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FLORAL RELATIONS AMONG THE GALAPAGOS ISLANDS

BY

A. L. KROEBER

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In Professor B. L. Robinson's valuable and fundamental treatise on the Flora of the Galapagos Islands,[1] he speaks repeatedly of the many unexplained anomalies between the florulae of the various islands of this group, and concludes his monograph by inferring from these differences and discrepancies that botanical evidence on the whole opposes the theory of the formation of the islands by subsidence and favors the hypothesis of their emergence.

> Of the species of Albemarle nearly half are common to Charles and Chatham, and about one-third to James, while scarcely more than one-fifth have been found on Indefatigable, although it attains about the same height and lies directly between Albemarle and Chatham.
>
> Of its [Barrington's] 40 species, 26 occur upon Charles and Chatham islands, while but 18 have been found on the nearer Indefatigable.
>
> More than half the plants of Bindloe occur upon Charles, Chatham, and Albemarle respectively, while the proportion found on Abingdon and Tower [nearer islands] is considerably less.
>
> It is another of the unaccountable anomalies in the florulae of these islands that the common element between Duncan and Charles or Chatham is greater than between Duncan and the nearer islands of Albemarle, Indefatigable, and James.
>
> It is a curious fact that of the twenty-two plants observed on this island [Jervis] only nine have been found on the adjacent James Island, although twelve have been collected upon Chatham, and no less than fifteen on Charles,, both much more distant.
>
> It is noteworthy that less than half the plants of the Seymour Islands have as yet been found upon Indefatigable, near as it is; indeed the common element is considerably greater with the much more distant islands of Charles, Chatham, and Albemarle.

[1] Proc. Am. Acad. Arts and Sciences, 38, 77–269, 1902.

The most noteworthy feature of these differences is not, however, their extent, but rather the fact that for the most part they stand in no relation to the distance of the islands from each other or to the depth of the intervening channels. Thus the florulae of Albemarle and Chatham at opposite sides of the archipelago are more alike than either is to that of the intervening Indefatigable; Jervis lying near James has a greater common floral element with the more distant Charles; the florulae of the Seymour Islands have a greater number of plants in common with Charles, Chatham, and Albemarle than with Indefatigable, of which the Seymour Islands are merely a detached spur. Although a high percentage of ferns has been recorded on James, not a single representative of this group has thus far been found on the adjacent Indefatigable. The common floral element between Duncan and the relatively remote Chatham is greater than with any of the three large islands, James, Indefatigable, and Albemarle, which to a considerable extent surround it. In fact, the only cases in which it appears that proximity between two islands has brought about any marked similarity in their floras are on the one hand Narborough and Albemarle, and on the other Gardner and Charles, and even in the former of these pairs, the likeness is by no means close, for not over 71 per cent of the plants of Narborough have been observed on Albemarle.

These anomalies in the different florulae must find their explanation in peculiarities of climate and soil, together with an element of chance—arising partly from imperfect exploration, and partly from the accidents of seed-dispersal. Although they are not fully explained by the theory that these are islands of emergence casually seeded, they are much less in accord with the Baur theory of subsidence; for, were the florulae remnants of a common flora persisting upon islands separated by gradual subsidence, it is evident that those islands would possess the most floral similarity which were nearest together and divided by the shallowest channels, since these would have been separated from each other more recently than the remoter islands, which are cut off by a greater depth of ocean. As we find no such relation prevailing in the Galapagos Islands, but have observed just the reverse, namely, that the more distant islands, separated by relatively deep channels, often show greater floral similarity than the nearer ones, it is necessary to conclude that the botanical evidence, so far as it has been made out, is opposed rather than favorable to the subsidence theory.[2]

On the respective hypotheses of subsidence and emergence of the Galapagos group, I have no particular conviction and no view to press. But the basis of Professor Robinson's inferences on this point seems questionable; and a re-examination of the facts presented by him has led me to a very different opinion of the irregularity of the inter-island floral relations of the Galapagos.

The statistical summary on which Professor Robinson bases most of his conclusions is the following table of species and forms common to the several islands.[3]

[2] *Ibid.*, pp. 244–259.

[3] *Ibid.*, p. 253.

TABLE I

Island	Abingdon	Albemarle	Barrington	Bindloe	Charles	Chatham	Culpepper	Duncan	Gardner	Hood	Indefatigable	James	Jervis	Narborough	Seymour	Tower	Wenman
Abingdon	50	34	11	15	36	31	0	10	13	14	18	26	9	14	7	11	1
Albemarle	....	205	23	24	100	93	2	29	17	33	46	74	13	42	25	7	2
Barrington	....	.....	40	11	26	26	2	13	14	20	18	19	5	15	16	10	0
Bindloe	....	.....	....	42	25	22	1	7	8	13	15	14	5	15	8	9	1
Charles	....	.....	....	....	267	126	2	35	31	40	48	78	19	38	30	13	2
Chatham	....	.....	....	....	.....	231	2	34	22	42	51	64	12	33	31	15	4
Culpepper	....	.....	....	....	.....	.....	5	2	1	2	0	0	0	2	2	1	1
Duncan	....	.....	....	....	.....	.....	..	51	17	26	20	21	8	9	16	7	1
Gardner	....	.....	....	....	.....	.....	..	....	33	22	17	15	6	7	13	9	1
Hood	....	.....	....	....	.....	.....	..	....	....	59	20	29	8	15	20	10	0
Indefatigable	....	.....	....	....	.....	.....	..	....	....	....	76	33	12	14	23	9	2
James	....	.....	....	....	.....	.....	..	....	....	....	....	153	10	27	19	10	1
Jervis	....	.....	....	....	.....	.....	..	....	....	....	....	.....	22	1	7	3	1
Narborough	....	.....	....	....	.....	.....	..	....	....	....	....	.....	....	59	8	7	0
Seymour	....	.....	....	....	.....	.....	..	....	....	....	....	.....	....	....	47	6	2
Tower	....	.....	....	....	.....	.....	..	....	....	....	....	.....	....	....	....	19	2
Wenman	....	.....	....	....	.....	.....	..	....	....	....	....	.....	....	....	....	....	11

It is true that at first sight this table seems to show many surprising anomalies. Bindloe island was known to have forty-two species of vascular plants at the time of Professor Robinson's writing, and James, which is one of the nearest to it, 153; fourteen species being common to the two. Charles, with 267 species, is much farther from Bindloe than is James; but Charles and Bindloe share twenty-five species. But it is clear that the absolute numbers are misleading in this connection, on account of the enormous difference between the numbers of species, or known species, on the several islands. Charles, according to these figures, is florally nearly twice as rich as James; and, conditions being reasonably equal, a greater number of its plants than of those of James should therefore recur on Bindloe. As a matter of fact, the *proportion* of fourteen James-Bindloe to twenty-five Charles-Bindloe is less than that of 153 James to 267 Charles; so that a greater similarity between adjacent James and Bindloe than between distant Charles and Bindloe could be more properly asserted than the contrary finding of Professor Robinson.

TABLE II

	Narborough	Albemarle	Jervis	Duncan	Barrington	Seymour	James	Indefatigable	Charles	Hood	Gardner	Chatham	Abingdon	Bindloe	Tower
Narborough (59)	....	20	9	18	*37*	17	18	18	14	26	21	14	28	*35*	41
Albemarle (205)	***71***	....	59	57	57	53	49	***61***	38	56	52	40	***68***	57	41
Jervis (22)	2	6	....	16	12	15	7	16	7	14	*18*	5	*18*	12	16
Duncan (51)	15	14	*36*	....	32	34	20	25	13	16	*52*	15	20	17	*37*
Barrington (40)	25	11	23	25	....	*34*	12	22	10	12	*42*	11	22	26	*53*
Seymour (47)	14	12	*32*	31	*40*	....	12	30	11	15	*39*	13	14	19	*32*
James (153)	46	37	45	41	47	40	....	43	29	*49*	15	28	*52*	33	*53*
Indefatigable (76)	24	22	*55*	39	45	*49*	22	....	18	34	*52*	23	48	36	47
Charles (267)	64	49	***86***	69	65	64	51	63	....	68	***94***	50	***72***	60	68
Hood (59)	25	16	36	*51*	50	43	18	26	15	....	***67***	18	28	31	*53*
Gardner (33)	12	8	27	*33*	28	*29*	10	22	12	18	....	9	26	19	*47*
Chatham (231)	56	45	55	67	65	66	42	67	47	***71***	67	....	62	52	***78***
Abingdon (50)	24	16	*41*	20	27	15	17	24	13	24	39	13	....	*36*	***58***
Bindloe (42)	*25*	12	23	14	27	17	9	20	9	22	24	9	*30*	....	*47*
Tower (19)	12	3	14	14	*25*	13	7	12	5	17	*27*	6	*22*	11	....

In Table II, Professor Robinson's figures have been converted into percentages. The islands have also been listed in approximate geographical instead of alphabetical order. Since any number denoting the species common to two islands can be expressed as a percentage of the total number of species on each island, the horizontal rows and vertical columns of figures are not identical. As one reads downward, one encounters the various percentages of the number of species found on the island heading the column, occurring also on the various other islands. Thus, of Narborough's fifty-nine forms, forty-two, or 71 per cent, recur on Albemarle, one, or 2 per cent, on Jervis, nine, or 15 per cent, on Duncan, and so on. Reading horizontally for Narborough, however, one encounters the figures twenty, nine, eighteen, and so forth; which denote that the forty-two Narborough-Albemarle species constitute 20 per cent of Albemarle's total of 205, the two Narborough-Jervis 9 per cent of the twenty-two on Jervis, etc.

But these percentages are also unsatisfactory, since it is obvious that when they are read vertically the high figures are regularly encountered for large and florally well-stocked islands, and that when they are read horizontally the figures run higher just in proportion as the islands referred to are small or poor in variety of vegetation. This is made clear by the italic and bold-faced numerals introduced

into the table. The three highest numbers in each column have been printed in black type. A glance shows that these heavy numerals all come in rows for Charles, Chatham, and Albemarle, the three islands which with respectively 267, 261, and 205 species are the richest in the group. Even the three vacancies caused by the intersection of the row and the column for each of these islands are instructive; their place is taken in each case by a black number in the row for James, the next richest island, with 153 species. The only two exceptions are for Gardner, 67 per cent of whose species recur on nearby Hood as against only 52 on richer but much more distant Albemarle; and isolated and scantily vegetated Tower, for which nearby Abingdon with 58 per cent also replaces Albemarle with 41. These two exceptions are interesting, it is true, because they indicate the influence of geographical position, contrary to Professor Robinson's statements. But they are too few to be of much significance; and in general, the results reveal too little, other than the overwhelming influence exerted on the results by the absolute number of species growing on each island, to endow the method employed with much validity as a means of determining inter-island relationships.

The same is true when the largest numbers encountered in each horizontal row are selected, as has been done in the table by the use of italics; only in this case it is of course the poor or small islands that appear most frequently. Thus it will be seen that Charles, Chatham, Albemarle, and James are not represented at all by italics; while Tower, Gardner, Abingdon, and Jervis, with only nineteen, thirty-three, fifty, and twenty-two species respectively, appear from ten to five times.

It therefore occured to me to combine the two sets of percentages given in the rows and columns of Table II into their means. Mathematically this procedure does not seem justifiable, as this mean does not express anything intrinsic. It would have been preferable, perhaps, to give the percentage which the number of species, common to each pair of islands, formed of the total number of distinct species found on the two islands. But this plan, besides involving some computation, seemed open to the objection that after all its results would depend too directly on the wealth of the various floras. Thus, only 3 per cent of all the species found on Albemarle (205) and Tower (19) are common to both; but 11 per cent of those occurring on Albemarle and Seymour (47), and as much as 27 per cent of those on

Albemarle and Charles (267). The first method suggested was therefore followed, and the results are given in Table III. The figure forty-five which appears at both intersections of Narborough and Albemarle is thus the mean of the 71 per cent of the Narborough flora recurring on Albemarle and of the 20 per cent of the Albemarle flora found on Narborough: that is, half of seventy-one and twenty.

TABLE III

	Narborough	Albemarle	Jervis	Duncan	Barrington	Seymour	James	Indefatigable	Charles	Hood	Gardner	Chatham	Abingdon	Bindloe	Tower
Narborough (59)	....	45	3	16	31	15	**36**	21	**39**	25	16	35	26	30	26
Albemarle (205)	45	....	32	35	34	32	**43**	41	**43**	36	30	42	42	34	22
Jervis (22)	3	**32**	....	26	17	23	26	**35**	**47**	25	22	30	29	17	15
Duncan (51)	16	35	26	....	28	32	30	32	**41**	33	**42**	**41**	21	15	26
Barrington (40)	31	34	17	28	....	37	29	33	**37**	31	35	**38**	24	26	**39**
Seymour (47)	15	32	23	32	**37**	....	26	**39**	**37**	29	34	**39**	14	18	22
James (153)	**36**	**43**	26	30	29	26	....	32	40	33	12	35	34	21	30
Indefatigable (76)	21	41	35	32	33	39	32	....	40	30	37	45	36	28	29
Charles (267)	39	43	**47**	41	37	37	40	40	....	41	**53**	**48**	42	34	36
Hood (59)	25	36	25	33	31	29	33	30	41	....	42	44	26	26	35
Gardner (33)	16	30	22	**42**	35	34	12	37	**53**	**42**	....	38	33	21	37
Chatham (231)	35	42	30	41	38	39	35	45	48	44	38	....	37	30	42
Abingdon (50)	26	42	29	21	24	14	34	36	42	26	33	37	....	33	**40**
Bindloe (42)	30	34	17	15	26	18	21	28	34	26	21	30	**33**	....	29
Tower (19)	26	22	15	26	**39**	22	30	29	36	35	37	42	**40**	29	....

In this table the three highest numbers appearing in each horizontal row have been indicated by heavy type. Charles, the island with the largest number of species, keeps its lead in high numbers in its vertical column, but Chatham begins to fall behind, and Albemarle still more so. It is also apparent at a glance that geographical position is not without influence. The group of southeastern islands, appearing in the third framed square in the table, particularly evidence a close relationship to one another: of the twelve high numbers relating to them, nine are confined to themselves. The distinct northern group also has three, out of the six numbers appearing in its frame, of the "highest" or bold-face type. Narborough and Albemarle, constituting a western group, show a higher common figure (45), than either does with any other island. Only the central group has miscellaneous affinities in all directions.

The situation is still clearer if we regard only the nine larger islands. In Table IV these are given, arranged by geographical groups, each followed by the three islands with which its mean percentage relation is highest according to Table III; and each of these three names is followed by a number from 1 to 8, indicating the respective degrees of geographical proximity of these islands to the one in question. Those of the same group are in heavy type.

TABLE IV

Island	Resemblances					
Narborough	**Albemarle**	1	Charles	6	**James**	2
Albemarle	**Narborough**	1	Charles	4	James	2
James	Albemarle	1	Charles	6	Narborough	3
Indefatigable	Chatham	4	Albemarle	2	Charles	3
Charles	**Chatham**	4	Albemarle	2	Abingdon	8
Hood	**Chatham**	1	**Charles**	2	Albemarle	4
Chatham	**Charles**	3	Indefatigable	2	**Hood**	1
Abingdon	[Albemarle	3	Charles	6]	Chatham	7
Bindloe	[Albemarle	3	Charles	7]	**Abingdon**	1
		24		34		31

Again the western group is a unit, not only in its internal relation, but in the fact that the same non-western islands come next in each case. Much the same holds of the northern group. The three southern islands are again clearly linked together. The addition of the numbers indicating proximity points in the same direction: 24, 34, and 31 total 89. Divide by 27 (3 numbers each for 9 islands), the product is 3.3. If, however, geographical relations did not exist, the numbers would have appeared at random, and their average would have been the mean of the sequence 1 to 8, or 4.5. The difference between 4.5 and 3.3 is some index of the effect of geographical proximity in increasing floral relationship between islands.

Another and more nearly correct method of demonstrating such influence of geography upon flora as there might be, subsequently occurred to me. This was to arrange the islands, not in alphabetical sequence as Professor Robinson had done, nor in geographical order, as in Tables II, III, and IV, but in the order of their wealth of

TABLE V

	Total Species	Chatham	Hood	Charles	Gardner	Indefatigable	James	Brattle	Barrington	Duncan	Jervis	Seymour	Albemarle	Narborough	Abingdon	Bindloe	Tower	Wenman	Culpepper
Total Species	.....	306	79	319	48	193	224	16	48	103	42	52	325	80	119	47	22	14	7
Chatham	306	.....	60	188	31	128	121	13	36	69	30	38	175	56	80	29	18	7	2
Hood	79	60	....	66	37	49	47	10	29	45	16	26	58	26	35	18	13	4	3
Charles	319	188	66	.....	44	123	124	12	33	75	32	38	173	52	79	33	16	6	4
Gardner	48	31	37	44	....	30	27	6	23	24	13	20	35	13	23	14	11	4	4
Indefatigable	193	128	49	123	30	.....	111	11	27	59	32	38	145	45	75	27	13	7	2
James	224	121	47	124	27	111	.....	10	22	64	29	27	169	46	80	24	13	6	2
Brattle	16	13	10	12	6	11	10	....	7	4	3	7	10	6	11	4	5	5	1
Barrington	48	36	29	33	23	27	22	7	....	20	14	19	29	18	18	11	10	2	2
Duncan	103	69	45	75	24	59	64	4	20	....	24	23	75	25	49	13	9	4	2
Jervis	42	30	16	32	13	32	29	3	14	24	....	13	32	14	25	10	7	1	1
Seymour	52	38	26	38	20	38	27	7	19	23	13	....	34	15	26	11	8	5	2
Albemarle	325	175	58	173	35	145	169	10	29	75	32	34	.....	69	99	36	15	7	2
Narborough	80	56	26	52	13	45	46	6	18	25	14	15	69	....	34	18	8	4	2
Abingdon	119	80	35	79	23	75	80	11	18	49	25	26	99	34	....	26	16	6	3
Bindloe	47	29	18	33	14	27	24	4	11	13	10	11	36	18	26	....	10	5	2
Tower	22	18	13	16	11	13	13	5	10	9	7	8	15	8	16	10	....	6	1
Wenman	14	7	4	6	4	7	6	5	2	4	1	5	7	4	6	5	6	..	1
Culpepper	7	2	3	4	4	2	2	1	2	2	1	2	2	2	3	2	1	1	..

species. Meanwhile, however, a large body of fresh information on the botany of the Galapagos had been released for use through the publication of Dr. Alban Stewart's "A Botanical Survey of the Galapagos Islands,"[4] which it had been my lot to conduct on its course through the press. This monograph not only incorporates all the data available to Professor Robinson, but includes a wealth of new material secured by the author during a stay of more than a year in the archipelago. Many irregularities in Professor Robinson's data, due to imperfect exploration up to his time of writing, are corrected by Dr. Stewart. Thus Albemarle, by far the largest of the islands, now is known to have also the largest number of species, whereas before it was reckoned only third. So also Indefatigable, the second greatest in area, was formerly represented by less than a third as many species as much smaller Chatham, whereas now the figures are 193 and 306. It is therefore preferable to use Dr. Stewart's data. These are first shown in Table V, which is a direct reproduction from Dr. Stewart's monograph,[5] except that it is geographically rearranged.

Dr. Stewart's essay is only part of what he hopes to issue on Galapagos botany,[6] and his discussion of botanical conditions on each island is reserved for the unpublished portion of his work. His table from which my Table V is taken is, however, based on the same unfortunate alphabetical arrangement as Professor Robinson's; and at the only point where he touches on the question of inter-island relationships, he seems to incline to Professor Robinson's view that the distribution of Galapagean plants runs counter to the geographical position of and distances between the islands. Thus:[7]

> If oceanic currents were an important factor in the transport of seeds . . . the several islands of each group [in the archipelago] should have a larger floral element common among themselves than with any of the islands of the other group. The following table shows the percentages of floral relationships between the islands of the northern group, as well as their relationships with some of the more important islands of the southern[8] group.

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[4] Proc. California Acad. Sciences, ser. 4, I, 7–288, 1911: Expedition to the Galapagos Islands, 1905–1906, II.

[5] *Ibid.*, p. 237.

[6] *Ibid.*, p. 9.

[7] *Ibid.*, p. 240.

[8] Dr. Stewart's "groups" here are different from mine. His "northern" islands are Abingdon, Bindloe, Tower, Wenman, Culpepper, his "southern" ones all the remaining islands of the archipelago.

Floral Relationships of Northern Islands

	Abingdon	Albemarle	Barrington	Bindloe	Brattle	Charles	Chatham	Tower
Abingdon	.....	83.1	.....	.....	.....	66.3	67.2	.....
Bindloe	55.3	76.5	.....	.....	.....	68.5	61	.....
Tower	72.7	68.1	48.4	48.4	.....	72.7	81.8	.....
Wenman	38.5	50	.....	35.7	35.7	38.6	50	38.5

From the above table it is seen that in the majority of instances the islands of the northern group have a larger percentage of their floras common with the islands of the southern group than with each other.

These computations by Dr. Stewart suffer from the same defect as my Table II. Abingdon and Albemarle have ninety-nine forms in common; this joint element forms 83 per cent of the flora of Abingdon, it is true, but only 30 per cent of that of Albemarle. Furthermore, his table ignores the all-important factor of size of the floras. Abingdon, indeed, is only half as distant from Tower as is Albemarle; but this does not raise any presumption in favor of a higher percentage of common forms for Abingdon, as soon as it is borne in mind that the flora of Albemarle is nearly three times as rich as that of Abingdon. When in view of this latter difference 73 per cent of Tower's flora is found to occur on Abingdon and only 68 per cent on Albemarle, it is clear that the distance between the islands, or other geographical factors such as the oceanic currents which Dr. Stewart is discussing in the passage cited, are of considerable influence in determining the various island floras. If the geographical relations of Abingdon and Albemarle to Tower were exactly alike, the infinitely richer flora of Albemarle would certainly be more abundantly represented on meagerly clothed little Tower than that of Abingdon.

Table VI, then, gives Dr. Stewart's data with the islands arranged in order of the richness of their floras. It is obvious from this at once that in general the number of species common to any two islands depends not so much on their location relative to each other, nor their altitude, rainfall, or position in certain winds or currents, nor on any as yet unknown or mysterious cause, but on the mere wealth and variety of their plant lives. This is the all-important factor, beside which every other is comparatively insignificant. When this element is considered, the internal floral relations of the Galapagos are substantially accounted for; when it is disregarded, they become unintelligible. The general regularity of the decreasing series from left

TABLE VI

	Total species	Albemarle	Charles	Chatham	James	Indefatigable	Abingdon	Duncan	Narborough	Hood	Seymour	Barrington	Gardner	Bindloe	Jervis	Tower	Brattle	Wenman	Culpepper
Total species	......	325	319	306	224	193	119	103	80	79	52	48	48	47	42	22	16	14	7
Albemarle	325	......	173	175	169	145	99	75	69	58	34	29	35	36	32	15	10	7	2
Charles	319	173	......	188	124	123	79	75	52	66	38	33	44	33	32	16	12	6	4
Chatham	306	175	188	......	121	128	80	69	56	60	38	36	31	29	30	18	13	7	2
James	224	169	124	121	......	111	80	64	46	47	27	22	27	24	29	13	10	6	2
Indefatigable	193	145	123	128	111	......	75	59	45	49	38	27	30	27	32	13	11	7	2
Abingdon	119	99	79	80	80	75	......	49	34	35	26	18	23	26	25	16	11	6	3
Duncan	103	75	75	69	64	59	49	......	25	45	23	20	24	13	24	9	4	4	2
Narborough ..	80	69	52	56	46	45	34	25	....	26	15	18	13	18	14	8	6	4	2
Hood	79	58	66	60	47	49	35	45	26	....	26	29	37	18	16	13	10	4	3
Seymour	52	34	38	38	27	38	26	23	15	26	....	19	20	11	13	8	7	5	2
Barrington ..	48	29	33	36	22	27	18	20	18	29	19	....	23	11	14	10	7	2	2
Gardner	48	35	44	31	27	30	23	24	13	37	20	23	....	14	13	11	6	4	4
Bindloe	47	36	33	29	24	27	26	13	18	18	11	11	14	....	10	10	4	5	2
Jervis	42	32	32	30	29	32	25	24	14	16	13	14	13	10	....	7	3	1	1
Tower	22	15	16	18	13	13	16	9	8	13	8	10	11	10	7	....	5	6	1
Brattle	16	10	12	13	10	11	11	4	6	10	7	7	6	4	3	5	....	5	1
Wenman	14	7	6	7	6	7	6	4	4	4	5	2	4	5	1	6	5	....	1
Culpepper	7	2	4	2	2	2	3	2	2	3	2	2	4	2	1	1	1	1	....
Sum	....	1163	1098	1081	922	922	685	584	451	542	350	320	359	291	296	179	125	80	36

to right, or from above downward, leaves no other inference possible. It is true that there are some important exceptions to this regularity; and these, as will be shown, possess a positive meaning; but they acquire this significance only with reference to the general trend of relationship as based on absolute number of species. It would be possible to establish an exact, quantitatively expressed correlation between the numbers of species on the various islands and the numbers of species possessed jointly by them with any given island. The range of floral wealth, however, is great, and the series are small; so that the degree of their trend, and its uniformity, are readily visible without more elaborate mathematical treatment. The point of the basic importance of richness of flora can therefore be accepted as established without further analysis or discussion; and I will proceed to examine briefly for each island the meaning of the departures from normal tendency of its series.

ALBEMARLE

The fairly considerable though secondary effect of geographical nearness is evident from the first three figures in Table VI. Nearly as many Albemarle species have been found on nearby James as on more remote Charles and Chatham, though these are almost half as rich again in total species as James. Narborough and Hood point the same moral. Their total species number the same—eighty and seventy-nine, to be exact; those which they share with Albemarle are, however, sixty-nine and fifty-eight. Hood, however, is about a hundred miles distant, while Narborough is separated from Albemarle by only a narrow channel, and moreover is shielded by it from all the remainder of the group. In view of this location it might be presumed that the difference between the Narborough and the Hood identities would be much greater: evidently position, while a factor, is not the primarily determining one.

Five islands have a flora of nearly the same size: Seymour with fifty-two species, Barrington with forty-eight, Gardner near Hood[9] with forty-eight, Bindloe with forty-seven, Jervis with forty-two. Their forms held in common with Albemarle are respectively thirty-four, twenty-nine, thirty-five, thirty-six, and thirty-two. The one signifi-

[9] Dr. Stewart gives figures also for Gardner near Charles, but as the number of species reported from this island is minimal, I have omitted all reference to it. Professor Robinson mentions only "Gardner Island," and treats it as if near Charles, but the number of species attributed by him to it shows that his data probably pertain to Gardner near Hood.

cant break in this series is the twenty-nine of Barrington. This I cannot explain by location, for while Barrington is much farther from Albemarle than is Jervis, it is much nearer than Gardner; and if it is near enough to Indefatigable to have been especially stocked by local species from that large island, Seymour is nearer still, and Gardner is almost a part of Hood, yet these both show the presence of more Albemarle forms. Such cases as this, of which several occur, must therefore be set down as due to "accident," as we may call the various unknown minor causes that it is impossible to follow in detail.

CHARLES

Charles shows more affinity with Chatham—188 to 173—than with nearer, larger, and florally richer Albemarle. This is the first instance of several pointing to a special relationship between the southeastern islands of Charles, Chatham, Hood, and Gardner, which constitute a fairly defined botanical province of the Galapagos. It is clear for one thing that the conditions at least for the variety of plant life are on the whole more favorable in these islands than elsewhere in the archipelago. Charles and Chatham are very much smaller than Albemarle, yet contain virtually as many species as it; they are considerably surpassed in area by Indefatigable, yet, according to available information are fully half as rich again in forms. Hood has as many species as Narborough, yet is only a fraction as large. Gardner seems to be distinctly the smallest and lowest of the five islands referred to in the preceding paragraph, yet it has no fewer different forms.

Narborough and Hood stand in a relation to Charles opposite to that which they hold towards Albemarle. From sixty-nine and fifty-eight, the figures reverse to fifty-two and sixty-six. It is probably not so much that Hood is nearer in miles than Narborough, as that it forms part with Charles of the southeastern province just referred to, whereas Narborough from its peculiar position must be in some measure especially dependent on Albemarle. The same may be said concerning the high figure (forty-four) which Gardner shows toward Charles as compared with the thirty-eight, thirty three, thirty-three, thirty-two of the four other islands of similar floral wealth.

CHATHAM

Chatham reveals the same affinities with the members of its own province as Charles, though not in so pronounced a form: species in common with Albemarle (325), 175, with Charles (319), 188; with

Narborough (80), 56, with Hood (79), 60. There is, however, no closer affinity to Gardner than to Seymour, Barrington, Bindloe, and Jervis.

JAMES

The nearness of this large island to Albemarle and Indefatigable is clearly reflected in the figures: Albemarle (325), 169, Charles (319), 124, Chatham (306), 121, Indefatigable (193), 111. Again, Jervis is only a few miles from James: the common species number twenty-nine while Seymour, Barrington, Gardner, and Bindloe, all slightly richer in species but more remote, share twenty-seven, twenty-two, twenty-seven, and twenty-four forms with James. I must admit that these differences are in themselves not very impressive; but my contention is that absolute wealth of flora is the primary factor, and geographical position only the chief of the secondary causes governing distribution.

INDEFATIGABLE

This great but apparently either unusually arid or botanically unduly neglected island of the central group shows somewhat the same effects of location as James, though in less marked form as regards the other large islands, no doubt owing to somewhat greater proximity to both Charles and Chatham. For the five smaller islands the significant figures are: Seymour thirty-eight, Barrington twenty-seven, Gardner thirty, Bindloe twenty-seven, Jervis, thirty-two. Seymour is almost on top of Indefatigable; and Jervis, while as far removed as Barrington, lies toward allied James, while with Barrington the more alien southeastern group is approached.

ABINGDON

This, not the largest but the highest and by far the richest island of the northern group, appears to have fairly uniform relations with the other groups, as might be expected from its rather detached position. There is, however, a perceptible leaning toward the nearer western and central flora rather than toward the farther southeastern. Compare Albemarle ninety-nine, Charles seventy-nine, Chatham eighty, James eighty, Indefatigable seventy-five. As James and Indefatigable run to only two-thirds as many species as Charles and Chatham, the practical equality of the present figures is certainly not accidental.

So, also, compare Seymour twenty-six, and Jervis twenty-five—both in James–Indefatigable waters—with Gardner twenty-three, and Barrington eighteen, one in and the other near the southeastern province.

Abingdon clearly has some direct affinity with the two other northern islands; but this is less marked than might be surmised, until one remembers that the three northern islands are rather small and not closely grouped, so that in the long run the chances would be more favorable of their receiving species from the large islands of the mass of the archipelago than from one another. Even if the Galapagos are not risen volcanoes but a gradually sunken land-mass, distinct local species must have been often communicated from one island to another; so that the point would hold. Proximity to Abingdon has, however, had some influence in shaping the floras of Bindloe and Tower, as will be shown; but on the other hand they are both too poor to have affected Abingdon appreciably.

DUNCAN

Duncan, considering its size, has a remarkably varied flora, due perhaps to the comparative variety of environment afforded by its unusual altitude. It lies between Albemarle and Indefatigable and near James. Its affinities are distributed about as one might expect from its position and the relative wealth of species of the other islands, except that the figure for Albemarle—seventy-five as compared with seventy-five and sixty-nine for distant Charles and Chatham—sinks rather low, and that for Narborough is surprisingly small. Evidently Duncan has not been stocked in any great measure from the west, and is itself too small to have had much influence on the larger western islands.

NARBOROUGH

The unusual position of this island is of interest. It is the most westerly of the Galapagos, and is half surrounded, and shut off from all the remainder of the archipelago, by crescent-shaped Albemarle. Of the large islands, it is distinctly the poorest in flora, according to our data. A large part of its area is covered by recent lava flows. It might therefore be anticipated that Narborough would show a very high degree of dependence on Albemarle, and little except the most general relationship to the other islands. This is only partially true, 86 per cent of its species are found on Albemarle; but this ratio is substantially equalled by the 84 per cent of Hood species occurring

also on Charles; and Hood is by no means as closely linked geographically to Charles as Narborough is to Albemarle. Again, therefore, location appears to be of only subsidiary potency.

HOOD

The bonds between all the southeastern islands are revealed again by Hood. Thus, Albemarle fifty-eight, Charles sixty-six, Chatham sixty; and adjacent Gardner thirty-seven, but four more distant islands of similar floral range, twenty-nine to sixteen. With Indefatigable, possessing 193 species, Hood shares forty-nine; with James, possessing 224 but lying on the farther side of Indefatigable, forty-seven. The narrowness of the difference is as significant as its existence. Duncan (103), near Indefatigable, has forty-five Hood species; Abingdon (119), far to the north, only thirty-five; Narborough (eighty), twenty-six. Barrington, on the Hood side of Indefatigable, has twenty-nine Hood forms out of a total of forty-eight; Seymour and Jervis, on the James side of the same island, twenty-six out of fifty-two and sixteen out of forty-two.

SEYMOUR

Seymour is a small island, or rather pair of islets, separated from the north shore of Indefatigable by the narrowest and shallowest of straits. 73 per cent of its species, or thirty-eight out of fifty-two, are found on Indefatigable. For Charles and Chatham to the southwest, the figures are the same; for Albemarle and James to the west, only thirty-four and twenty-seven. Again it is apparent that specific abundance is the most influential cause in the establishment of inter-island relationships, and that proximity, especially when close, comes second. As a third factor we can add the greater potency of the southeast than of the remainder of the archipelago, especially upon the central province. Thus Hood has twenty-six Seymour species, to fifteen on Narborough and twenty-three on nearer and more varied Duncan; Barrington and Gardner show nineteen and twenty Seymour identities, Bindloe and Jervis only eleven and thirteen.

BARRINGTON

I have heretofore reckoned Barrington as one of the smaller central islands, on the basis of its geographical situation; but its affinities tend somewhat to the southeastern group, towards which it lies off Indefatigable. Thus:

Albemarle	29 of 325	Charles	33 of 319
James	22 of 224	Chatham	36 of 306
Narborough	18 of 80	Hood	29 of 79
Duncan	20 of 103		
Jervis	14 of 42	Gardner	23 of 48
Seymour	19 of 52		

The nearest land is Indefatigable, 14 per cent of whose flora it possesses, as against 12 per cent of Charles', 10 of Chatham's, 10 of James', and 9 of Albemarle's. After all, close proximity counts for more than distinct exposure to the strong southeastern influence.

GARDNER

This island lies close by Hood and fifty miles from Charles; but it has forty-four of the larger island's species and only thirty-seven of the nearer ones.

Within its usual limits, however, location makes itself observable: compare forty-four species shared with Charles, thirty-five with Albemarle; thirty with Indefatigable, twenty-seven with James; twenty-four with Duncan, twenty-three with Abingdon—the more remote island being in each case also the richer, though less represented on Gardner.

I cannot explain the low number (thirty-one) of Chatham species on Gardner as compared with the forty-four from Charles. Usually Charles and Chatham appear substantially as a unit in their relationship with other islands; and even in the case of Hood—to which Gardner is attached—the difference in favor of Charles is comparatively slight.

BINDLOE

Bindloe is the largest of the northern islands and the nearest to the central group, but, either on account of a lower elevation or for some unknown reason, it has less than half as many species as Abingdon. The affinities of its flora are very evenly distributed, except for somewhat higher percentages for species shared with the other northern islands, as indeed is only natural and might be expected, though Dr. Stewart's cited passage professes the opposite for the northern islands in general. Thus it has twenty-six of Abingdon's species, as against twenty-seven, twenty-four and twenty-nine of Indefatigable's, James' and Chatham's, although these average more than twice as many total forms; and similarly, the figures for Tower are ten out of twenty-two, as against ten out of forty-two for Jervis and eleven out of fifty-two for Seymour.

JERVIS

Jervis lies closest to James, but is also near Indefatigable and Albemarle. Its proximity to the two former is reflected by the figures in Table VI—twenty-nine and thirty-two—but the number for Albemarle species is unexpectedly low (thirty-two) and substantially equalled by the numbers of distant Charles and James. Exactly the same status holds for Duncan, the nearest small island to Jervis.

TOWER

This smallest and poorest of the northern islands shows a special affinity with Abingdon, 13 per cent of whose species it possesses as against, for instance, 6 of James', 5 of Albemarle's, 6 of Chatham's, and 9 of smaller Duncan's.

The southeastern influence is perhaps slightly stronger on Tower than that of the central and western groups. Compare Albemarle fifteen with Charles sixteen and Chatham eighteen; Duncan nine and Narborough eight, with Hood thirteen; Seymour eight, Barrington ten, and Jervis seven, with Gardner eleven.

BRATTLE

The little island of Brattle lies off that shore of Albemarle which faces Charles. Only sixteen plants have been reported from it. Considering the proximity of Brattle to Albemarle, it is significant that it possesses only ten species of that large island but twelve and thirteen from Charles and Chatham. The number shared with Hood is above the average. Evidently the southeastern influence has operated much as in the case of Jervis and Duncan, which also lie not far east of Albemarle.

WENMAN AND CULPEPPER

These two islets lie far to the north of the main Galapagos archipelago, and must not be confounded with what I have heretofore called the northern group, consisting of Abingdon, Bindloe, and Tower. Their flora is so monotonous that little inference can be drawn from the few species, out of their total fourteen and seven, which they share with the other islands. It does appear, however, that the southeastern group is again represented a little more than proportionately, although it is the most remote; and that on the other hand the three northern

islands, no doubt because they are nearer, also share more, on the whole, in the floras of Wenman and Culpepper than the western and central groups.

For the sake of completeness, though it does not seem to add much that is new, I have included Table VII. This is a computation, along the lines suggested above, of the proportion which the number of species common to each pair of islands bears to the total number of different species known from the same two islands. The percentages are based on Dr. Stewart's data, with the islands rearranged in order as in my Table VI.

It is obvious that in a percentage table of this sort the high numbers will not all be at the heads of the columns and at the left of the rows, as in Table VI, but must cluster about the intersections of columns and rows. For instance, if all of the forty species on a given island are found also on a second island whose total number of forms is forty, and again on a third island whose wealth of species however reaches 200, the percentage for islands one and two will be 100, and for one and three only twenty. I have indicated by heavy type the highest percentage occurring in each column. It will be seen that these bold-face numbers practically all occur about where they should come as a matter of mathematical probability; namely, in close proximity to the row of spaces which diagonally bisects the table. (If corresponding entries had been made also in the horizontal rows, the arrangement of the heavy-type numbers would of course have been symmetrical to this diagonal axis.) This distribution once more corroborates mere floral wealth as the fundamental factor in island relationships. At the same time, the notable perturbations from probability are practically all due to geographical situation. Compare the high figures for Bindloe–Abingdon and Jervis–Duncan, to which Narborough–Albemarle just fails of being added.

If the distribution of the heavy-type numbers were mathematically regular, the entry of the one such number in each column should result in their appearance also one in each row; which is approximately the case. The one conspicious deviation from this theoretical rule is afforded by Gardner, whose horizontal row will be seen to contain as many as five heavy numbers. This can scarcely be an accident, and I am inclined to attribute it to the slightly preponderating influence of the southeastern islands on the remainder of the archipelago. A similar influence appears deducible as regards southeastern Hood, with

TABLE VII

	Total species	Albemarle	Charles	Chatham	James	Indefatigable	Abingdon	Duncan	Narborough	Hood	Seymour	Barrington	Bindloe	Gardner	Jervis	Tower	Brattle	Wenman	Culpepper
Albemarle	325	....	37	38	**44**	**39**	29	21	21	17	10	8	10	11	10	5	3	2	1
Charles	319	37	....	**48**	30	32	22	22	15	20	11	10	14	10	10	5	4	2	1
Chatham	306	38	**48**	....	30	35	23	20	17	18	12	11	10	9	9	6	4	2	1
James	224	**44**	30	30	....	36	30	24	18	18	11	9	11	10	12	6	4	3	1
Indefatigable ..	193	39	32	35	36	....	**32**	25	20	22	18	13	14	13	16	6	6	3	1
Abingdon	119	29	22	23	30	32	....	28	**21**	21	18	12	16	**19**	19	11	9	5	2
Duncan	103	21	22	20	24	25	28	....	16	33	17	15	19	9	**20**	8	4	4	2
Narborough	80	21	15	17	18	20	21	16	....	20	13	16	14	17	13	8	7	4	2
Hood	79	17	20	18	18	22	21	**33**	20	....	25	30	**41**	17	15	15	12	4	4
Seymour	52	10	11	12	11	18	18	17	13	25	....	23	29	12	16	12	11	8	2
Barrington	48	8	10	11	9	13	12	15	16	30	23	....	33	13	18	17	**12**	7	4
Gardner	48	10	14	10	11	14	16	19	14	**41**	**29**	**33**	....	17	17	19	10	7	**8**
Bindloe	47	11	10	9	10	13	19	9	17	17	12	13	17	....	13	17	7	9	4
Jervis	42	10	10	9	12	16	19	20	13	15	16	18	17	13	....	12	5	2	2
Tower	22	5	5	6	6	6	11	8	8	15	12	17	19	17	12	....	15	**20**	4
Brattle	16	3	4	4	4	6	9	4	7	12	11	12	10	7	5	15	....	5	5
Wenman	14	2	2	2	3	3	5	4	4	4	8	7	7	9	2	**20**	5	....	5
Culpepper	7	1	1	1	1	1	2	2	2	4	2	4	8	4	2	4	5	5	..

two entries in its row, as compared with western Narborough, which possesses an equal number of species but has no entry in its row.

Examination of the individual figures in Table VII also shows a distinct but definitely limited influence of proximity paralleling that which has been established on the basis of Table VI. Only it must be remembered that in the present tabulation the high numbers must be expected to come not near the edges of the table but along the diagonal axis, dwindling away from this in all directions. A high percentage, such as that of thirty-three between Hood and Duncan, is therefore not indicative of operation of proximity, but is an effect of the similar number of species, seventy-nine and 103, occurring on the two islands. Viewing the figures with this point in mind, it could be pointed out, for instance, that the percentage of species common to Albemarle and James, and Albemarle and Indefatigable, is greater than the percentage common to Albemarle and Charles, and Albemarle and Chatham—unquestionably as a result of proximity, since theoretical probability would reverse the figures. In the same way scarcely a row or a column can be followed through without analogous deviations due to the same cause. The relationships established in this way, however, follow so closely those already discovered in Table VI and discussed at length, that it would be mere repetition to cite and analyze them.

CONCLUSIONS

It follows, therefore, that, so far as the number of joint species is concerned, the floras of the various Galapagos islands do not show any unaccountable relations or mysteries, but almost exactly such connections as might be expected.

The first and fundamental element that determines the number of species which two islands have in common, is clearly the number of species found on each. So obvious is this both from my own tables and those of Professor Robinson and Dr. Stewart, that practically all of the foregoing discussion of the characteristics of individual islands has concerned departures from this rule. A given island will always share more of its species with an island containing 300 species than with one containing fifty. This is clearly the result of the working of mathematical probability, and just in proportion as the influence of this element transcends that of any other, are these more specific causes relegated to a subsidiary station.

Secondly, though far behind, comes the factor of geographical position. Islands in proximity have more species in common than those that are far apart—at least in most cases, and to some degree.

Thirdly, there appears to be a slightly greater influence of the southeastern than of the western and central groups upon most of the smaller islands. This may be due to the southeastern islands being nearer the continent, or being the first to be washed by the flow of the Humboldt current, or lying to the windward of the others. At best, however, this southeastern preponderance is little more than nominal.

As regards the origin of the islands—a question which is primarily a geological one, though of interest to the biologist because its answer will enable him better to trace the processes of evolution of animal and plant life—Professor Robinson inclines rather to the emergence theory, Dr. Stewart favors that of subsidence, and I do not believe that a satisfactory answer can be given on botanical grounds, at least not without some new method of attack. If the islands arose from the ocean, and were gradually stocked with plants, different species would be bound to reach the individual islands at various times; but some, at least, of these would again be communicated to other islands. On the other hand, if the archipelago should be the remnant of a larger sunken block of land, there would no doubt have been greater original uniformity of distribution; but with the lapse of time there would be increasing diversity due to the formation of local varieties as well as the dying out in certain islands of species originally occurring there; while on the other hand the factor of dispersal and transmission of species from island to island would be operating simultaneously. It thus seems impossible to decide from a mere knowledge that such and such species are or are not now common to such and such islands, how far each of these various and conflicting processes has been at work.

The origin of the Galapagos Islands, then, is scarcely a soluble botanical problem. As regards the internal floral relationships of the archipelago, it appears that there is little that is not explainable on the basis of mathematical chance operating evenly as if all the islands formed a unit; with this factor disturbed in some measure by ordinary geographical influences.

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