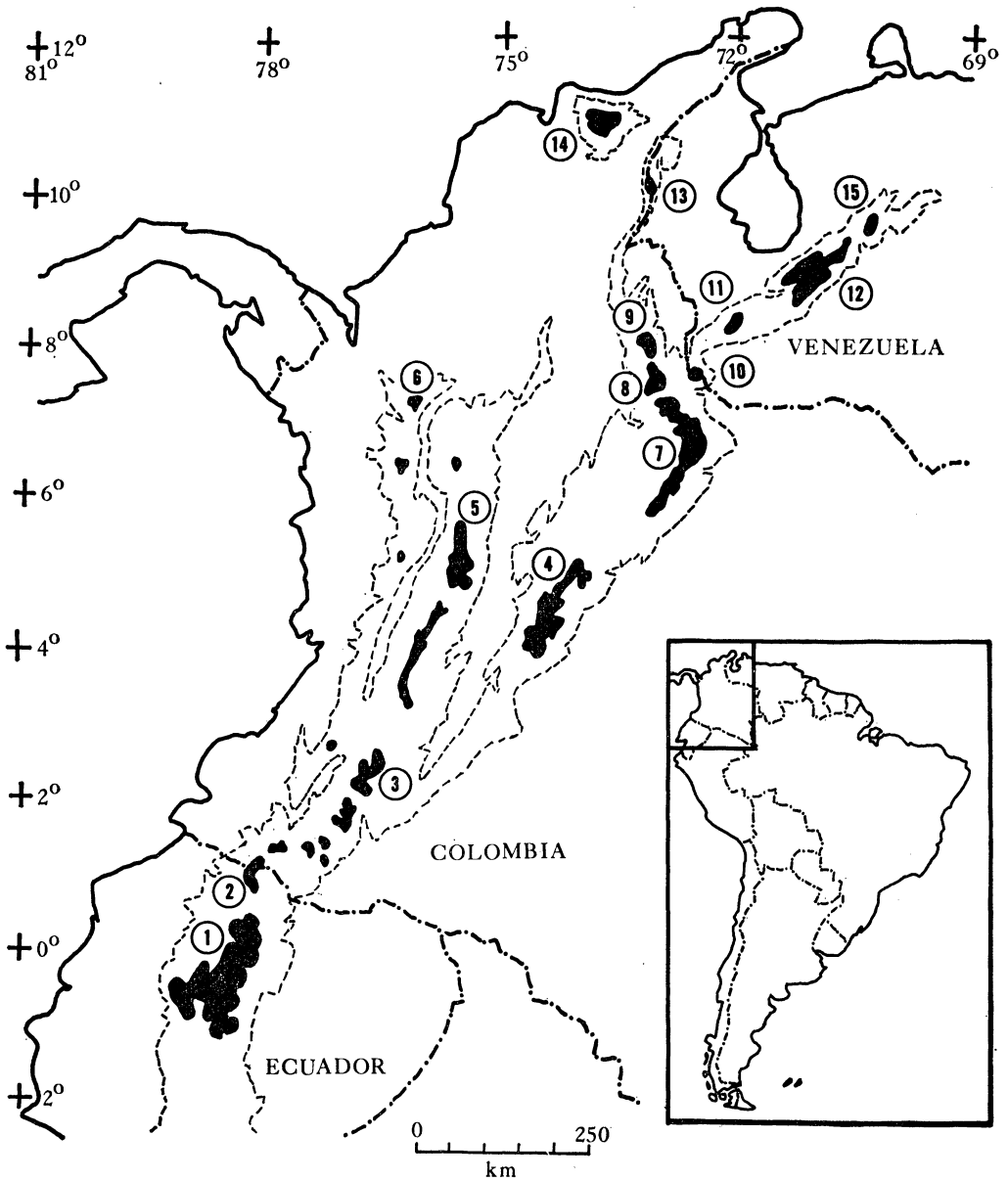


FIG. 1.—The northern Andes, with the islands of páramo vegetation in black; the 1,000-m contour represented by a dotted line. Further data on islands 1–15 can be found in table 1 (dependent and independent variables).

promise, taking into account the observed differences, and was set at 3,000, 3,250, or 3,500 m.

The contour line of each island was traced, after selection of the base altitude, on the following maps: "Agustín Codazzi" (Instituto Geográfico, 1963), scale 1:1,500,000 (Colombia), millionth map of the Americas (American Geographical Society) (Venezuela and Ecuador), and millionth map of Ecuador (Instituto Geográfico Militar, 1950).

All páramo islands mapped are shown by black areas on figure 1, but only those numbered 1 through 15 were analyzed in this study. The remainder were excluded because no faunal list could be compiled, or because faunal sampling appeared to be grossly incomplete. For each of the 15 islands retained, the following three measurements (presumably reflecting environmental diversity) were taken into consideration in the prediction of bird species numbers: area (measured in square kilometers as the plane area bounded by the horizontal contour line at the base elevation; no effort was made to measure the actual surface area), elevation (vertical distance in meters from base altitude to the highest summit of a given island), and base altitude. Four measures of interisland isolation (in kilometers) were calculated as follows: distance from source (shortest map distance between island number 1 and island considered), distance to the nearest island whether that island was one of the 15 sampled or not), distance to the nearest island to the south, and distance to the nearest large island (more than 200 sq km). The seven variables listed above are considered the independent variables for each island, and are given in table 1.

THE PÁRAMO AVIFAUNA

Species lists for the 15 islands included in this paper were compiled from the works of Chapman (1917, 1926), Phelps and Phelps (1958, 1963), de Schauensee (1948–1951, 1964), Todd and Carriker (1922), and Wetmore (1946), and from lists obtained during my own field studies. The total number of species included in the páramo avifauna, and distributed among the 15 islands of figure 1, is 83. Of these, 77 are land birds occurring in one of the following ecological categories: (a) grassland only, (b) grassland and open scrub, (c) grassland, scrub, and upper edge of the montane forests (ceja forests), and (d) edge only. The remaining six species are freshwater birds living on lakes or ponds within the páramo vegetation.

From the total species list (83 species) I determined that eight species might not be of South American origin, so their inclusion in the analysis might distort the distance effect. These species are believed to be of North American origin, or of doubtful origin.

Endemism among the birds of the páramo fauna was analyzed by a combination of literature review and personal comparative studies of museum specimens (Vuilleumier 1968, 1969*a*, in press, and manuscript in preparation). An endemic taxon is defined here as a species or subspecies restricted to a single island of páramo vegetation.

TABLE 1
DEPENDENT AND INDEPENDENT VARIABLES FOR THE 15 ISLANDS OF PÁRAMO VEGETATION ANALYZED

ISLANDS OF PÁRAMO VEGETATION	DEPENDENT VARIABLES			INDEPENDENT VARIABLES								PREDICTED VALUES OF DEPENDENT VARIABLES			
	N_1	N_2	E_1	E_2	AR	BA	EL	DEc	DNI	DNIS	DNLI	N_1	N_2	E_1	E_2
1. Ecuador	65	57	1	1.5	3,487	3,500	2,397	1*	1*	1*	1*	66	58	1	-4.7
2. Chiles	36	31	1	2.7	326	3,500	1,264	36	14	36	36	32	28	1	9.2
3. Las Papas-Cocoenuco	30	25	1	3.3	501	3,500	1,170	234	13	26	26	30	26	2	3.7
4. Sumapaz	37	32	3	8.1	2,031	3,500	1,060	543	83	80	116	38	32	3	9.2
5. Tolima-Quindío	35	33	9	25.7	989	3,500	1,900	551	23	25	25	32	29	7	18.6
6. Paramillo	11	10	1	9.0	25	3,500	460	773	45	45	186	14	12	1	9.9
7. Cocuy	21	18	1	4.7	2,168	3,500	1,998	801	14	108	14	25	22	2	18.8
8. Pamplona	11	9	1	9.0	217	3,500	700	950	14	14	14	12	10	0	-4.7
9. Cachira	13	12	0	0.0	143	3,250	735	958	5	19	19	15	13	-1	-2.1
10. Tamá	17	14	0	0.0	46	3,000	613	995	29	29	29	20	18	1	2.8
11. Batallón	13	10	0	0.0	66	3,250	662	1,065	55	65	55	13	11	1	12.9
12. Mérida	29	26	6	20.6	1,798	3,500	1,502	1,167	35	55	204	23	20	7	19.2
13. Perijá	4	4	2	50.0	167	3,000	750	1,182	75	197	75	3	2	0	37.5
14. Santa Marta	18	16	12	66.6	606	3,500	2,275	1,238	75	75	330	20	19	12	66.5
15. Cendé	15	13	0	0.0	70	3,000	552	1,380	35	35	35	12	10	0	4.4

NOTE.— N_1 = total number of species; N_2 = number of species of South American origin; E_1 = number of endemic taxa (species and subspecies); E_2 = percentage of endemic taxa; AR = area in square kilometers; BA = base altitude in meters; EL = elevation in meters; DEc = distance from páramo 1 in kilometers; DNI = distance to nearest island of páramo vegetation in kilometers; DNIS = distance to nearest island to the south, in kilometers; DNLI = distance to nearest large island (large = more than 200 sq km).

* Since páramo 1 is considered the source area, all measures of isolation (DEc, DNI, DNIS, and DNLI) are actually 0, but arbitrary values of 1 were assigned in order to avoid working with the log of 0.

The four variables concerning the páramo avifauna (species numbers, and number and percentage of endemic taxa) are considered the dependent variables (see table 1). Complete faunal lists for each of the 15 islands can be obtained from the author.

ASSUMPTIONS AND METHODS

The analysis of species numbers and numbers of endemics is based on two expectations derived from studies of archipelago situations. First, assumed measures of environmental diversity (area, base altitude, elevation) and of isolation (distance from source) may be important in regulating the number of species. An increase in environmental diversity should bring about an increase in species numbers, and an increased distance from the source a decrease in such numbers.

Second, measures of interisland isolation may be significant in regulating dispersal (and hence gene flow), and influence numbers of endemics. In the case of páramo islands, faunal exchange should lessen as distance to nearest island, to nearest island to the south, and to nearest large island increases.

To test these assumptions, and in order to ascertain which of the several independent variables contributes most to species numbers and endemism, stepwise multiple regressions were carried out at the Harvard Computing Center. The program used was BMD02R (Dixon 1968). In this program, the independent variable entered into the regression equation at each step is that which makes the greatest reduction in the error sum of squares, has highest partial correlation with the dependent variable, and has the highest F value (Dixon 1968, p. 233). Three models were tested: linear (untransformed data), semilog (long-transformed independent variables), and log-log (log-transformed data). The multiple correlation coefficient (R^2) was the statistic used to estimate how much variance in the predicted values of the dependent variables is due to the regression (Snedecor and Cochran 1968, p. 402).

RESULTS

Species Diversity

The number of species is positively correlated with area (fig. 2). Only the total number of species (N_1) is illustrated, but the pattern for the number of species of South American origin (N_2) is similar. The partial correlation coefficients are .798 for N_1 and .800 for N_2 , both significant at the 1% level ($df = 13$).

The slope of the regression (z value) and its standard error is 0.286 (± 0.089) for N_1 and 0.302 (± 0.085) for N_2 . That is, $N_1 = 1.716 \text{ Area}^{0.286}$, and $N_2 = 1.595 \text{ Area}^{0.302}$. On figure 3, the percentage of saturation plotted against distance from páramo 1 (distance effect curve) is apparently more linear than the plot for Pacific island birds (MacArthur and Wilson

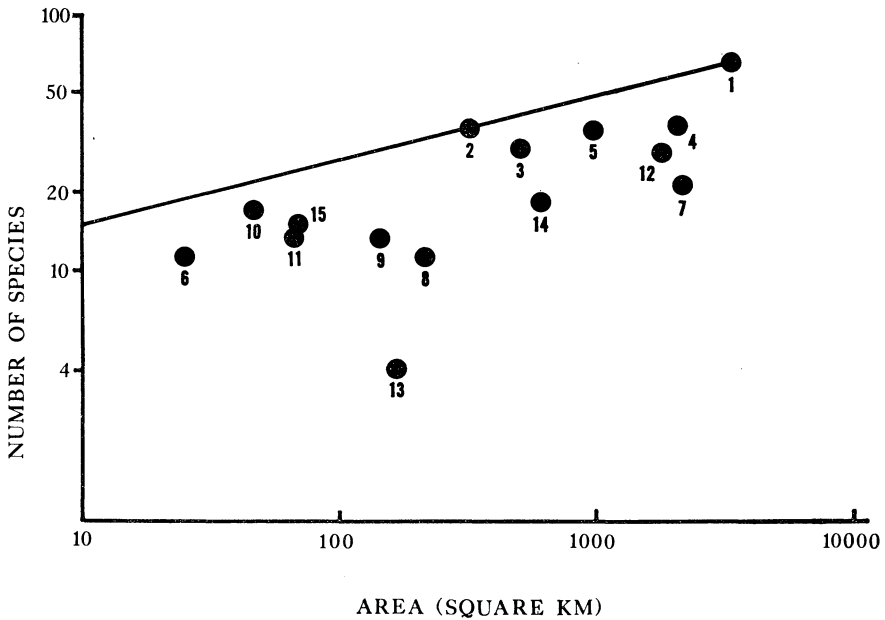


FIG. 2.—Double logarithmic plot of total number of species of birds against area for the 15 islands of páramo vegetation listed in table 1. The “saturation curve,” drawn from páramo 1 (considered the source area) to the geographically closest, páramo 2, represents the predicted “saturation” values, around which the actual values should fall were it not for the distance effect. The very small number of species on Perijá (páramo 13) may reflect insufficient collecting there.

1963). The saturation values for the number of species of each island were computed by extrapolating from the observed number of species to the number predicted from the saturation curve of figure 2 (see MacArthur and Wilson 1963). Here again, only N_1 is illustrated, but the distance effect is similar for N_2 . Numbers of species are negatively correlated with distance from páramo 1, the partial correlation coefficients being $-.776$ for N_1 and $-.763$ for N_2 , both significant at the 1% level (13 df). The partial correlation coefficients are slightly higher with untransformed N_1 and N_2 but log-transformed distance from páramo 1: $-.853$ for N_1 , and $-.841$ for N_2 . The partial correlation is lowest when both species numbers and area are log-transformed: $-.652$ for N_1 and $-.660$ for N_2 (still significant at the 1% level).

The predictions of species numbers N_1 and N_2 by multiple regression are presented in table 1. In both cases, the linear model, using untransformed data, gave the best fit, judging by the high coefficients of multiple correlation obtained (R^2), varying from about .96 to .97. In other words, from 96% to 97% of the variance in species numbers can be explained on the basis of the seven independent variables entered in the equation. The semi-log model (log-transformed independent variables) gave a slightly poorer

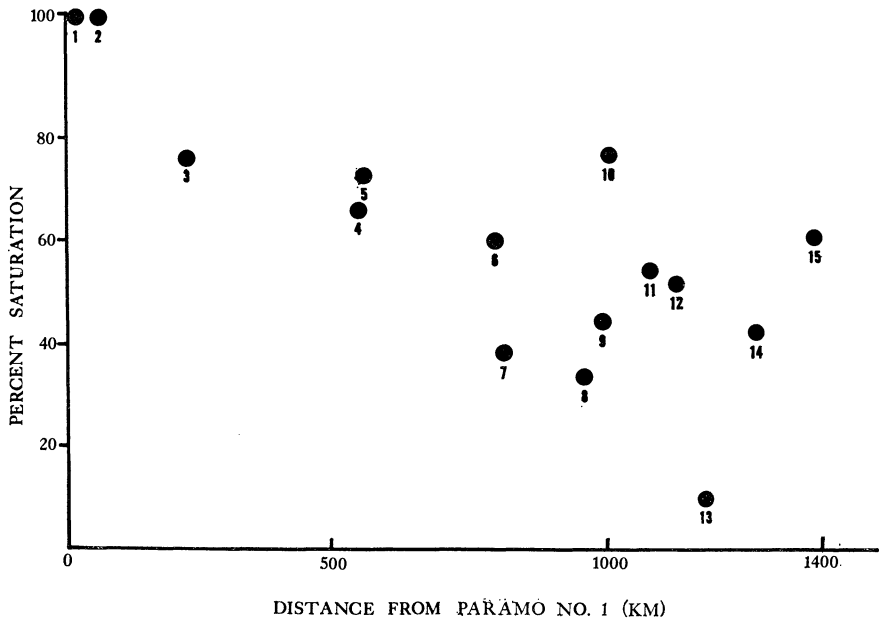


FIG. 3.—Percentage of faunal saturation plotted against distance from páramo 1 for the 15 islands of páramo vegetation listed in table 1. The percentage of saturation is obtained by calculating the predicted saturation values (B_i) from the observed values (s_i) for each island lying under the saturation curve of figure 2, then computing $s_i \times 100/B_i$ (MacArthur and Wilson 1963).

fit, with R^2 varying from 91% to 92%. Table 2 shows the results of the multiple stepwise regressions for the prediction of N_1 , with the respective contributions to R^2 of each independent variable. The results from the curvilinear model are not shown in the table, since R^2 was only .7016 in the case of N_1 and .7284 in N_2 . Since the results are similar whether N_1 or N_2 was the dependent variable selected, only prediction of N_1 is shown in table 2.

The chief results from the stepwise multiple regression analysis are as follows (table 2). With a linear model, area is the best single predictor of species number, contributing .6364 to R^2 , while distance from páramo 1 contributes .2181. Two additional variables, distance to nearest island to the south and elevation, contribute a small but significant value to R^2 . Thus four of seven independent variables can be singled out as important components in variance in species numbers. With a semilog model, however, distance from páramo 1 is a far more important predictor of species number, since it alone contributes .7268 to R^2 , whereas area contributes only .1449. A third variable, distance to nearest island, contributes a small, but significant fraction to R^2 . Thus three of a total of seven variables are the most useful in predicting the number of species.

A comparison of the partial correlation coefficients helps explain, in part, the discrepancy between the results obtained with two different models.

TABLE 2
RELATIVE CONTRIBUTIONS OF INDEPENDENT VARIABLES TO THE MULTIPLE CORRELATION
COEFFICIENT (R^2) WHEN PREDICTING THE NUMBER OF BIRD SPECIES (N_1) ON 15
ISLANDS OF PÁRAMO VEGETATION BY MEANS OF MULTIPLE REGRESSION EQUATIONS

INDEPENDENT VARIABLE	LINEAR MODEL			SEMILOG MODEL		
	Contri- bution to R^2	F Value	Order Entered in Equa- tion	Contri- bution to R^2	F Value	Order Entered in Equa- tion
Area (AR)6364	22.75**	1	.1449	13.54**	2
Distance from páramo 1 (DEc)2181	17.99**	2	.7268	34.57**	1
Distance to nearest island to the south (DNIS) ..	.0433	4.65*	3	.0078	0.71	3
Elevation (EL)0264	5.96*	6	.0003	0.03	6
Base altitude (BA)0205	2.98	5	.0002	0.01	7
Distance to nearest island (DNI)0200	2.43	4	.0356	4.18*	4
Distance to nearest large island (DNLI)0009	0.17	7	.0012	0.13	5
Total R^296569168

NOTE.—The multiple linear regression equation is $N_1 = 105.71455 + 0.00768$ (AR) $-$ 0.02278 (BA) $+ 0.00556$ (EL) $- 0.02116$ (DEc) $+ 0.13110$ (DNI) $- 0.13040$ (DNIS) $= 0.00990$ (DNLI). The multiple semilog regression equation is $N_1 = 77.48402 + 12.13713$ (log AR) $- 12.37374$ (log BA) $- 2.59854$ (log EL) $- 11.46990$ (log DEc) $+ 9.42757$ (log DNI) $- 12.68230$ (log DNIS) $+ 2.58680$ (log DNLI).

* Significant at the 5% level.
** Significant at the 1% level.

With untransformed data, the two highest partial correlations with species numbers are, first with area, and second with distance from páramo 1. With log-transformed data, these two variables again have the highest partial correlation with species numbers, but in the reverse order. Thus the distance effect is clearly not entirely linear, so that distance from source will be favored more when using a semilog regression equation. (Incidentally, a semilog model using only distance from páramo 1 as a log-transformed independent variable gave R^2 values of .9292 for N_1 and .9194 for N_2 . Thus a linear model is clearly better than semilog models.) It is therefore justified to conclude that both area and distance from source are the chief predictors of species numbers, with some other measure of isolation (either distance to nearest island to the south, or distance to nearest island) adding another small value to R^2 .

Endemism

The number and percentage of endemic taxa are not (or at best only weakly) correlated with area. The highest partial correlation coefficient is between log area and number of endemic taxa (E_1), but its value of .412 is not significant at the 5% level. Figure 4 shows a double logarithmic plot of

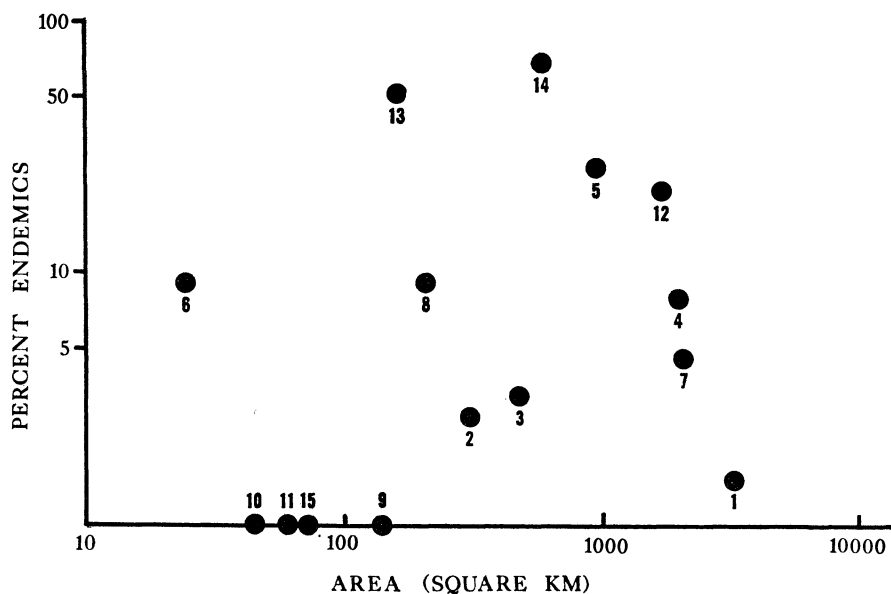


FIG. 4.—Double logarithmic plot of percentage of endemic species and sub-species of birds against area for the 15 islands of páramo vegetation listed in table 1. Islands 9, 10, 11, and 15, have no endemic taxa, but were assigned token values of 1% for the purpose of this diagram.

percentage of endemic taxa (E_2) and area. The scatter is enormous, and no correlation is apparent.

The predictions of number and percentage of endemic taxa by multiple regression analysis are shown in table 1. The best model to predict number of endemics is semilog (with log-transformed independent variables), while a linear model is better in the case of percentage of endemics. The R^2 values obtained in predicting endemism are lower than those for species numbers. The highest R^2 for number of endemics is .9225 (see table 3), comparable only to the second-best estimate for total species numbers. The highest R^2 for percentage of endemics is .8434, and is lower than the lowest estimate for number of endemics. I conclude that it is more difficult to predict endemism than species numbers, either because "endemism" is a more subjective concept than species number, for any given island, or because the independent variables selected in this analysis more effectively regulate species numbers than endemism.

Table 3 summarizes the results of the stepwise regressions used to predict numbers of endemic taxa. With a linear model (total $R^2 = .8566$), distance to the nearest large island contributes the largest amount to R^2 , .4656, and elevation the next highest value, .2328. Of the remaining variables, only area contributes significantly to R^2 . Thus three of seven variables are the most relevant in predicting number of endemics.

With a semilog model (total $R^2 = .9225$), distance and elevation are,

TABLE 3
RELATIVE CONTRIBUTIONS OF INDEPENDENT VARIABLES TO THE MULTIPLE CORRELATION
COEFFICIENT (R^2) WHEN PREDICTING THE NUMBER OF ENDEMIC TAXA (E_1) AMONG
BIRDS ON 15 ISLANDS OF PÁRAMO VEGETATION BY MEANS OF
MULTIPLE REGRESSION EQUATIONS

INDEPENDENT VARIABLE	LINEAR MODEL			SEMILOG MODEL		
	Contri- bution to R^2	F Value	Order Entered in Equa- tion	Contri- bution to R^2	F Value	Order Entered in Equa- tion
Distance to nearest large island (DNLI)4656	11.32**	1	.3692	16.67**	2
Elevation (EL)2328	9.26*	2	.3652	7.47*	1
Distance from páramo 1 (DEc)0138	0.68	6	.0795	5.55*	4
Distance to nearest island to the south (DNIS) ..	.0230	1.18	5	.0428	2.11	3
Distance to nearest island (DNI)0261	1.31	4	.0425	3.79*	5
Area (AR)0774	3.79*	3	.0222	2.26	6
Base altitude (BA)0179	0.87	7	.0011	0.09	7
Total R^285669225

NOTE.—The multiple linear regression equation is $E_1 = -19.53279 - 0.00175 (AR) + 0.00401 (BA) + 0.00558 (EL) + 0.00238 (DEc) + 0.06998 (DNI) - 0.01880 (DNIS) + 0.00077 (DNLI)$. The multiple semilog regression equation is $E_1 = -34.27844 - 1.61446 (\log AR) - 6.2635 (\log BA) + 18.72641 (\log EL) + 2.07809 (\log DEc) + 3.97772 (\log DNI) - 5.75494 (\log DNIS) + 2.82140 (\log DNLI)$.

* Significant at the 5% level.
** Significant at the 1% level.

again, the two most important contributors to R^2 , but this time both bring about equal increments, .3692 and .3652, respectively. Two additional variables contribute small but significant values to R^2 —distance from páramo 1 and distance to nearest island. Four of seven variables permit prediction of number of endemics. Note that here, as in the case of prediction of species numbers, the model with highest R^2 , and hence presumably best predictive power, uses four of seven variables, while the next best model uses only three.

The results show clearly that both distance to nearest large island (a measure of isolation) and elevation (a measure of environmental diversity) are the most important independent variables regulating the number of endemics on a given island. Interestingly, multiple regression (linear model) with percentage of endemics as the dependent variable results in elevation not being a significant contributor to R^2 , while area is (.1215). The single most important variable predicting percentage of endemics is, however, also distance to nearest large island (.4710).

It should be noted here that only two models (linear and semilog) were used in the prediction of endemism. Since several islands have zero endemism, log transformation of all the dependent variables would not have been possible.

TABLE 4
A COMPARISON OF BIOGEOGRAPHIC PATTERNS IN OCEANIC ARCHIPELAGOS WITH
THOSE OF THE ISLANDS OF PÁRAMO VEGETATION IN THE NORTHERN ANDES

Oceanic Archipelagos	Islands of Páramo Vegetation
Numbers of species:	
Species-area curve permits a reasonable prediction of species numbers (slope, z , varies between 0.20 and 0.40)	Similar
Distance-effect curve is exponential when percentage of faunal saturation is plotted on the ordinate	Curve is more rectilinear
Endemism:	
Number of endemics can be predicted by some measure of isolation, such as interisland distance	Similar
Percentage of endemics is positively correlated with area of island	No correlation

DISCUSSION

If the results of this study are compared with those from true archipelago situations (table 4) both similarities and differences become evident. I will discuss them in the order listed in table 4.

Species-Area Curve

In most, and probably all, truly insular biota, plant and animal species numbers show a positive correlation with area of island when both are plotted logarithmically. This generalization appears valid for the Andean avifauna of the páramo islands. The slope (z) of this curve was predicted by Preston (1962*a*, 1962*b*) to be about 0.27, but MacArthur and Wilson (1963, 1967), and Johnson, Mason and Raven (1968) have shown that in archipelagos the values of z varied between 0.20 and 0.40 (being even higher occasionally), while in mainland situations z oscillated between 0.12 and 0.20. The values obtained in this study are 0.29 and 0.30, and fall consequently close to the predicted value of Preston's, and within the range given by MacArthur and Wilson (1967, table 2).

That area is the best single predictor of species numbers when used in multiple regression analysis, is a generalization derived from studies on archipelago faunas and floras, and seems to hold true for the birds of the West Indies, East Indies, Pacific Islands, and Gulf of Guinea Islands (Hamilton, Barth, and Rubinoff 1964; Hamilton and Armstrong 1965), and the plants of the islands along the coast of California (Johnson, Mason, and Raven 1968).

Exceptions are the land plants and the Darwin's finches of the Galápagos Islands (Hamilton et al. 1963; Hamilton and Rubinoff 1963, 1964, 1967). Plant species diversity is best predicted by elevation, and finch species diversity by interisland distance. The Galápagos flora is not as well known as that of the California islands and better data might possibly lessen the importance of elevation in predicting the species numbers of land plants. The Darwin's finches are a single, monophyletic assemblage, and not a complex, polyphyletic assemblage (fauna) as in the other island groups

studied so far. Thus it is not surprising that a measure of isolation should predict their numbers better than island area. Full sympatry, and increased species diversity on any island, among such closely related species, can only be achieved after speciation has been completed. This process depends to a considerable degree on the amount of extrinsic isolation between populations (Mayr 1963).

If these arguments are valid, and the two instances just cited are considered atypical of archipelagos where an entire well-known flora or fauna is analyzed, we can accept the conclusion that area is generally the most important independent variable permitting prediction of species numbers. As shown above, the páramo islands conform to this rule only when a linear regression equation is used. When the independent variables are log-transformed, however, distance from páramo 1, instead of area, is the best predictor of species numbers.

The reason that distance does not seem more important in most oceanic archipelagos is that distance from source is not given by a single measure. Indeed, several source areas may contribute to species diversity on given islands, so that taking the distance solely from one potential source area is misleading, as MacArthur and Wilson (1963) pointed out.

In the Andes, the distribution patterns of the islands of páramo vegetation are mostly linear (roughly south-north, fig. 1), and the faunal flow has been mostly from south to north. Consequently, the single measure—distance from páramo 1—can be taken to accurately represent distance from source. I therefore feel that the páramo islands are no less “insular” than those of true archipelagos, but merely represent a specialized case.

The Distance-Effect Curve

In the birds of the East Central Pacific, the percentage of faunal saturation, when plotted against the distance from source, shows an exponential decrease with increasing distance (MacArthur and Wilson 1963). In the páramo birds, this decrease appears to be more linear (fig. 3). If the distance-effect curve is a function of the probability of dispersal away from a source area and the probability of reaching a potential recipient island at a certain distance away from the source area, then the observed differences between Pacific birds and Andean birds may indicate that these processes are different in the two situations. This possibility will be explored in greater detail in a later section.

Endemism Can Be Predicted by Isolation

This conclusion appears true in both archipelago and continental situations. The results of the multiple regressions carried out during this study are comparable to those of the only other similar study, that of the Darwin's finches (Hamilton and Rubinoﬀ 1963, 1964, 1967). In both instances, some measure of interisland distance appears to be an important

contributor to R^2 , whether the model used is linear or nonlinear, but the total value of R^2 is considerably increased in the Andean avifauna when some measure of environmental diversity is also added—elevation.

Endemism is Positively Correlated with Area

Mayr (1965), MacArthur and Wilson (1967), and Greenslade (1968) presented evidence that endemism and area are correlated in the case of birds, ants, beetles, butterflies, and bugs of the Pacific archipelagos. This conclusion cannot be applied to the avifauna of the páramo islands, as figure 4 shows. There is no statistically significant correlation between area and percentage or number of endemics, whether the data are log-transformed or not, yet area does contribute 0.1215 to the variance in percentage of endemics when a linear model is used.

CONCLUSIONS

1. The similarities between oceanic and continental insular situations suggest that the following generalizations are true in both:

a) Propagules have a greater probability of reaching an island, and of becoming established on it (colonizing), the greater the area of that island. This is due partly to the greater target area available to a propagule, regardless of its colonizing potential, and also to the greater environmental diversity, which will increase the probability that the recipient island is ecologically suitable enough for the propagule to survive and reproduce.

b) The probability that a propagule reaches an island far away from the source area is inversely correlated with the distance from that source, but the probability distribution may be different in the oceanic and in the continental situation, as will be argued later.

c) The probability that a taxon differentiates on a given island and becomes endemic there is positively correlated with the isolation of that island from source areas which might serve for faunal exchange.

2. What about the differences observed between oceanic and continental patterns? I venture to conclude that these discrepancies reflect genuine differences in two related phenomena, isolation and dispersal.

a) In oceanic archipelagos, the probability of a propagule falling in the sea and dying before it reaches a potential recipient island is always high. Birds (the organisms considered here) will tend to fly until exhausted, maintaining either a fixed or a changing direction. The probability distribution of their reaching another island will consequently be either exponential or normal (see MacArthur and Wilson 1967).

In continental islands, however, the probability of an avian propagule dying before it reaches another island is considerably lower, because the islands are not isolated from each other by sea, but by different vegetation, where the propagule may "rest." Thus, even though the barrier is unsuitable for the species' establishment (in the genetic sense), it is suitable

as a stepping stone. Consequently, the probability distribution will be uniform (MacArthur and Wilson 1967), or will tend to be so. If the probability distribution is reflected by the shape of the distance effect curve, it is interesting that the latter should be exponential in Pacific birds, and more linear in Andean birds. Notice, however, that since species numbers have a higher correlation with distance when the latter is log-transformed, the probability distribution for Andean birds may not be entirely linear but tend toward an exponential. This would mean that the vegetation separating páramo islands is not as drastic an obstacle for páramo birds as the sea, but it is not as benign as páramo itself.

b) In oceanic archipelagos, dispersal from a source area has a high probability of proceeding equally at all times, and in all directions away from it, in a concentric fashion. Area and distance are therefore very important as determinants of the probability of faunal exchange. Over time, the larger and closer islands have a greater probability of receiving propagules than smaller and more distant islands.

In the Andes, however, dispersal proceeds in a concentric fashion only periodically, as during interglacials (as now), when the páramo vegetation and its fauna are, indeed, insular in geographical distribution (see fig. 1). During glacial periods of the Pleistocene, however, a lowering of timberline would have permitted direct connection between at least some of the "islands" of figure 1. Therefore, as I argued in a previous paper (1969b), more dispersal takes place during glacial periods. An interesting consequence is that dispersal will be enhanced mostly or only in a geographically linear fashion between neighboring islands, as should be obvious in figure 1. As a result, one may expect that both small and large "islands" will have at that time more equal probabilities of receiving new propagules. Whether these propagules will remain, differentiate and eventually become endemic will depend more on the relative isolation of a given island after the dispersal phase, than on the area of that island, hence the scatter in figure 4.

SUMMARY

In order to test whether the theory of insular biogeography also applies to a continental situation, species diversity and endemism were studied among the birds living in islands of páramo vegetation above timberline in the northern Andes of South America. Stepwise regression analyses were performed, assuming that measures of environmental diversity (especially area) and of isolation (interisland distances) permit prediction of species numbers and numbers of endemics in a continental situation, as they do in archipelagos.

With seven independent variables included in the equations, prediction of species diversity and endemism was extremely good. From 92% to 97% of the variance in species numbers can be accounted for by regression, the best fit (97%) being obtained with a linear model. From 87% to 93% of

the variance in number of endemics can be predicted by regression, a semi-log model providing the best fit (93%).

The Andean islands conform to archipelagos in two ways: first, because the species-area curve offers a reasonable prediction, as a first approximation, of species numbers; and second, because the numbers of endemics can best be predicted by some measure of interisland distance. The páramo islands differ from oceanic islands, however, because the distance effect curve is more linear than exponential, and because there is no statistically significant correlation between endemism and area of islands. These differences can be explained if isolation between islands is less absolute, so that the probability distribution of dispersal away from a source area is uniform, instead of exponential or normal.

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