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Glacial Migrations of Plants: Island Biogeographical Evidence

Abstract. *Analyses of the floras of the high north Andean habitat islands (paramos) and the Galápagos Islands show that plant species diversity conforms to the MacArthur and Wilson model of island biogeography but that immigration occurred primarily during glacial periods. Modern plant species diversity is more significantly correlated with area and distance measures of the glacial forms of the islands than with similar measures of the present-day islands.*

According to the MacArthur and Wilson (*1*) theory of island biogeography (*2*), the number of species on an oceanic island, or on a continental habitat island (*1–3*), is primarily correlated to, and a function of, the area of that island and its distance from a source of propagules. This relation holds only when enough time has elapsed to allow an approach toward an equilibrium state, or a balance between constant rates of immigration and extinction (*1, 2*). Assuming that there is such an equilibrium, a function of S (species number), unique for each set of islands and taxonomic group, can be derived with the area of the islands and their distances from source areas as the principal independent variables. Stepwise multiple regression has been the most common method employed for determining this function (*3–7*). In interpreting the results of such a regression analysis, it is important not only to obtain a high coefficient of correlation (R^2), but also to ascertain the contributions made to the equation by both area and distance measures.

Table 1. Results of multiple regression analyses. All analyses were made with BMD-02R, UCLA biomedical computer programs. The islands are shown in Figs. 1 and 2; S is the number of species. In parts (a) and (b) the abbreviations are as follows: A, planar area of island; DL, distance to nearest paramo with area $\geqq 200$ km²; ELE, elevation from tree line to highest peak of mountain massif; DS, distance to nearest paramo to the south; AVD, average distance to nearest two paramos; DE, distance to Ecuador. In parts (c) and (d) the abbreviations are: A, area of island; ELE, elevation of island; DNI, distance to nearest island; DSC, distance to Santa Cruz; $AADJ$, area of adjacent island; $DISA$, distance to Isabela.

Dependent variable	Independent variables in order entered into equation	R^2
	(a) *Modern paramo habitat islands*	
S (linear)	A**, DL, ELE, DS, DE, AVD	.6584
Log S (log-log)	Log A**, log DL, log ELE, log AVD, log DE	.7111
S (semilog)	Log A**, log DS, log AVD, log DL, log DE, log ELE	.7337
	(b) *Glacial paramo habitat islands*	
S (semilog)	Log A*, log ELE, log DL	.7169
Log S (log-log)	Log ELE*, log DL, log A	.8410
S (linear)	A**, ELE*, DL	.9565
	(c) *Modern Galápagos Islands (16)*	
S (semilog)	Log A**, log DSC*, log AADJ, log DISA; log DNI, log ELE	.7748
S (linear)	ELE**, AADJ**, DSC, DISA, A, DNI	.8101
Log S (log-log)	Log A**, log ELE**, log DNI, log DSC, log AADJ	.8127
	(d) *Glacial Galápagos Islands*	
S (linear)	A*, DSC*, DNI, ELE, DISA	.6085
Log S (log-log)	Log A**, log DSC, log ELE, log DNI*, log DISA	.8969
S (semilog)	Log A**, log DSC**, log DNI, log ELE**, log DISA*	.9287

* Variables with a partial regression coefficient significant at $P = .05$. ** Variables with a partial regression coefficient significant at $P = .01$.

Failures in previous studies to find significant correlations between area, distance, and species diversity have been ascribed to low vagility of the organisms, essentially nonconstant rates of immigration (bursts of colonization), or insufficient time for extinction to have produced an equilibrium with the modern area of an island or its present immigration rate (*3, 5, 8, 9*). Studies in which historical changes have been hypothesized as causal factors have involved either continental areas drastically affected by glacial phenomena (*8*) or islands connected directly to a mainland by glacial land bridges (*9*). Until now, there has been no positive evidence for the role of paleoecological events in the determination of modern species diversity in island situations where the islands were less severely altered or have not been connected to a continent since at least early Tertiary times.

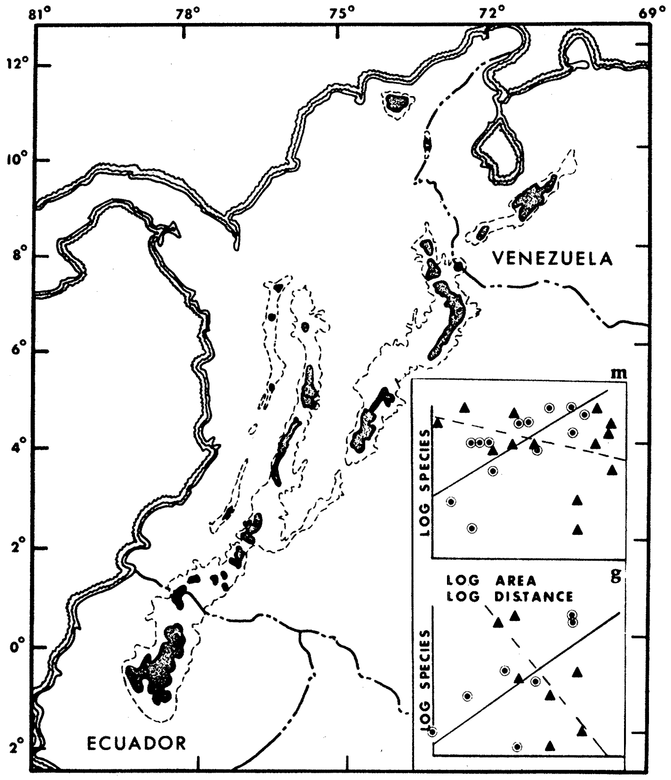
This report provides evidence that in at least two situations, the continental paramo habitat islands and the oceanic Galápagos Islands, plant colonization has occurred through dynamic dispersal over unfavorable areas, but modern species diversity reflects an approach toward equilibrium achieved during glacial times. Stepwise multiple regression analyses made with the modern island parameters have shown that these parameters account for a large amount of the variation in species numbers of birds in both areas (*3, 6*). It was likely, therefore, that plant species diversity was also related to island area and distance measures. The point under investigation here is whether angiosperms, a less dynamic group of organisms than birds, show similar patterns of diversity or whether the modern flora shows stronger correlations with former island conditions.

In the first study, 151 plant species of the Colombian and Venezuelan paramos (Fig. 1), a large subsample of the total flora, were used in a stepwise multiple regression analysis with the variables listed in Table 1a (*5*). A former study of the avifauna (*3*) had shown that more than 95 percent of the current variation in species numbers from paramo to paramo could be accounted for by using these modern areas and distances as the principal independent variables. The multiple regression analysis of paramo plant species against these variables also showed a rather high coefficient of determination ($R^2 = .73$) with only area contributing significantly to the equations (Table 1a). Moreover, pairwise correlations showed that distance was not highly correlated with species diversity (Fig. 1m).

From paleobotanical evidence (*10*), we know that within the last 30,000 years, and probably several times earlier in the Pleistocene, the extent of the paramo patches and their distances from one another have been greatly altered. Consequently, rates of immigration could not have remained constant for more than about 10,000 years. Since these microfossil studies allow a reasonable estimate of the lowering of the tree line, the glacial areas of the paramos and their past distances from one another can be determined (Fig. 1). A second set of regression analyses was therefore made with the parameters of the paramos during a glacial period (Table 1b). Table 1b shows that models using these historical parameters account for much more of the modern variation ($R^2 = .96$) in species numbers of plants than do the modern paramo areas and distances. As in the previous case, only area contributed significantly to the equations, but pairwise correlations showed that glacial distances were more highly correlated with species diversity than modern distances (compare Fig. 1m and Fig. 1g).

A similar analysis was tried with the Galápagos Islands (Fig. 2). Studies of the modern avifauna have shown that 87 to 89 percent of the species diversity is accounted for by modern island parameters. A report using an updated flora and precise modern area and distance measures (*7*) showed that these parameters could account for a maximum of 81 percent of the present plant diversity. However, only area contributed significantly to the multiple regression equations (Table 1c); distance measures were not correlated to species numbers in simple pairwise correlations (Fig. 2m).

During maximum glacial times, sea level dropped 100 m in tropical latitudes (*11*), and this must have altered both the areas of the Galápagos Islands and their distances from one another (Fig. 2). Consequently, a second analysis was made with reconstructed glacial islands. As in the case of the paramos, this analysis provided more significant results (Table 1d) than were obtained with the modern areas and distances (Table 1c). With the glacial parameters, distance as well as area (as predicted by the theory of island biogeography) contributed significantly to the equation. Furthermore, in pairwise combinations, glacial distances were also significantly correlated with species diversity (Fig. 2g).



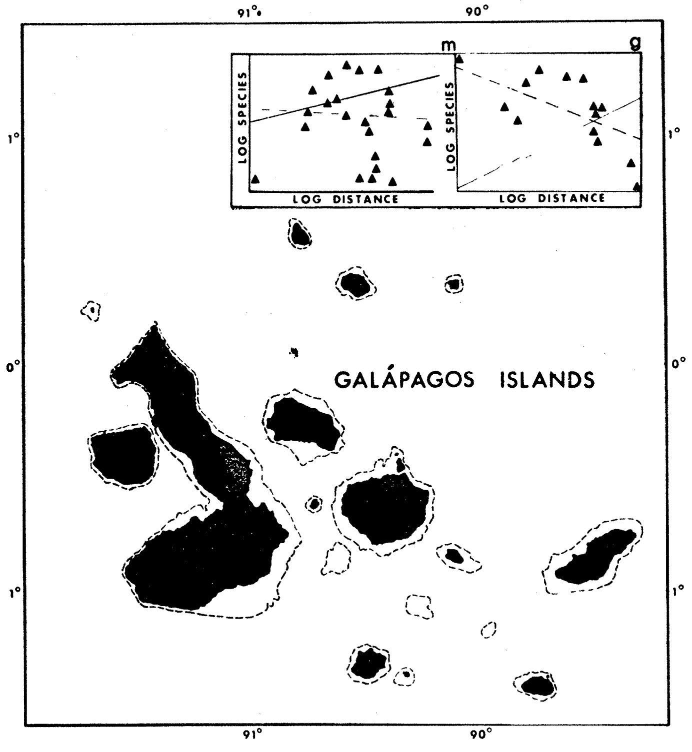


Fig. 1 (left). Distribution of areas of paramo habitat in northern South America. Dark areas enclosed by solid lines indicate the present distribution. Areas enclosed by dashed lines indicate the distribution in glacial times, assuming a tree line depression of 1500 m (*10*). (Inset m) Regression of log S against the logarithm of the modern area (circles and solid line, $r = .755$, significant at $P = .01$) and against the logarithm of the modern distance of each paramo to the nearest paramo to the south (triangles and dashed line, $r = -.366$, not significant). (Inset g) Regression of log S against the logarithm of the glacial area (circles and solid line, $r = .763$, significant at $P = .05$) and against the logarithm of the glacial distance of a paramo to the nearest large paramo (triangles and dashed line, $r = -.720$, almost significant at $P = .05$). Horizontal axes are the same in both m and g. [Map used: Republica de Colombia by Instituto Geografico de Colombia, Agustin Codazzi, 1963]

Fig. 2 (right). The modern Galápagos Islands (dark areas enclosed by solid lines) and their glacial forms (areas enclosed by dashed lines), assuming a 100-m drop in sea level (*11*). (Inset m) Regression of log S against the logarithm of the modern distance to Santa Cruz (triangles and dashed line, $r = -.131$, not significant). (Inset g) Regression of log S against the logarithm of the glacial distance to Santa Cruz (triangles and dashed line, $r = -.637$, significant at $P = .05$). The solid lines in m and g are the regressions of log S against the logarithm of the area for the modern and glacial islands (*14*) ($r = .884$ and $.849$, respectively, both significant at $P = .01$). [Millionth map of the American Geographical Society, NA 17 (1948/1956), plus U.S. Navy Oceanographic Office Chart 22000 (ed. 14)]

It seems justifiable to conclude that vascular plants of continental habitat islands affected by climatic shifts, and oceanic islands affected by sea level drop, colonized principally in glacial periods, when immigration was facilitated by larger island areas, smaller distances to source areas, and stronger wind and ocean currents (*12*). During such periods, the islands would have acquired an "hyperequilibrial" number of species relative to modern island areas and distances. The present number of species per island, representing a nonequilibrium situation, has apparently departed little from the high level reached during glacial times. A decay in species numbers to an equilibrium consistent with modern island parameters would depend more heavily on the reduction in the area of an island following climatic change than on the changed distances. Consequently, one would expect to find a stronger correlation of the numbers of species with modern areas than modern distances. Figures 1 and 2 show this to be the case.

Very rapid readjustment of species numbers following changes in island areas (or artificial manipulation of species) is known in several groups of animals which are highly mobile and exhibit considerable amounts of interspecific competition (*13*). As a result, modern species diversity of such animal taxa is quite strongly correlated with both modern areas and distances (*1–3, 13*). The contrasting lack of rapid extinctions in the flora of the paramos or the Galápagos Islands following glacial retreat and sea level rise might be due to several factors (*14*). First, plants are long-lived relative to birds and insects and would require a longer time to readjust to a new immigration rate. Second, the number of individuals of a plant species is often higher than that of an animal species. Again, more time would be required for complete extinction of a plant species. Finally, competition between species, although an important element, is often not as taxon-directed in plants as it is in animals and would only slowly eradicate all the individuals of a particular species. The correlations of modern plant species diversity with the present areas and distances from source areas of both the Galápagos Islands and the paramos, previously considered to constitute a reasonable fit to the MacArthur and Wilson equilibrium model, probably reflect the fact that, in these cases, the modern areas and distances are often proportional to their glacial counterparts (Figs. 1 and 2).

These results show that historical factors such as geological changes in island areas and the distances of the islands from sources of propagules, as well as the relative life span, population size, vagility, and extent of interspecific competition of the island taxa involved, must all be considered in determining the applicability of the model of island biogeography to either present or past situations.

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15. Several of these ideas resulted from discussions with B. Holt, A. Schoener, and J. Terborgh. I particularly thank N. Roth and J. Terborgh for help and E. Wilson and T. P. Webster for kindly reading the manuscript. The Information Systems Division, Smithsonian Institution, provided facilities and advice.

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Hyporheic Communities of Two Montana Rivers

Abstract. *Collections of stream organisms from a domestic water supply system adjacent to the Tobacco River revealed that a detritus-based community exists in subterranean waters circulating through floodplain gravels at least 4.2 meters below and 50 meters laterally from the river channel. Several stone fly species spend their entire nymphal life cycles in underground habitats of the Flathead and Tobacco rivers.*

One of the most interesting aspects of stream ecology is the manner in which aquatic organisms segregate across and within stream bed substrata in response to preferences for specific microhabitats encompassed by the lotic environment. Complex horizontal distributions of animals determined by availability of food and suitable shelter are well documented (*1*; *2*, pp. 206–216). Riverine water may circulate deep within the substrata and to some distance laterally from the stream channel in areas of extensive fluvial deposition of small rocks and gravel. Interstices in the channel substrata are often sufficiently wide to allow vertical and lateral colonization of subterranean water by surface macrobenthos (*3, 4*). Subterranean habitat of streams has been referred to as the hyporheic area, and the indigenous faunas are usually composed of many very small individuals of species also common on the surface of the stream bottom (*4, 5*). Common riverine invertebrates may be distributed as deep as 70 cm vertically within substrata (*3, 4*) and to 60 cm laterally in shore groundwaters (*2*, p. 407). We report here the hyporheic habitats of two rubble-bottom rivers in northwestern Montana; the habitats extend to at least 4.2 m in depth and up to 50 m laterally from the river channel. The hyporheic community is dominated by large stone flies, which spend all except the adult stage of their life cycles deep in subterranean waters.

For the past 2 years we have been studying stone fly (Plecoptera) ecology in the Flathead River and its three forks in the area above Flathead Lake,