be used to achieve an accuracy of 1'. Petrie hints that astronomical parallax would have to be overcome by taking records 6 months apart, but it should be possible to get an alignment of the required accuracy in a single night.

There are no other remains in Egypt which can give corroborative results; the other pyramids are smaller and of less accuracy, and many other buildings have solar or stellar alignments. The two pyramids that give us this unique result were built at the zenith of pyramid construction, and it is not surprising that they alone yield such accuracy.

Giza is situated approximately 30°E, 30°N; hence, we can say that the pole of about 4500 years ago (as seen from the center of the earth) is now 3.5' ± 0.9' along longitude 60°W toward Greenland, and with an unknown component along longitude 30°E. At the time of building, the "pole star" would have been Vega. Being at an elevation of 30°, Vega would be ideal for alignment, but it would be worthwhile to conduct an experiment on the actual site so that all possible sources of error could be investigated.

It is now well documented that the true pole moves at 0.0032" annually along longitude 60°W (3). This would amount to 0.24' over 4500 years, is far too small, and is of the wrong sign. Some variation is thought to be caused by the melting of the ice on Greenland and Antarctica. Other variations of the polar position are oscillatory in nature and are of very small amplitude (4).

Continental drift can cause the direction of true north to vary with respect to the moving block. The Americas have been separating from Africa and Europe owing to the spreading of the sea floor. This movement has a hinge southwest of Iceland, and is about 5 cm per year between South America and Africa. If this causes only the latter to rotate and if the rotation is uniform, in 4500 years the pyramids would be rotated 0.1' in the observed sense.

Africa and the Arabian peninsula are moving apart as if hinged near the north end of the Red Sea. This suggests a rotation of the pyramids in the wrong sense, but again of a magnitude far too small. Both these movements are shown in Fig. 2.

Earthquakes are a possible mechanism for a local reorientation. The Mediterranean and Red Sea areas are well known for earthquakes, but a single quake of unprecedented magnitude

Fig. 2. The pattern of continental drift, showing two hinge points.

would be needed to move the pyramids by strain release. Expert geological opinion would be worthwhile on this point as the local fault system must be understood in detail, as also the effect of the quake thought to have occurred in 908 B.C.

An observation of the movement of the pole exists on a time scale which is rare to modern science. The continental drift theory is based on very recent measurements, and there is controversy over whether drift is continuous or jerky. In this debate the pyramid observation may make a contribution, as it should be explainable in geophysical terms.

If we accept the evidence of the pyramids as valid we may well ask what other archeological remains can give further information. There are some extremely accurate yet unexplained plateau markings in Peru, made by the Nasca people, and these are in danger of destruction. The megalithic sites in Britain and Brittany are also candidates for study, but first we must be convinced of the arguments that these are solar and lunar observatories (5). The best of these may be accurate enough, although this is doubtful. The pyramids probably yield the most accurate record, and it would be a pity if this unique fact was lost in the rush of science.

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References

1. F. Petrie, Wisdom of the Egyptians (Quaritch, London, 1940).
2. I. E. S. Edwards, The Pyramids of Egypt (Pelican, New Orleans, ed. 2, 1961).
3. W. Markowitz and B. Guinot, Eds., Continental Drift (Reidel, Dordrecht, Netherlands, 1968).
4. J. Coulomb and G. Jobert, The Physical Constitution of the Earth (Oliver and Boyd, Edinburgh, 1963).
5. A. Thom, Megalithic Lunar Observatories (Oxford Univ. Press, New York, 1971).

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Species Number and Endemism: The Galápagos Archipelago Revisited

Abstract. Regression analyses to determine plant species number are repeated for the Galápagos Islands with new data. The multiple curvilinear regression gives the best prediction of species number, with island area making the only significant contribution. The proportion of species endemic to the Galápagos is highest in the arid, transition zone and on small islands, and lowest in the littoral and mesic zones. This is explained in terms of zone-specific immigration and extinction rates and the very recent appearance of moist upland climates in the archipelago.

The major factors determining the number of plant species on the Galápagos Archipelago were analyzed and discussed by Hamilton et al. (1). They concluded that ecologic diversity (estimated by topographic relief) and isolation (estimated by interisland distances) were the two most important regulators of species number. While island area was the best single predictor of the number of plant species on each island (when logarithms of the species number and area were used), the multiple regression that best predicted the island species number was a linear one to which area did not make a significant contribution. Elevation made the major contribution to the determination of the number of species on each island in that linear regression. Area may also be considered a measure of ecologic diversity and has been the better predictor of plant species numbers in other island groups (2, 3). Do the Galápagos differ from other island groups in the determination of species number and, if so, why?

A major criticism of the results of

Hamilton *et al.* is that the data for island species number at that time were quite incomplete. A new flora of the Galápagos has been published by Wiggins and Porter (*4*). This flora is still not complete, but is a vast improvement over the data available to Hamilton *et al.* Using data taken from Wiggins and Porter, we have repeated the analyses done by Hamilton *et al.* Plants known only from cultivation in the Galápagos Islands were deleted from the island species lists. As a result, our figures are slightly different from those given in the book. We have lists for 29 islands, compared to 17 in the earlier analyses. The independent variables initially used in our analysis are those of Hamilton *et al.*:

area of the island, A_1; topographic relief expressed by elevation, E; distance from the nearest island, D_1; distance from the center of the archipelago taken at Santa Cruz, D_2; and area of the adjacent island, A_2. The elevation could not be determined for six of the islands. All analyses with elevation have a sample size, n, of 23. The data are summarized in Table 1.

The following regression analyses were computed with the species number of each island as the dependent variable: (i) simple linear, (ii) simple curvilinear (logarithmic data), (iii) multiple linear, and (iv) multiple curvilinear. The correlation matrices are given in Table 2 and the results of

the multiple regression analyses in Table 3.

The results differ markedly from those of Hamilton *et al.* The best prediction of species numbers is obtained with the multiple curvilinear equation. With this equation only area makes a significant contribution to the determination of species number (S). In simple linear regressions, elevation remains a better predictor than area (for S and E, $r^2 = .5047$, $n = 23$, $P < .001$; for S and A_1, $r^2 = .3795$, $n = 29$, $P < .001$), but the best single predictor is area in the curvilinear relationship (for $\ln S$ and $\ln A_1$, $r^2 = .7797$). These new results fit those obtained for the California islands (*2*) and for the British Isles (*3, 5*) except that isolation, as measured according to Hamilton *et al.*, is not a significant contributor to the regressions. We have estimated isolation using different criteria and more elaborate parameters. These analyses follow the approach of Thornton (*6*) and demonstrate a significant decrease in species number with increasing isolation.

While both area and elevation are parameters estimating ecologic diversity, area consistently gives the higher correlation with species number. We suggest that this is true because area includes the forms of environmental heterogeneity measured by elevation, and additional heterogeneity not resulting from elevational changes. It is important to note that elevation consistently has a better linear correlation with species number than does area. An increase in elevation is expected to produce a difference in habitat. However, when area is sampled in successive increments the probability of finding new habitats decreases. The elevation–species number relationship is therefore linear, whereas the area–species number relationship is curvilinear.

In the British Isles and in the California islands, environmental richness was shown to increase species number. On the Galápagos Islands the high-elevation islands receive much more rainfall than the low-elevation islands. Elevation may be indicating environmental richness in addition to ecologic diversity. This dual role would account for the greater importance of elevation in determining species number in the Galápagos as compared to other island groups that have been studied.

An interesting observation is the distribution of endemics among the islands, on each island, and taxonomically. The numbers of species endemic

Table 1. List of islands and variables.

Island	Observed species Total S	Observed species Endemics	Area A_1 (km²)	Elevation E (m)	Distance (km) From nearest island D_1	Distance (km) From Santa Cruz D_2	Area of adjacent island A_2 (km²)
Baltra	58	23	25.09		0.6	0.6	1.84
Bartolomé	31	21	1.24	109	0.6	26.3	572.33
Caldwell	3	3	0.21	114	2.8	58.7	0.78
Champion	25	9	0.10	46	1.9	47.4	0.18
Coamaño	2	1	0.05		1.9	1.9	903.82
Daphne Major	18	11	0.34		8.0	8.0	1.84
Darwin	10	7	2.33	168	34.1	290.2	2.85
Eden	8	4	0.03		0.4	0.4	17.95
Enderby	2	2	0.18	112	2.6	50.2	0.10
Española	97	26	58.27	198	1.1	88.3	0.57
Fernandina	93	35	634.49	1494	4.3	95.3	4669.32
Gardner*	58	17	0.57	49	1.1	93.1	58.27
Gardner†	5	4	0.78	227	4.6	62.2	0.21
Genovesa	40	19	17.35	76	47.4	92.2	129.49
Isabela	347	89	4669.32	1707	0.7	28.1	634.49
Marchena	51	23	129.49	343	29.1	85.9	59.56
Onslow	2	2	0.01	25	3.3	45.9	0.10
Pinta	104	37	59.56	777	29.1	119.6	129.49
Pinzon	108	33	17.95	458	10.7	10.7	0.03
Las Plazas	12	9	0.23		0.5	0.6	25.09
Rabida	70	30	4.89	367	4.4	24.4	572.33
San Cristóbal	280	65	551.62	716	45.2	66.6	0.57
San Salvador	237	81	572.33	906	0.2	19.8	4.89
Santa Cruz	444	95	903.82	864	0.6	0.0	0.52
Santa Fé	62	28	24.08	259	16.5	16.5	0.52
Santa Maria	285	73	170.92	640	2.6	49.2	0.10
Seymour	44	16	1.84		0.6	9.6	25.09
Tortuga	16	8	1.24	186	6.8	50.9	17.95
Wolf	21	12	2.85	253	34.1	254.7	2.33

* Near Española. † Near Santa Maria.

Table 2. Correlation matrices. The right triangular matrix is for raw values and the left triangular matrix for logarithmic values. For correlations with E, $n = 23$; for all other correlations, $n = 29$.

Variable	S	A_1	E	D_1	D_2	A_2
S		0.616	0.710	−0.018	−0.186	0.012
A_1	0.883		0.753	−0.114	−0.109	0.177
E	0.724	0.893		−0.110	−0.174	0.558
D_1	−0.040	0.104	−0.036		0.613	−0.120
D_2	0.181	0.313	−0.127	0.540		0.045
A_2	0.051	0.092	0.227	−0.080	−0.094	

to the Galápagos Archipelago (Galápagos endemics) found on each island is given in Table 1. These species make up 25.7 percent of the total flora—much less than original estimates (7)—but the mean percentage of Galápagos endemics in the individual island floras in 49.7 percent. The Galápagos endemics are found on more islands, on the average, than species not endemic to the Galápagos. The mean number of islands per species for the Galápagos endemics is 4.73 ± 0.33 (2 S.E.) whereas the mean for all species is 3.69 ± 0.30. The percentage of Galápagos endemics in the individual island floras decreases significantly as the area of the island increases ($r = -.6813$, $n = 29$, $P < .001$). On individual islands the approximate percentages of Galápagos endemics in the ecological zones from sea level to high mountains are: littoral zone, 12 percent; arid zone, 64 percent; transition zone, 43 percent; Scalesia zone, 23 percent; Miconia zone, 27 percent; and fern-sedge zone, 8 percent. These figures are only approximate as the zonal distributions of species are not well known. The proportion of Galápagos endemics among dicots (34 percent) is higher than that among monocots (12 percent). In both ecological and evolutionary aspects, the Galápagos endemics are not a random subset of the total Galápagos flora.

We suggest the following explanation of the pattern of endemism. The archipelago consists of three major ecological zones that differ in their immigration and extinction rates (8) and in their ages. In the first of these zones, the littoral zone, immigration by drift is very important and the rate is quite high. Many of the species in this zone are drift-disseminated littoral species with wide geographical distributions. Storm disturbance and the small area of this zone result in a high extinction rate. The high immigration and extinction rates reduce the opportunity for endemism, which is observed to be lowest in this zone.

The second major zone is the arid lowlands (arid and transition zones). This zone makes up the major portion of the land area of the archipelago and is found on all islands. These conditions would lower the extinction rate and increase the opportunity for endemism.

The unusual observation is the relatively low proportion of endemics in the moist uplands. For most other island groups studied, the highest proportion

of endemics has been found in the moist uplands. These endemics consist largely of forms that have evolved from related species occurring at lower elevations. In the Galápagos Archipelago, the moist uplands have been populated chiefly by immigrants from the mainland. Colinvaux (9), on the basis of his analysis of a core of sediments from a lake on San Cristóbal, has shown that the period from about 10,000 to 30,000 years ago (radiocarbon dates) was very much drier than the present. In the light of his findings, we propose that the great majority of the nonendemic plants in the moist uplands have reached the Galápagos Archipelago within the past 10,000 years. Moist uplands in their present form seem to have existed in the archipelago only during this period of time. There has evidently not been sufficient time for the evolution of many endemics in situ. A very high proportion of the plants found away from the immediate coast are disseminated by birds, only a few by wind (10).

As to the age of the archipelago itself, the radioisotope ages of a number of lava samples suggest an age of several million years for the eastern islands, such as San Cristóbal (11), and an age of less than 0.7 million years for the western ones (12). Ages of 30 million (13) or even 40 million years (14) have been proposed for islands in the vicinity, and Holden and Dietz (14) have argued that the "endemic birds and bizarre animals" of the Galápagos have required millions of years for their evolution in isolation. In comparison with the Hawaiian Islands, where many genera and over 90 percent of the vascular plant species are endemic, the figures presented in this report suggest on the contrary that several million years would have been adequate for the evolution of the endemic flora. The endemic plants and animals (15) of the Galápagos do not illuminate the question of the possible existence of islands in the vicinity before the Pleistocene.

Even the modestly developed species swarms found in these islands—such as those in *Acalypha, Alternanthera, Chamaesyce, Coldenia, Mollugo, Opuntia,* and *Polygala*—are mainly confined to low elevations, with a very few such groups weakly developed in the moist uplands (*Cordia, Scalesia,* and *Verbena*). This pattern of low endemism in the moist uplands is one that sets the Galápagos aside from almost all other islands that have been studied in detail.

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References and Notes

1. T. H. Hamilton, I. Rubinoff, R. H. Barth, Jr., G. L. Bush, *Science* 142, 1575 (1963).
2. M. P. Johnson, L. G. Mason, P. A. Raven, *Amer. Natur.* 102, 297 (1968).
3. M. P. Johnson and P. H. Raven, *Evol. Biol.* 4, 127 (1970).
4. I. L. Wiggins and D. M. Porter, *Flora of the Galápagos Islands* (Stanford Univ. Press, Stanford, Calif., 1971), pp. 1–998.
5. M. P. Johnson and D. S. Simberloff, in preparation.
6. I. W. B. Thornton, *Evolution* 21, 842 (1967).
7. C. Darwin, in *Essays in Social Biology*, B. Wallace, Ed. (Prentice-Hall, Englewood Cliffs, N.J., 1972), vol. 2, p. 77.
8. Our definitions of immigration and extinction rates are modified instances of definitions given by R. H. MacArthur and E. O. Wilson [*Evolution* 17, 373 (1963)]. We have partitioned the Galápagos Archipelago into ecological zones rather than islands in a manner similar to that of D. R. Whitehead and C. E. Jones [*ibid.* 23, 171 (1969)].
9. P. A. Colinvaux, *Nature*, in press.
10. J. D. Hooker, *Trans. Linn. Soc. London* 20, 235 (1847); S. Carlquist, *Bull. Torrey Bot. Club* 94, 129 (1967).
11. A. Cox, *Earth Planet. Sci. Lett.* 11, 152 (1971).
12. —— and G. B. Dalrymple, *Nature* 209, 776 (1966).
13. R. N. Hey, K. S. Deffeyes, G. L. Johnson, A. Lowrie, *ibid.* 237, 20 (1972).
14. J. C. Holden and R. S. Dietz, *ibid.* 235, 266 (1972).
15. W. J. Bock [*Evolution* 24, 704 (1970)] has calculated that the endemic honeycreepers (*Drepanidae*) of Hawaii could have differentiated from a common ancestor within a million years; in the absence of fossil evidence, assumptions about rates of evolution should be made with great reserve.
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Table 3. Summary of results of multiple regression analyses.

Dependent variable	n	Independent variables	Coefficient of determination R^2
S	29	A_1^*, D_1, D_2, A_2	.4218
ln S	29	ln A_1^*, ln D_1, ln D_2, ln A_2	.8000
S	23	$A_1, E^*, D_1, D_2, A_2^*$	.7635
ln S	23	ln A_1^*, ln E, ln D_1, ln D_2, ln A_2	.8142

* Independent variables with significant partial regression coefficients ($P < .05$).