CHAPTER I

The flora of Great Britain

The presentation of our subject being somewhat new, it may be well to begin with a well-known flora. BRITAIN has, by various estimates, about 100 families, 475 genera, and 1500-2000 species. Where not cultivated, it is covered by different ecological communities of plants (122), composed of many species, varying in abundance from dominant to very rare. No taxonomic relationship shows among them any more clearly than if they had been chosen at random, unless, as at times, two or three members of a genus or family occur together. Climate varies; the soil may be rich or poor in humus, in lime, and in other things, and may differ in degree of humidity, acidity, and consistency. It may bear different types of vegetation, such as trees, shrubs, or herbs, causing different conditions at ground level, and so on.

Under these various conditions, one may get moors, fens, heaths, woods, chalk-pastures, sand-dunes, &c, each having its own type of flora, one often differing widely from another in its composition. In any one country there are usually many types of situation, so that there is a large total flora, the local flora varying from place to place with the communities that there occur. The composition of the latter finally depends upon the total flora, for they are made up out of it, or out of such of it as occurs within reasonable distance, by natural selection of the most suitable, just as the inhabitants of a village are made up from their various qualifications of suitability, chiefly that of having been born and brought up among the conditions there prevailing. Ecology studies

the local conditions, the location and composition, of these communities, while distribution proper studies the total floras, with their composition, sources, and origin, a study long left neglected.

Even in a complete and "closed" community, the composition will not always remain the same. Sooner or later, and largely as a result of the continued growth in the same spot of the same plants, soil changes will appear, bringing about changes in relative abundance, some species even disappearing, perhaps, some new ones appearing, so that a species that has long lived near by without being able to join the community may now get its chance to move forward. Probably, on the whole, in large areas (where there are usually many communities), and in long time, each species of a total flora may get a chance of spreading that does not differ so very much from that of others. But one must not forget that the early comers will have the first chance at becoming accustomed to new conditions, and so will have the first chance with yet others before the communities are fully made up, and will thus become the most widely spread of all ("the early bird gets the worm"; "to him that hath shall be given").

Such ecological changes may occur in what are comparatively short periods, while the movement of species over large areas may take up what are relatively geological periods. Ecology deals with recent events, and variation under local conditions, distribution proper with slow and on the whole steady movements spread out over long periods, during which several ecological changes may occur at the same place. Evolution creates the plants, while distribution studies the way in which they move about the world. These two necessarily go together, while ecology studies the way in which the plants settle in any given spot after arrival. The distribution of plants upon the large scale cannot be intelligently visualised without a proper knowledge of the way in which they came into being. If, for example, a given plant proved to have been independently born in two quite different places, any study based upon the idea that it had only begun in one would be rendered of much less value.

Most often, perhaps, a plant will travel with the community to which it belongs. This will travel as a whole so long as the conditions remain fully favourable to all its members,

but as probably no two species have just the same functional adaptability, the community will gradually become altered, some species dropping out, their places being often taken by newcomers, to whom the altered conditions are now suitable. But these changes do not involve any structural change or adaptation, unless a new mutation should happen to coincide with them, and even then there is no reason to look upon it in the light of an adaptation. Such a change will probably involve a slight adaptational change, but it must not be serious, or the species may be killed out by natural selection as soon as it arrives.

If the junction with the continent were once at the southeastern part of BRITAIN, as seems probable, plants arriving there would find little or no immediate change in conditions, but to go thence to the north or west they would have to become suited to different soil and climate. That this is possible is shown by the figures in the *London Catalogue* (11th ed.), which give with great accuracy the distribution of every British species into the " vice-counties ", the more natural divisions made by H. C. WATSON, who began this work, to replace the political counties. Owing to its geological formation, and its nearness to the ATLANTIC, BRITAIN differs so much in different parts that species that occupy many must have become suited to them by some functional or internal process as they moved about. The number of vice-counties in BRITAIN, not including IRELAND, is 112, and the mean is 56.5.

As the chief illustration of this chapter let us take the well known family *Ranunculaceae*. One is very apt to fall into the slipshod habit of saying that the family is well represented and well distributed in BRITAIN. What one really means is that some, but not all, of its genera and species are so. Taking the vice-county figures, and placing a bar at the mean point of 56.5, one gets as the dispersal of its species :

Distribution of Ranunculaceae in Britain

Anemoneae							*Helleboreae*		
Clematis		49					Caltha	112	21
Thalictrum	76	39	38	30	6	4	Helleborus		33 19
Anemone	109	19					Trollius	66	
Myosurus		46					Aquilegia	65	
Ranunculus 112	112	112	112	112			Aconitum		9
112 104 97 93 87	87	83					Actaea		5
76 75 71 62 57	55	51^1	16	13					
	10	4	3	3					

Average dispersal : *Anemoneae* 61.   *Helleboreae* 41.1.

Of the 43 species 21 are below the mean, and the family average, 57.3, is just above it, while if *Ranunculus* were removed, it would fall to 41.   The next table gives the species above-below and the family average, for various large families :

Large families in Britain

Below mean dispersal			*Above mean dispersal*		
Cruciferae	23/35	Av. 49	Ranunculaceae	22/21	Av.57.3
Caryophyllaceae	32/36	50	Compositae [2]	64/48	58
Leguminosae	34/38	52	Labiatae	33/21	60
Umbelliferae	28/31	55			
Liliaceae	7/22	32	Total Dicots	236/230	
Orchidaceae	16/28	42	Monos	81/123	
Gramineae	58/73	53			

Most of these large families, regarded by the old school as very " successful ", thus show dispersal rather below than above the mean, especially in Monocots, where the only ones above are a few small families like *Lemnaceae* (water

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[1] A gap like this is common in large genera; in the first fifteen it averaged 33, or more than the ten or fifteen one might expect.   Its meaning is not clear (? a narrowing of the isthmus at some time).

[2] Small Hieracia omitted.

plants) or *Dioscoreaceae* (one species).   We shall come upon a good many marked differences between Dicots and Monocots (*cf.* Index).

If one accept the view, put forward in *Age and Area*, that small dispersal means late arrival, rather than lack of adaptation, one will not expect any family with many species to be much above the mean, though one of late arrival may well be below it.

One of the first things that one notices in the British (or other European) flora is the great number of the large subfamilies and tribes that are represented.   Of the three in *Ranunculaceae* the only one not represented is the unimportant group of the *Paeonieae*, whose leader, *Paeonia*, occurs in the centre and south of FRANCE.   We shall return later to the consideration of this phenomenon, which is hardly what one would expect under selection.   There is little evidence to show that adaptation takes any serious part in the distribution.   Recent work seems to show that a species that is polyploid may be more rapidly distributed than one that is not, but one would hardly, upon present evidence, consider this as adaptation.

The " unsuccessful " British families that have only one genus and one species each, show the dispersal : above the mean 112, 112, 108, 105, 93, 93, 89, 89, 86, 78, 78, 73, 70, 68, 64, 62, 59, and below the mean 41, 26, 23, 12, 8, 7, 6, 6, 3, 2. Thus 17 are above and only 10 below the mean, and the average of 60 is about the same as that of the large families quoted above.   There is no evidence for any inferiority in dispersal.   The two 112s are *Hedera*, a small genus, and *Oxalis*, a very large.   The division between successful and not so must be, if anywhere, within the genus or species. But as success in one country is usually accompanied by success in others, where there is not too great a difference in conditions, the solution of the problem by reference to natural selection is not possible, and it is simpler to adopt that offered by age and area, which puts down distribution to age rather than to adaptation, abandoning the theory that the latter governed dispersal over large areas and long time. Under the Darwinian theory there is no production of new forms without the urge of adaptational improvement, and the new forms kill out their predecessors.   Under the theories that we advocate here (156), adaptation to its place of birth

is born with a new species, and is rather functional than
structural, if at all the latter in most cases. Those not
born with it are killed out. With the adaptation itself must
go a certain amount of adaptability, to enable the organism
to withstand the continual small changes of conditions, and
this adaptability enables it to spread to a greater or less
distance from its birth place. The ancestors are not necess-
arily killed out.

The current theory, that dispersal is due to adaptation
acquired by gradual structural evolution, uses what HUXLEY
termed " the verbal anodynes by which the discomfort of
ignorance is dulled ", but cannot explain the facts. To
what is *Ranunculus*, or any of its species, really adapted?
Reference to a couple of British floras shows that they
inhabit " ponds, ditches, running streams, deep still waters,
rivers, marshes, salt-marshes, wet places, sandy shores of
lakes, bogs, thickets, pastures, meadows, cornfields, waste
places, woods, bushy places, and most of all cultivated places
and slovenly farms ". How did they become suited to all
these places, except by the passage of time? To suit what
conditions were they really evolved? What made some
species so " successful ", some so unsuccessful? Why is
the genus so cosmopolitan? Why did it need so many
species (it has about 325)? Our solution is simply that it
is an old genus, and that its older (more widely dispersed)
species have therefore had time to adapt themselves function-
ally to many different conditions. HUTCHINSON (**68**) calls
it " the most primitive of herbaceous Dicotyledons "; it
was probably a very early arrival in EUROPE, where it is
conspicuous in the far north, and also goes very high in the
ALPS, where, as *R. glacialis* near the summit of the FINSTER-
AARHORN, it is at the greatest height recorded for any plant
in SWITZERLAND (4270 m., or over 14.000 feet) (**113**). It
may even have been born originally somewhere in northern
EURASIA.

How did the common buttercups like *repens* become so
suited to cultivated places, when they must be much older
than cultivation? They must just have happened to suit
them, or have become functionally, not structurally, adapted
to them. But what adaptation caused them to become the
most widespread of the buttercups? To what were they
really adapted, and for what, upon the Darwinian plan, were

they evolved ? In BENTHAM's *British flora*, six buttercups are marked abundant, and eight are not. The distribution of these in the *world* is :

Abundant in Britain	*Not*
1. North temperate, Australia	1. North palaeotemperate
2. North temperate	2. North palaeotemperate
3. North temperate	3. North palaeotemperate
4. North palaeotemperate	4. Mediterranean, W.Europe
5. Europe and western Asia	5. Europe and W. As.
6. Europe and western Asia	6. Europe or part of it
	7. Europe or part of it
	8. Europe or part of it

The distribution abroad of the abundant species is much greater than that of the others, and this, so long as one works with groups of allied species, proves to be a general rule, that is practically fatal to the supposition that wide spread depends upon adaptation. This interesting fact was discovered long ago in the flora of CEYLON, where the writer found that " the most widely distributed species in CEYLON, *on the average*, are those that show a distribution abroad to a greater distance than merely to PENINSULAR INDIA; then follow those that only reach the peninsula, and the least widely distributed in CEYLON are those that are found in CEYLON only " (*Age and Area*, p. 60). These last, known as endemic species, are hardly noticeable in northern EUROPE. " This graduation of areas... showed not only for the grand total, but also for every family of 14 or more species... nothing but a mechanical explanation would serve. Natural selection could not act on all plants alike with even pressure. " (*l.c.*, p. 61). This phenomenon is so universal that it may be termed a law of distribution, and called the law of " first come, first served ", or " to him that hath shall be given ".

The abundant species in BRITAIN, as their distribution is so wide, must on the average have come from far away, and so, if they had any structural adaptation, they must have brought it with them. But to carry structural adaptation from a country A that will also suit B, C, D or E seems strange, though if it is only structure that is carried, it

probably makes little or no difference. The species could not have survived unless it had adaptation to start with, and it would acquire local adaptation as it travelled. But in so doing it does not necessarily alter its structural characters at all, the adaptation being primarily functional. The physiologists have long told us that structure and function are largely independent.

There are many *Ranunculi* with wide dispersal in BRITAIN. Six, the largest number in any single genus, reach the maximum possible of 112, but the average for the whole genus is but 68.7, because other and younger species continued to arrive in BRITAIN until the final separation.

It is of interest to note that the other ten British genera make up a list of localities not much inferior to *Ranunculus* itself—woods, open woods, moist copses, thickets, hedges, cornfields, chalk and limestone pastures, stony pastures, mountain pastures, parks, riverbanks, moist meadows, the sides of ditches, marshes, alpine bogs, sandy shores, chalk hills, dry limestone soils, waste places, old walls, ruins, &c. Similar variety may be found in other large families and genera in BRITAIN.

Evolution. DARWIN's great work, which unfortunately is not called by his name, has shown beyond any doubt that plants and animals owe their great variety of structural form to an evolution that has been going on since the beginning of life. It was originally intended to deal with it also in this work, but it became too bulky, and was published in 1940 as *The Course of Evolution*, where a summary of conclusions will be found on p. 191. In 34 crucial testcases between the Darwinian theory of progress by selection of small structural variations that possess adaptational value, and the pre-Darwinian theory that I have accepted and have called the theory of divergent mutation, I have shown that the evidence is almost overwhelming in favour of the latter. Under this theory, a single mutation, usually very divergent from the parent form, may give rise, at one step (not gradually as under Darwinism) to a new form, of family, generic, specific, or varietal rank. This reverses the course postulated by Darwinism, going from family down to species, not the other way. But if this be so, it is clear that selection cannot have controlled it, unless it work in some recondite way at present unknown, and it is simpler to take the view that

" evolution and natural selection are probably to a great extent independent, and they work at right angles to one another with (in plants at any rate) little mutual interference ". Evolution is evidently " working upon some definite law that we do not yet comprehend ", and the mutations " cause structural alterations, which may, but by no means necessarily must, have some functional advantage attached. If such an advantage appear in the mutation, natural selection will likely allow it to survive. There is no necessary reason why the immediate ancestor should die out ". " Evolution is no longer a matter of chance, but of law. It has no need of any support from natural selection. It thus comes into line with other sciences 'which have a mathematical basis. The theory of natural selection has been trying to work it backwards ". Or, in the words employed by YULE and the writer (159) " inasmuch as all families, both of plants and animals, show the same type of curve, whether graphic or logarithmic, it would appear that in general the manner in which evolution has unfolded itself has been relatively little affected by the various vital and other factors, these only causing deviations this way and that from the dominant plan. "

In plants, divergent mutation seems to hold very generally. A species with alternate leaves may give rise to one with opposite, or a 5-merous flower to a 4-merous. But as the species of a genus increase, the later tend to fill up the gaps between the earlier, making the divergences less distinct. The early, clearly marked species or genera have most descendants, and tend to become the heads of sub-genera, or tribes. In my work upon the *Podostemaceae* (*Evol.* p. 21), where under as completely uniform conditions as are known, evolution has yet produced the most divergent set of characters known (*cf.* the pictures in **148**), I came to the conclusion that, at least under certain circumstances, evolution must go on, whether there be any adaptational reason for it, or not. Such extreme cases of divergence as those just quoted offer no grip to selection, nor could it bring them to perfection as it is usually shown, for as this was approached, the urge would rapidly fall off, till the time needed for the finishing touches would rise to infinity. (*Cf.* Testcase X, *Evol.*, p. 114).

These objections also apply to gradual development by small mutations in series, each altering one feature, unless

one abandon selection, and consider these as controlled by some general law.   One might get *Myosurus* from *Ranunculus* in two such mutations, one changing the head of carpels to a cylinder, the other giving the petal a tubular base.   But there is no adaptational reason for the existence of *Myosurus*, which might ensure that one of these was followed by the other.   Probably mutations that change a genus are very rare, but as YULE showed (**158**), one new species, formed anywhere upon the globe, once in 15-30 years, is probably enough to account for all that are known, so that the chance of such an one being recognised is practically *nil*.

But if evolution proceeds upon these lines, adaptation must take a place completely different from that so far assigned to it (**136, 156**).   A species born in this sudden way, if not so far adapted to the place of birth as to be able to survive and reproduce, will at once be killed out by natural selection, so that any species that survives may be looked upon as adapted to the place where it grows.   How far it can spread from there will depend mainly upon the time available, and its adaptability to new conditions.   As this adaptability will presumably centre upon the conditions under which it was born, while that of its parent will centre upon some other place, it *may* be able, once established (which will take a long time, during which the parent may get a long start), to travel more rapidly than its parent, and may even at times pass the latter in its progress.   We shall return to this subject below.

Age and Area.   If then, evolution was largely independent of any urge from adaptational improvement, as seems highly probable, the latter can have but little influence upon dispersal and some more mechanical explanation must be found.   That which the writer proposed, and which he found to cover most of the phenomena of distribution, as yet simply the subject of vague speculation, he called *Age and Area* (*AA*), which may be briefly indicated in the phrase " the most widely dispersed plants, *each in its own circle of affinity*, and taken in groups of ten to cancel individual variation, are the oldest, the least so the youngest ".   Age in itself effects nothing, but it allows the time for the various active factors in distribution to produce their effects.   If in a long time and a large space, one factor produce an effect 1, then in twice the time it will probably produce 2, and the

same thing for the resultant of all the factors. In reality it will probably be not quite so simple, on account of the way in which all the conditions are liable to vary.

It was found for CEYLON, NEW ZEALAND, and elsewhere, that those species were the most widely distributed in a country which had the widest distribution outside, while the local or endemic species had the smallest areas, working always with averages of ten allied species, and comparing with allied. Wides, as I called the first named, showed a decrease in number in any country from large areas down to small, endemics an increase. " The facts call for a mechanical explanation, and the most reasonable seems to be that area occupied on the average increases with age, independently of the origin of the species. "

The system in space to which the earth belongs affords a good illustration. The sun may represent the original genus of the family, split off from an older and larger genus. The planets represent further new genera, split off from the sun, the furthest out being the oldest and " covering " the largest area, the nearest to the sun being the youngest with the smallest area; and the satellites of the planets in the same way may represent the species derived from the genera.

" I called this hypothesis by the convenient jingle of age and area, and from the very first I was careful to point out that this result was only strictly true when *averages* of about 10-15 *allied* species were taken (*AA.*, pp. 61-2, and seq.). " What has really surprised me ....is that the figures that have been given in many papers, by myself and others, show such clear and unmistakeable results that it is evident that mere age of species is a much more important factor in... distribution than we had been inclined to suppose... one can make so many predictions... especially within comparatively small areas, and find them correct within such small limits, that it is evident that mere age is a very important factor indeed, and consequently that distribution, when one works with groups of species and over enormous periods of time, is a much more mechanical phenomenon than we had been inclined to think ". One could therefore make predictions upon this simple basis. " For example, the flora of the outlying islands of NEW ZEALAND, being in general derived from the same sources as that of the main islands, must be

composed of species that were among the earliest arrivals, in their own affinity groups, in NEW ZEALAND, and should therefore... be very widespread there. This proved to be the case in a very striking manner, the species of the islands ranging on the average nearly 300 miles further in NEW ZEALAND than the species that did not reach the islands... Other predictions were equally successful... Age and area has been applied in this manner in over 90 cases without a failure... "

Some people seem to think that the argument just given has been vitiated by the fact that if one have a large space of land, such as must probably have existed when the CHATHAMS, AUCKLANDS, &c formed part of NEW ZEALAND (cf. the soundings, 140,33: 479), covered by large or small circles of distribution, and then cut out a piece, say the CHATHAMS, that piece will obviously have more in proportion of the large than of the small circles. This is in reality the same argument as mine, and does not affect the prediction in the least. Nor does it in any way give any support to the theory that dispersal was due to the adaptation. It rather implies that the dispersal was more or less equally divided over the whole area, and makes no reference to the fact that the species must have reached NEW ZEALAND from the north, south, or west, while these islands are to the east in the case of the CHATHAMS, the chief island group. It shows that the same results as I obtained can be reached in other ways, but it does not give any evidence to show that my explanation is not correct, nor to show that dispersal depended upon adaptation. How did the NEW ZEALAND species get the adaptation to suit the CHATHAMS, unless they just acquired it upon the way across from NEW ZEALAND? This, and the general mechanical way of distribution, is what I am contending for, and the many ways in which similar results can be arrived at, such as by counting names in the telephone book, or hotels at different places in BRADSHAW, or the heaps of sand made by the holes in a sieve stretched in different degrees by a blow in the middle, the sizes of the stones in a heap of gravel, and so on and so on, that have been brought up in the endeavour to prove that my results are valueless or accidental, all go to show the same thing. The important point about the hollow curves is that every family shows the same curve when of more than just a few genera, and as that

curve when expressed in logarithms is a close approach to a straight line, its origin is due to a growth of those families upon the formula

$$1 — 2 — 4 — 8 — 16 — 32 — 64 — \text{and so on}$$

a formula which is somewhat difficult to reconcile with any system of growth by the selection of chance variations of adaptational value.

Though the notion that an older species should occupy more space than a younger one seemed almost axiomatic, the publication of *Age and Area* in 1922 was met with great opposition, and the principle was not accepted. This was perhaps because it was a direct contradiction of the Darwinian theory of evolution by gradual structural adaptation. As this was applied to distribution, it implied that species might be divided into " successes ", which were expanding, or had expanded, their areas of dispersal, and " failures ", which were contracting, or had contracted, theirs. The well known curves showed the weakness of this supposition, for where, upon an evenly running curve with the " successes " at one end and the " failures " at the other, could one draw a line indicating which was which? But if we abandon this notion, we may take in its place the supposition that allied species, say in groups of ten to cancel irregularities, will react to outside influences in the same general way as other groups allied to the first. Incidentally, the notion of a multitude of failures, exceeding the successes, does little credit to nature's capacity for turning out good work, which in other sciences has been so well brought out in the last twenty years.

Size and Space. Any table in which genera of the same family are arranged in order by the (world) numbers of their species, as for example that upon p. 30, shows that the larger genera, taken in groups as usual, show larger dispersal areas than the smaller. On the whole, the larger the genus, the larger the area (law of size and space). While the first three *Anemoneae* are cosmopolitan, and the fourth in both hemispheres, the genera below them show decreasing areas, and the small ones at the foot are quite local. The *Helleboreae* show the same thing, but they *begin* at a lower level. This law appears to be of universal application, and is a great

obstacle to supporters of dispersal by adaptation. Why should better adaptation need more species?

Comparing the first 25 British genera with more than 200 species in the world with the first 25 with less than 50, we find the average dispersal to be 97 to 65 vice-counties. In the larger ones there are 11 at 112, in the smaller 3. Of the 101 Dicots that reach 112, 78 are at least North Palaeotemperate in dispersal, while 12 more cover most of EUROPE and western ASIA, leaving only 11 for anything smaller. If in the British flora we average the number of vice-counties in which the most dispersed, the second most, &c species occur, in genera with different numbers of species, we get :

Distribution in Britain of genera of various sizes

Genera of	Average dispersal									
One species in Britain	62									
Two	80	36								
Three	95	60	27							
Four	92	63	37	15						
Five	102	80	47	23	13					
Six to ten	101	76	61	44	27	18	18	9	5	2
Over ten	108	97	88	81	74	67	53	48	37 &c to 1	

Monocots						
One	43					
Two	77	36				
Three	76	35	6			
Four	90	61	34	18		
Over four	111	105	92	75	60	49 &c

It is clear that the dispersal of the first species of any British genus goes on the whole, in Dicots and Monocots alike, with the local size of the genus *in Britain,* which in turn goes largely with the size in the world. This agrees with the law of size and space, but cannot be fitted into any adaptational scheme. And the second, third, and other species show a similar rise in dispersal from small to large. At the same time the larger genera show their species closer together, with a much greater proportion of very small

dispersal. In *Ranunculus*, for example, we have seen the dispersals of the species on p. 10; in *Hypericum* they are 111 106 102 101 91 80 77 63 | 48 5 5 4; in *Trifolium* 112 112 110 109 105 98 85 72 67 60 | 42 25 21 18 12 1 1 1 1; in *Salix* 111 110 107 105 104 103 95 93 62 62 | 38 35 35 35 22 18 12 11 10 8 4 3 3; while *Carex* has 32 above the mean and 42 below it, thus made up 53 52 48 45 44 40 38 34 32 32 25 24 20 19 19 17 16 15 15 14 12 12 11 7 6 6 4 3 3 3 3 2 2 1 1 1 1 1 1. How are all these tails of very local species in big genera to be explained upon the Darwinian supposition? The great bulk of the very local species occur, as we shall presently see with regard to endemics, in the largely represented genera, where there would be more arriving at the last minute, so to speak, and not in those with few species. This just reverses what one would expect under the theory of selection by adaptation, where small and local things are failures and relics.

The genera in the first half of the British flora that have species found in one vice-county only are *Fumaria*, *Arabis*, *Draba*, *Thlaspi*, *Viola*, *Dianthus*, *Arenaria*, *Sagina*, *Trifolium*, *Ornithopus*, *Rubus*, *Alchemilla*, *Sorbus*, *Cotoneaster*, *Saxifraga*, *Tillaea*, *Epilobium*, *Lonicera*, *Senecio*, *Carduus*, *Centaurea*, and *Hieracium*, a list with hardly a small or a local genus. Even without *Senecio* (2000 spp.) they average 186 in world size. It is the big genera that contain the bulk of the species of small dispersal. Of genera over four species, 92% show a species (or more) with dispersal less than 25, of genera with four 73%, genera with three 65%, and with two only 46%. The locally larger genera overlap the locally smaller at both ends—very wide and very local dispersal, a result that we should expect if dispersal be mechanical. The larger genera have their species closer together, as we saw in the table on p. 20, owing to the greater speed at which species spread as the genus gets older. If the big genera really owed their success to adaptation, one would have to explain why so few of their species succeed. The 42 *Carices* in the tail of that genus only average 16 vice-counties each; why are there so many below the mean of the " unsuccessful " genera? If species arrived in BRITAIN by reason of adaptation, rather than by the mere chance of relative age, and of nearness or the reverse, there would hardly be such numbers below 10. The most reasonable explanation

of the great numbers of local species in the big genera is that they are the most recent arrivals in BRITAIN.

The dispersal in BRITAIN of the small species of *Rubus* and *Hieracium* sets a somewhat awkward problem before the supporter of the older views upon dispersal. Why, of 237 *Hieracia* below the mean, and 118 *Rubi* (just half as many) are there 41 to 1 in one vice-county only, while in two the numbers are 28/3, the *Rubi* continually gaining till at 19 they go ahead of the *Hieracia*. The latter stop at 39, except for one at 111, while between these figures there are 25 *Rubi*, and the average dispersal is 28 for a *Rubus* and only 7 for a *Hieracium*. These are distinctions too clear to be ignored, and suggest that some kind of evolution of small varieties is actually going on, more recently in *Hieracium* than in *Rubus*, and also perhaps that the same, or approximately the same, mutation may take place in more than one locality. How at present these phenomena are to be explained without calling in age, as (29) and others have done, is not easy to see. And why, too, are there so many different taxonomic divisions of these genera represented?

The larger the genus in EUROPE, and therefore, as a little investigation will show, usually the larger in BRITAIN also, the smaller will be the gaps in time of arrival between its species. If from the last table we take these gaps, and arrange them in the same way, we get :

Gaps between times of arrival of species, as expressed by the number of vice-counties reached

	Dicots				Monocots			
Genus of one species	Nil				Nil			
two	44				41			
three	35	33			41	29		
four	29	26	22			29	27	16
five	22	33	24	10	Over, 17	13	6	4
6-10	25	15	17	17				
over	11	9	7	7				

a very fair indication that the prophecy was correct, showing the diminution of gaps from small genera to large.

The laws of ASA, or the Triangle of Distribution. Taking together the principles just discussed, it is clear that age goes with area, and so does size with space (area). It therefore follows that size goes with age. Age represents the resultant of all factors that are active, showing its results in size of genera, and the space that the genus occupies. Taking allied groups of ten to cancel out irregularities, the results

will be very similar, and may be expressed in a triangle. An old genus will have many species, and occupy much space; a genus with many species will be old, and cover much area; a genus occupying much space will be old and have many species. To save space, we shall in future call these the laws of ASA.

Age

Area   Size
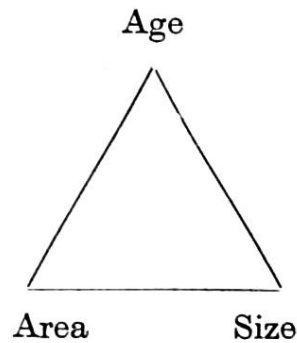
The basis, then, upon which our subject will be dealt with, is largely that indicated in the two preceding books, *Age and Area*, and *Evol.*, and we hope to show that by the application of the inductive method promising results may be obtained, which give hopes that the vast, and at present confused and unorganised mass of facts that makes up geographical distribution proper, as distinguished from its offshoot ecology, may be gradually reduced to something like order.

If these arithmetical rules hold generally, it should be possible to make successful predictions about the dispersal of the plants of a country, testing them afterwards upon the facts. It may be worth while to give another instance or two. For example, it is clear that if dispersal is thus mechanical, there should probably be a good many species in the British flora that have reached 112, and " have no more worlds to conquer ", whereas if BRITAIN had been large enough, they would have reached various figures beyond 112. In other words, there should be an accumulation of old species at 112, and perhaps another at 111 of species that for example reached the ORKNEYS, but were too late for the SHETLANDS. The figures show as follows, but one must not suppose that the whole flora of the SHETLANDS, for example, shows dispersal of 112, for many are missing in one or more vice-

counties further south, thus showing only a dispersal of 111
or less.

*Distribution of most widely dispersed species in Britain,
showing accumulations at the top*

Vice-counties reached	Dicots	Monocots	
112	101	29 (18 grasses) [3]	
111 [1]	23	15	8
110 [2]	13	10	3
109	15	5	—
108	11	4	2
107	14	1	1
106	6	4	1
105	13	2	2
	Total 196	70 (35 grasses)	

After the first two, or three in the Monocots, the numbers
begin to vary up and down in the irregular way that one
would expect, but there is a very definite accumulation at
112, and a smaller, but noticeable one, at 111. The Monocots
also seem to show a tendency to accumulate at 110, as if
many of their older species had not even been in time to
reach some far outlying islands of BRITAIN. The excess of
Dicots at 112 is greater than that of the Monocots. Half
the Monocots at 105 or more are grasses, and even more at
111 and 112. A large proportion of the dominant and abund-
ant species in the various plant associations also come into
these figures, so that the species concerned must evidently
appear in many associations.

One may see this accumulation of species at the top of a
column elsewhere and often. Thus in the HAWAIIAN Is. (62)

---

[1] SHETLANDS, or sometimes outer HEBRIDES, the most usual
omission.

[2] ORKNEYS also, most usual omission.

[3] And 4 *Carex*, 3 *Juncus*, and one each of *Iris, Potamogeton, Scilla,*
and *Sparganium*, a list which gives an idea of the kind of country
open to colonisation by the earliest Monocotyledons.

41 of the 581 local or endemic species occur on all the islands and there is a smart fall to the 8 that only occur on six islands, from which the numbers go steadily up, being 11 on five, 55 on four, 80 on three, 113 on two, and 273, or 47% of all, on one island only. Evidently the oldest endemics of all accumulated at the top, having nowhere further to go. Incidentally this seems to indicate that the group of islands was cut off very early.

It is evident that the figures of local distribution in BRITAIN, put together with such painstaking labour by WATSON and his successors, bid fair to prove of great value and importance in further study of dispersal.

Supposing that we take the sizes *in Britain* of those families that contain any species that reach 112, and place them in order, with the larger numbers rounded to the nearest five, we get, for Dicots only :

125 80 75 70 70 60 55 55 45 30 30 25 20 20 20 15 15 15 10 10 5 5 5 5 4 3 1 1   Total 874 spp.

Average 31 per fam., while the families with no 112s, but reaching 105-111, show

20 20 20 20 12 12 10 6 3 3 2 1 1   Total 130.

Average 10 (Small varieties of *Rubus* and *Hieracium* omitted).

If one note for each genus of the British flora the highest dispersal shown by any of its species, one gets a list of the figures at which each genus comes in. Of the 71 genera of Dicots that reach 112, 46, or 64.8%, belong to the *Compositae* (with 14), *Caryophyllaceae* and *Labiatae* (6 each), *Leguminosae* (5), *Cruciferae*, *Rosaceae*, and *Scrophulariaceae* (4 each) and *Umbelliferae* (3), a list of very large families which we shall find appearing again below in quite other connections (pp. 69—71 for instance).

By the rule of age and area, the most widely dispersed genera in BRITAIN should be the oldest, which again, by the rule of age and size will be the largest, whether in BRITAIN or even in the world. The genera with species reaching 112 are on the whole the largest in BRITAIN, and show an average size (*Dict.* figures) of 160 species in the world. Those

reaching 101-11 average 119, those reaching 91-100 average 71. The next lot, 61-90, is brought up by the presence of three enormous genera, *Aster*, *Astragalus*, and *Salvia*, to 85, but the genera from 31-60 only show 56, and those from 1-30 36 in the world. Clearly dispersal is largely dependent upon size in the *world*, a fact which puts " adaptation " very much out of court.

As the present British flora probably entered chiefly at the south-east, one will expect to find, in such an association as that of chalk-pasture, which is there very common, that it is very numerous, and that its most prominent species have a very wide dispersal. A glance at (**122**), p. 176, will show that the number of species (146 of them) is very large, and so is the dispersal in BRITAIN. The 91 dominant, abundant, and frequent species average 93 vice-counties, the 17 locally dominant &c average 67, both high figures. No fewer than 36 out of the 91 show a dispersal of 112 (shown by only 130 species in all).

A remarkable example of how greatly the species in any given community are determined by their range and commonness within BRITAIN is furnished by the arctic-alpine grassland above 2000 ft. (600 m.) (**122**, p. 300). To have been able to reach that height in the far north, these 48 plants (list B, not including A) must evidently be very old in BRITAIN, so that one will expect them to be widely dispersed there.

Dispersal of flora of arctic-alpine grassland in Britain

Distribution	Dicots	Monocots
112 v. c.	20 [1]	6 (5 grasses and a Carex)
102-11	9	10 (2 grasses, 4 Carices, one
and		each of Orchis, Juncus,
Antennaria dioica (89)		Luzula and Scirpus)
Viola lutea amoena (21)		and Avena pratensis (76)

[1] *Ranunculus* (6 British spp. at 112), *Cerastium* (2), *Sagina*, *Linum*, *Oxalis*, *Trifolium* (2), *Lotus*, *Potentilla* (2), *Heracleum*, *Scabiosa*, *Bellis*, *Achillea* (2), *Taraxacum*, *Leontodon*, *Veronica* (5), *Euphrasia*, *Thymus*, *Plantago* (2), and two spp. of *Rumex* (4). Thus no less than 36 (out of a Dicot total of 101) show 112, so must be among the oldest of the old in BRITAIN.

List A of the same habitat, the " Highland " species, on the other hand, only shows dispersals of 29,112 (*Festuca ovina*), 22, 40, 20, 20, 8, 20, 14, 20, 20, the usual figures for the dispersal of Highland species, which have not recently climbed from below.

The average dispersal of the 48 species in list B is 107, or very high indeed. The composition of the list of Monocots is worth study.

We may get a rough idea of the variation of conditions under which the members of the various communities grow, by taking the space devoted to them in the Index of (122). Taking only the genera in A and B, those mentioned once only in the index have an average dispersal of 67, twice of 83, 3-6 times of 84, 7-10 times of 95, and more than that of 101.

Outlying genera the largest. As BRITAIN lies at the edge of what has long been the ATLANTIC coast of EUROPE, with deep water beyond, one may make another important prediction about its flora. By the theory of evolution that we have set out, the oldest genera of a family will start at or towards its centre (the oldest of all of course at the very centre), and thus will on the whole be the first to reach the outer boundaries of the present distribution of the family, though at times, as we have suggested, the first genus may be overpassed by some younger one better suited to the conditions in that direction. In other words the most outlying genera of a family will tend to be its oldest or largest in the world. Of the 100 families in BRITAIN, it is therefore of considerable interest to find that this is the case in nearly three quarters. No less than 71 families are headed each by its largest genus in the world, while 10 more are headed by the second or third. This, as we shall see, is not an isolated phenomenon, but is universal.

The supposed operation of adaptation. If the adaptation theory worked as it is supposed to do, it is evident that a slight difference like that between two allied varieties would be ample to ensure that evolution should go on. Why then should one find generic differences at all, and still less why · larger ones? Yet these large differences are obviously a

part of nature's scheme in evolution. As upon the Darwinian supposition they must have some adaptational value, it is supposed that there must still be competition to widen the gaps between species until they become generic. But as differences become greater and more distinct the higher one goes, this would imply that the competition also increased, whereas it is in reality the other way. There may be great competition between two bootblacks, especially if their stands be near together, but not between a cabinet minister and a stationmaster, nor between a bootblack in LONDON and one in BRISTOL. Natural selection is primarily an individual phenomenon; A may win here, B there, but *all As do not defeat all Bs*, though there has in recent years been a recrudescence of this fallacy. There are no super-species. Had insect organisation been carried further, man would have had little chance, and as it is, a vast amount of skill and labour has to be expended in warring with them. Cotton, to take only one instance, is a vast industry in AMERICA, yet in different years from 10 to 25% of all the labour expended upon it goes to feed boll-weevil and other troublesome insects. Taking the world as a whole, we have estimated that labour equal to that of 30 millions of men is occupied in feeding noxious insects. It is well to remember such things when we pride ourselves too much upon our civilisation.

It is hard to conceive of competition between two species of buttercup *as a whole*, though it may be fierce between one individual of A and one of B. One is compelled to realise that distribution is individual, taking little or no account of the structural characters of the competitors, so long as they are not very unlike. Ecological distribution shows the same thing. What is there in the structure of any of them that should make *Lythrum Salicaria, Epilobium hirsutum, Sonchus palustris, Lysimachia vulgaris,* and *Typha angustifolia* become members of a reed-swamp association (**122**, p. 191) There is nothing in their structure to show what kind of habitat they affect, and they show great structural variety, even to the distinction of Dicot and Monocot. No evidence can be brought to show that distribution is seriously affected by structural differences. When one looks into the simple facts of distribution, they are soon found to clash hopelessly with the Darwinian explanation based

upon adaptation. There is no reason whatever to suppose that species of plants fight as units.

The tribes of Ranunculaceae. As we cannot describe the whole family of *Ranunculaceae* as being numerous, widespread, and successful in BRITAIN, let us go a step lower to the tribes, taking them from the *London Catalogue* 11th ed. for the figures. *Anemoneae*, which include *Ranunculus*, have 35 species, occupying in all 2135 vice-counties, against 8 *Helleboreae* in 330, an average of 61 against 41.1; both differences are too great to be accidental. If we call the *Anemoneae* the more successful, we must explain why some of them are rarer than any *Helleboreae*, though the *top* four are much superior to the uppermost *Helleboreae* in dispersal. But this fact, which by age and area implies that in this family the achene (the mark of *Anemoneae*) is older than the follicle (that of *Helleboreae*), flatly contradicts the current view, that the follicle is the older form. It would be very difficult to change an achene into a follicle by gradual changes, while a change in the other direction is possible; but to mutation, which we are here upholding, either way seems equally possible. It is clear that all the achene-bearers are not superior to all the follicle-bearers, and so far as 'I know, it is not possible to find a group, all whose members are superior to any of those of a related group. The simplest way to explain these contradictions is to adopt a supposition like age and area, for which abundant evidence has been adduced. It simply says that the lower genera in each list are on the whole younger than the upper, and therefore have smaller numbers and less dispersal. And one may ignore in this respect the structural differences between them, to which one cannot attach any adaptational value. But this of course is the negation of Darwinism. (*Cf.* also Testcase XV, Achenes and Follicles, in *Evol.*, p. 124).

We shall now give two tables of the genera in these great tribes, arranged in order of size, with their distribution, following it later with the hollow curves produced by plotting the numbers graphically.

Ranunculaceae; distribution and sizes of genera, Anemoneae

Size

300	Ranunculus	Br.	Cosmopolitan
220	Clematis	Br.	Cosmopolitan
130	Anemone	Br.	Cosmopolitan
75	Thalictrum	Br.	N. Temp., Natal
18	Viorna (Clematis p. p.)		N. Am.
10	Adonis	Fr.	N. palaeotemp.
10	Oxygraphis		N. As., N. Am.
10	Clematopsis (Clematis p. p.)		Madag., trop. Afr.
7	Myosurus	Br.	N. and S. temp.
7	Naravelia (Clematis p. p.)		Indo-malaya
7	Rhopalopodium (Ranunculus p.p.)		W. S. Am.
6	Knowltonia (Anemone p. p.)		South Africa
6	Trautvetteria		Japan, N. Am.
4	Barneoudia (Anemone p. p.)		Chile, Argentina
4	Hamadryas		Antarctic Am.
3	Halerpestes (Ranunculus p. p.)		N. Am.
3	Leucocoma (Thalictrum p. p.)		N. Am.
2	Anemonanthea (Anemone p. p.)		N. temp.
2	Capethia		W. S. Am.
1	Aiolon (Anemone p. p.)		N. Am.
1	Arcteranthis (Oxygraphis p. p.)		N. Am.
1	Aspidophyllum		Peru
1	Beckwithia (Ranunculus p. p.)		California
1	Gampsoceras (Ranunculus p. p.)		Asia Minor
1	Kingdonia		W. China
1	Kumlienia (Oxygraphis p. p.)		N.W. Am.
1	Laccopetalum (Anemone p. p.)		Peru
1	Paroxygraphis		Sikkim
1	Piuttia (Thalictrum p. p.)		Himalaya
1	Stipularia (Thalictrum p. p.)		Himalaya
1	Sumnera (Thalictrum p. p.)		N. Am.
1	Syndesmon (Anemone p. p.)		E. N. Am.
1	Viticella (Clematis p. p.)		Europe

33 genera, 838 spp. Average 25.

Genera reaching BRITAIN are marked Br., reaching FRANCE only, Fr. All British genera are found in FRANCE also.

Distribution and sizes of genera, Helleboreae

Size

175	Delphinium	Fr. N. temp.
110	Aconitum	Br. N. temp.
75	Aquilegia	Br. N. temp.
20	Caltha	Br. N. and S. temp.
20	Isopyrum	Fr. N. temp.
16	Nigella	Fr. Medit., Eur.
15	Actaea	Br. N. temp.
15	Helleborus	Br. Medit., Eur.
12	Cimicifuga (Actaea p. p.)	N. temp. ,
12	Trollius	Br. N. temp.
10	Coptis	N. temp., arctic
10	Consolida (Delphinium p. p.)	E. Medit.
7	Eranthis	Fr. Medit., As.
5	Callianthemum	Mts. Eur., C. As.
5	Enemion (Isopyrum p. p.)	E. As., N. Am.
4	Paraquilegia	S. C. As.
2	Asteropyrum (Isopyrum p. p.)	China
1	Anemonopsis	Japan
1	Bodiniera	China
1	Calathodes (Trollius p. p.)	Himalaya
1	Chrysocoptis (Coptis p. p.)	N.W. Am.
1	Komaroffia (Nigella p. p.)	Turkestan
1	Leptopyrum (Isopyrum p. p.)	C. As.
1	Paropyrum (Isopyrum p. p.)	Turkestan, N.W. Himalaya
1	Semiaquilegia (Isopyrum p. p.)	Japan
1	Souliea	China
1	Urophysum (Isopyrum p. p.)	Szechyan (China)
1	Xanthorrhiza	Atl. N. Am.

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28 genera, 524 spp. Average 18.7

This table is of interest in various ways. One observes at once the extraordinary parallelism of the two sub-families, both in sizes of genera and in areas of distribution. Each list, as we shall see, gives a hollow curve. More than half the total have three species or less in one list, five or less in the other. The larger the number of possible parents, the larger tends to be the number of ones and twos, for these small genera are slow in getting established and in increasing their numbers.

The genera are from my *Dictionary*, with such revision as has been done up to date. Many people do not accept them all as genera, but each represents a group which has been regarded as a somewhat separate group of species, and that is all that really matters in this connection, for we have no definition, but only a description, of a genus. Each lot are probably the descendants of a mutation which we usually describe as somewhat larger than usual. The lists are admittedly not quite up to date, but as COCKAYNE said years ago, in a letter to the writer, " all recent systematic work simply makes age and area stand out more clearly ", inasmuch as almost all recent additions to the list are at or near the bottom, thus making the hollow curve more evident. For example, the new genera of *Acanthaceae* in two recent supplements to the *Index Kewensis* are 14/1 and 3/2. Most of the new and small genera are formed by splitting off from the older, so that they are in general satellites, not relics.

Each surviving species started with adaptation to its surrounding conditions, or it could not have survived. It must at the same time have had some range of adaptability, to resist the continual changes in conditions from day to day. Its further distribution would then depend upon how far this adaptation and adaptability would carry it, and how long a time had been available in which to spread. To these must of course be added the great retarding influences of barriers of every kind, as described in *Age and Area*, chaps. II-V.

The exceptions in the table are easily understood with a little thought. *Delphinium*, for example, is much larger than *Caltha*, which reaches both hemispheres, but probably arose a long way from any easy connection to the south, and was perhaps a very slow traveller, or had unusually small adaptability. It is to cancel out irregularities of this kind that even allies must be taken in groups.

HOLLOW CURVES SHOWN BY SUB-FAMILIES OF RANUNCULACEAE
AND BY FAMILY OF DIPTEROCARPACEAE
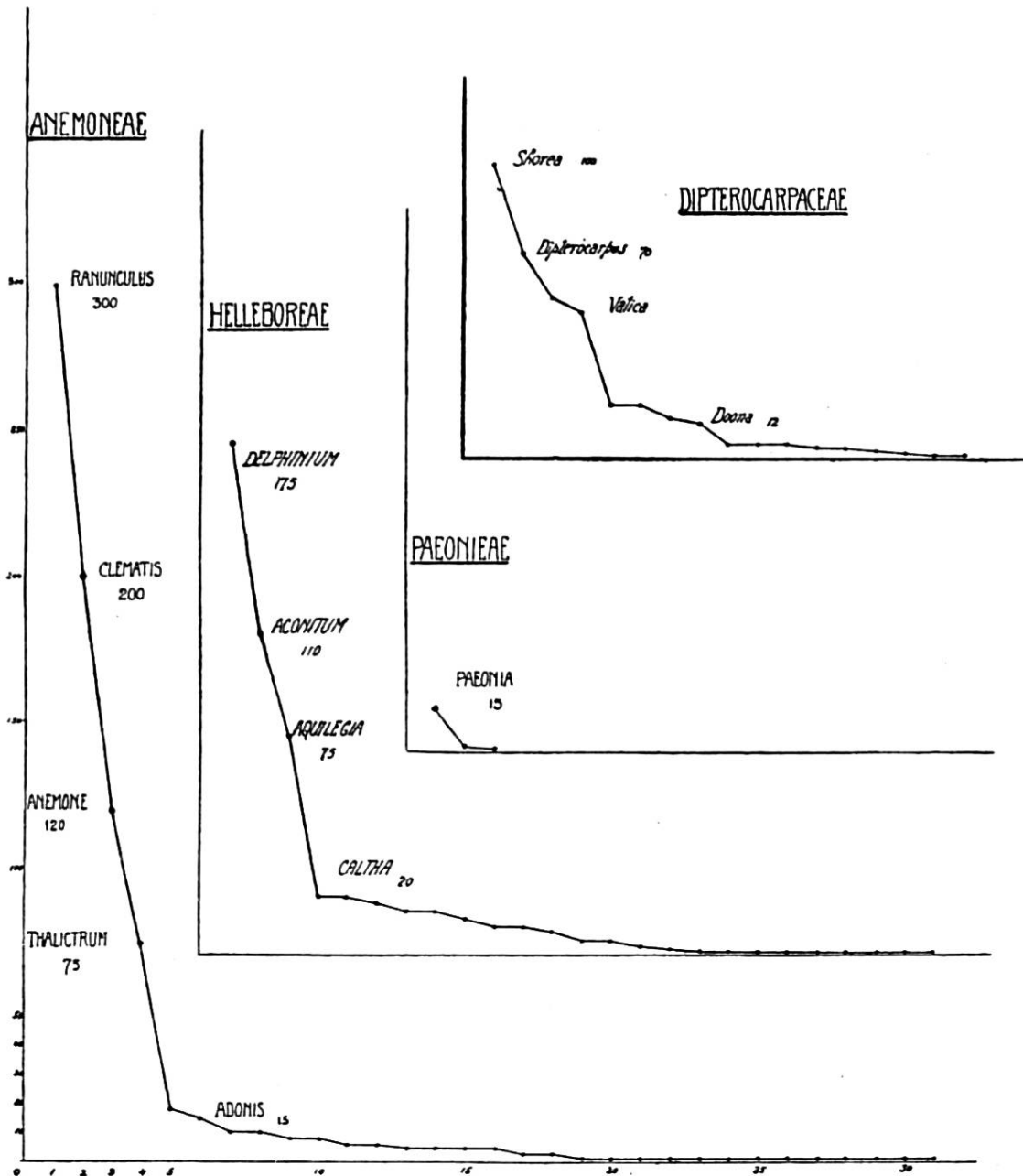
Let us now turn these two lists into graphic curves in the usual way, by the numbers of species in the genera, and add to the two British sub-families the third, *Paeonieae*, composed of *Paeonia* with 15 in EUROPE, ASIA, and NW AMERICA, and *Glaucidium* with 2 in CHINA and JAPAN. We have shown in *Evol.*, p. 84, that they cannot be regarded as equal in rank to the other two sub-families. The mutation that split off *Paeonieae* was a "larger" one than usual, combining two characters, fleshy ovary wall and loss of honey leaves, which may at times be seen singly in other *Helleboreae*, so that *Paeonieae* presumably came from this group, rather than from *Anemoneae*, as is suggested by the key on p. 85 in *Evol.* This again at once suggests what will be considered later, that a family may possess what one may term a set of characters for kaleidoscopic use.

Size and space shows best in the vertical, age and area in the horizontal direction, in these curves. The smaller and the least dispersed genera are at the bottom right hand end of the curve, the larger and the most dispersed at the top left hand end. Darwinism, as we have been pointing out for many years, is quite helpless to explain these curves, which show, as do many other facts that we have brought up, that if dispersal depends upon adaptation, that adaptation must be generic. But if so, why does the genus need so many species to cover the greater variety of conditions into which greater dispersal takes it?

To show how the hollow curve is formed, let us just consider the possible future growth of the *Paeonieae*. If a new genus form by splitting off from either of the other two, it will necessarily be a "one", and as 15 + 1 is more than twice 2 (the size of *Glaucidium*), the curve will at once be a hollow one. As each new genus begins as a one, and its early stages will be very slow, there will be an increasing number of ones at the bottom of the curve, while at the top, as the genera grow larger, and thus increase the number of their species in an expanding ratio (on account of the increase in the number of potential parent species), the positions of the genera on the curve will become continually further and further apart, thus lengthening the curve at that end also. (Cf. Testcases III and IV *Evol.*, p. 95, especially the reference to gaps between genera on p. 97.)

Most of the genera split off in the tables, and given as

X, p. p., are from large ones, like *Clematis*, *Anemone*, or *Delphinium*. In the *Anemoneae*, the larger and older group, there are 18 such, and the average size of the parents (*now*) is 145; in the younger group these figures become 8 and 47. The parents in the older group have grown more than those in the younger, of course, on the whole. But this splitting of new genera from older ones by mutations that are larger than usual is exactly the process of evolution that the writer has proposed in his book *The Course of Evolution*, 1940, and is a process that can not be reconciled with the theory of selection upon adaptational (and structural) improvement. It surrounds each genus of importance, which represents some mutation of long ago, with a group of smaller satellites, the result of more recent mutations. As the group thus formed increases in number and size, it goes through the stages of more and more definite recognition. The Supplements to the *Index Kewensis* show clearly how continually new and small genera, usually ones, are being split off from the larger genera. The relic explanation is thus continually being made to look more and more improbable.

All over the northern hemisphere, *Anemoneae* and *Helleboreae* occur together, the former (the larger and older group) always on the whole the best represented. There is little evidence for any dying out of genera or species, *once they have covered an area sufficiently large* for it to be very unlikely that the whole genus or species should be killed out by some geological or other catastrophe. Up to the present time, the evidence of fossils has been interpreted in a way suitable to the current theory of the course of evolution, and they have been looked upon mainly as ancestors, or ancestral relatives, of things now existing. But age and area makes clear that things with small areas of dispersal are in general young themselves, while any descendants to which they have given rise will be younger still, and will occupy smaller areas, usually well within the range of the first. It follows, therefore, that it is entirely unsafe to regard a fossil with small area as being the ancestor of any now existing form—if the small area is all that it has ever occupied, then its descendants, if any, will also be extinct. As most fossils of flowering plants, with which alone we are at present concerned, are known only from comparatively small areas, this discounts very much any evidence to be derived from

them as to ancestry. They are far more probably sidelines of evolution that have died out completely, not from any lack of adaptation, but on account of some misfortune that has overtaken them.

The migration to and fro that has marked the floras nearer to the poles, probably more than those in the tropics, seems often to have resulted in the extinction of small genera that could not get away quickly enough, while in the case of large genera only species would be destroyed. Water plants, with fewer species and larger ranges, would be less likely to suffer in this way. These extinct genera may then be found as fossils, but cannot be regarded as ancestral to anything now living, for their descendants, if any, would occupy lesser areas than themselves, and would be destroyed also. Thus the larger genera might go on as before with reduced numbers, while small and local ones might disappear altogether; the larger ones would increase again, and produce a new crop of small descendants.

In this connection it is of interest to read the account of the Pliocene flora of BRITAIN by Mrs REID (105-6). Of the 37 families mentioned, 28 are headed, as regards world size, by the following genera : *Acer, Atriplex, Betula, Carex, Ceratophyllum, Cornus, Elatine, Euphorbia, Galium, Hippuris, Hypericum, Myriophyllum, Naias, Nymphaea, Polygonum, Potamogeton, Potentilla, Quercus, Ranunculus, Rhamnus, Sagittaria, Salix, Solanum, Sparganium, Ulmus, Urtica, Valeriana, Viola,* all of them heading the families at the present day, and the largest (or largest available so far north) genera in them. The other nine, with the genera that now replace them, are : —

Old heads	*Present dispersal*	*New Heads*	*Present dispersal*
Centaurea	one at 112,11 others	Senecio	two 112,9 other
Circaea	106	Epilobium	one 112,11 oth.
Corema	only reaches Spain	Empetrum	73
Heracleum	112	Eryngium	55,9
Hypecoum	only to S. France	Corydalis	94
Menyanthes	110	Gentiana	97
Stachys	two 112,4 others	Salvia	64,6, one Chan-
Stellaria	112, 111, 111, 109,		nel Is.
	&c	Silene	104. 80, 60, 53, &c
Veronica	five 112, many othr.	Pedicularis	two 112 only

None of the second column appear at all in Mrs REID's list, though all of them are the numerical heads of their families, now found in BRITAIN, where most of them have evidently been later arrivals, as shown by their smaller distribution, than those in the first column. They appear to have been passed on the way from the south by younger genera, thus affording full support to the views that I have here brought forward, that such things can and do happen. In the cases of *Corema* and *Hypecoum*, the old genus has not again come so far north as BRITAIN, a fact which may mean slow dispersal, or slow adaptation to the colder climate, or which might mean that the climate was not so warm as formerly.

In considering such a list as this, with its 87 genera, none with more than a few species (largest *Carex* 8, *Ranunculus* 6, *Rumex* 5), one must not forget that coming from one locality, it probably does not represent more than a few, or even one, of the associations of plants that grew in the country at the time. Suppose that at some future date a deposit of the association now growing upon chalk grassland (122, p. 176) is unearthed. It is so large an association that one would be apt to think that one had made a good " haul ", yet it would in reality be less than 10% of the flora of the country, and one would not find the following families at all :

Berb., Nymph., Papav., Crucif., Franken., Portul., Elat., Hyper., Malv., Tili., Geran., Aquif., Celast., Rham., Acer., Saxi., Dros., Hippur., Halor., Callit., Lyth., Onagr., Cucurb., Aral., Corn., Caprif., Valer., Eric., Pyrol., Plumb., Ol., Apoc., Polem., Conv., Solan., Lentib., Verb., Chenop., Polygon., Arist., Thymel., Elaeag., Loranth., Euph., Ulm., Mor., Urtic., Myric., Bet., Fag., Salic., Empetr., Ceratoph., nor *Amaryll., Diosc., Lili., Typh., Sparg., Ar., Lemn., Alism., Butom., Scheuch., Potamog., Erioc.,* or 65 families in all out of the 99 of the British flora. And not only would one not find these families, nor anything to head them, but one would not find such genera as *Potentilla, Eryngium, Pedicularis, Gladiolus, Juncus,* or *Panicum,* genera actually heading families in BRITAIN. This point has been somewhat neglected in regard to fossils.

Ranunculaceae are " the most primitive type of herbaceous Dicotyledons " (68, p. 94), and *Ranunculus* itself is usually looked upon as very primitive, yet it is cosmopolitan in its

dispersal and has more species than any other of the family, being only passed by about 60 genera in the flora of the world. How did it come to reach almost all of such outlying islands as CEYLON, NEW ZEALAND, and the HAWAIIANS, in which last it is the only genus of the family? How did it go so far north, and to such heights in the mountains? If so old, why has it not been killed out by some more recent and better " adapted " type? Wide dispersal is usually put down to " the possession of some advantage that enables it to spread ", but no one has ever been able to suggest such, especially as it must evidently be generic. Even the supporters of selection are compelled to call in age, as DARWIN did (**29**, pp. 358-9), though they reject age and area, which is a direct contradiction of " Darwinism ". They also try to have a foot in either camp by explaining small genera as relics (failures) or as local adaptations (successes), thus showing our lack of real knowledge and understanding.

The explanation of the distribution of the *Ranunculaceae*, and if so, of other families also, to and in BRITAIN, where the flora is so recent that there has not been enough time for the formation of many endemic forms (that is, forms so recent that they have had neither time nor opportunity to get beyond the frontier), thus rests very largely upon the mechanical explanations that we have indicated. In any given small area of a country, at any given time, the local distribution is largely determined by the local conditions that there exist, working upon the actual flora that has so far arrived in the country and within reasonable distance of the area concerned. Gradually, in the course of time, natural selection picks out from this those species whose inherited or inborn adaptation and adaptability make them most suitable to whatever conditions may there be found. Supposing that a species arrived at the British frontier with some special adaptation to something that did not occur in BRITAIN, *e.g.* such a metal as selenium, it would be stopped at the frontier, and would get no further unless it developed a form suited to growth without selenium; but if it were adapted to chalk, it would probably commence life upon chalkpasture very soon, and whether it remained there so as to form a member of the chalkpasture association, when that became filled up, would depend upon its degree of adaptation to chalk, as modified by its capacities in the way of adaptability.

It thus comes about that an area A gradually becomes occupied by a community *a*, and an area B by *b*, which will slowly take in new members till the association becomes " closed ", just as the human communities with which BRAZIL was first colonised, not a miscellaneous crowd, as in most British colonies, but made up of a definite proportion of agriculturists, mechanics, and so on, might be so described. Both, with changing conditions, are obviously liable to alter in their composition. One might, in western European spots, match the conditions very closely in which certain associations grow in BRITAIN, but as there would be more plants available in the flora, it is improbable that the association would be made up of just the same species. To reach this closed condition, it is clear that much time must be allowed (age and area), and as it is therefore the large genera (age and size) that have spread the furthest (size and space), it is they that will have been able to occupy the most places in the associations which they first joined. As time goes on, their adaptability will enable them to join other associations, and thus still further to extend their numbers and dispersal (" to him that hath shall be given "), whereas newcomers will be likely to be found entirely, or nearly so, in communities like the one in which they first arrived.

Monocots—Gramineae. Let us now take a large and well represented Monocot family, the *Gramineae.* It has in BRITAIN proper 45 genera with 131 species. Of these 18 species in 16 genera reach the maximum possible dispersal of 112, and another 5 genera, besides some species of the 16, show a dispersal of 111, so that nearly half the genera are very widely dispersed, an advance upon the *Ranunculaceae*, probably due to the rather cold and wet conditions that first prevailed after the disappearance of the ice. On the other hand, there are a number of late arrivals, like *Panicum*, the largest genus in the family, which reaches only 6 vice-counties in the south of ENGLAND, *Leersia* (4 only), *Mibora* (3), and one genus *Lagurus*, which only reaches the CHANNEL Is., and cannot strictly be considered British.

As in all large British families, a striking thing is the great proportion of the subgroups that are represented. This is a necessary consequence of the simple fact that, as we have shown in *Evol.* (Testcases III, IX, XIV, XX, &c),

the larger (older) genera tend to be divided by larger divergences than do the smaller (younger), and it is they therefore that give the characters to the subgroups; and as they tend to appear in any country more or less in order of size, many subgroups will appear in the flora. Adaptation has little or nothing to do with it, and it cannot be explained by the help of that supposition. The sooner that we get rid of the notion of an adaptational reason for every small individual step in the differentiation of families, genera, and species, the better.

There are in BRITAIN no less than eight of the thirteen subgroups of the grasses, and it is worth while to look at a table of them :

Representation in Britain of the sub-groups of Gramineae

Group	World size about	Gen.spp. in Britain	Dispersal, in order of world size of the most widely dispersed sp. in each genus
Festuceae	120 gen.	15/67	112 112 112? 112 99 111 112 11 100 112 112 104 112 97 111. Average 102.
Agrostideae	60	10/27	71 112 112 111 7 93 65 19 25 3. Average 61.
Aveneae	40	7/14	98 98 112 111 112 112 6. Average 92.
Hordeae	30	6/14	112 46 80 112 53 108. Average 85.
Paniceae	70	1/1	6. Average 6.
Chlorideae	50	2/4	11 3. Average 7.
Phalarideae	7	3/3	111 112 3. Average 75.
Oryzeae	7	1/1	4. Average 4.
Andropogoneae	70	—	
Bambuseae	40	—	
Zoysieae	20	—	
Tristegineae	10	—	
Maydeae	6	—	

Such a table gives food for thought. The four top groups, which are essentially grasses of cool and even cold climates, are represented in BRITAIN in order of their size, and they

also show more species per genus in the larger (older) groups
by reason mainly of the longer time that has been available
for arrivals. It is fairly evident that the *Festuceae* is much
the most important group, though the grasses, to judge by
Panicum and the *Paniceae*, seem to have begun in warm
climates. The leading genera of *Festuceae, Poa* (200+),
Eragrostis, Festuca, and *Bromus,* are definitely grasses of
the colder climates, though being old, they have had time
also to reach the tropics, where however, they are not at
home except in the hills. Much the same may be said about
Agrostideae, though it seems to have been a good deal later
in BRITAIN, and its leading genus, *Calamagrostis,* is probably
younger than *Poa. Hordeae* is headed by *Danthonia,* which
is largely southern (S. AFR. &c), and is headed in EUROPE
by *Avena,* its second genus, which occurs in BRITAIN with
five others. Except for the marked drop in dispersal in
Agrostideae, which much needs explanation, each group
shows smaller representation and dispersal than the one
before it, so that if dispersal is to be explained by adaptation,
some adaptational reason, which must be generic, is needed
to explain the frequent small dispersal. Age is by far the
simplest explanation of all the figures that we are bringing up.

Looking at the other nine subgroups, the first four of
them in the list have a small representation in BRITAIN.
Paniceae is a marked group of tropical and subtropical
climates, only spreading much beyond in AMERICA. Its
leading genus, the head of all the grasses, *Panicum* with
over 500 species, has just been old enough to reach a few
districts in the south of ENGLAND, and has not produced
in the old world a genus more suited to the cold. *Chlorideae,*
headed by *Chloris* with 60 species in warm climates, is repre-
sented in BRITAIN by *Spartina* (11 vice-counties) and *Cynodon*
(3), both coast plants. *Oryzeae* is a very small group, headed
by *Oryza* (rice) with 7 tropical species, but the genus that
reaches BRITAIN, *Leersia* (4 vice-counties) was apparently
born further north. Finally *Phalarideae* is represented by
Hierochloe (20 spp., 1 in BRIT., 3 v. c.), *Anthoxanthum* (15 spp.,
1 BRIT., 112 v. c.), and *Phalaris* (10,1 in BRIT., 111 v. c.).
It is difficult to associate this group of northern genera with
Ehrharta (30 mainly S. AFR.) as a parent, and it is by no
means impossible that they arose from a separate but parallel
mutation, for we have no evidence of any destruction of the

transitional forms which would be needed under the Darwinian conceptions.

We may end with a comparison of Dicots and Monocots in BRITAIN by genera :

Distribution of Dicots and Monocots in Britain compared

Vice-counties	Dicots	Monocots	Grasses only
91-112	177 or 52%	49 or 40%	29 or 64%
61-90	71 20%	17 14%	3 7%
31-60	42 12%	16 13%	2 5%
1-30	53 15%	41 33%	11 24%

Thus 72% of the Dicots reach 61 or more, while only 54% of Monocots do so, or, if one omit the grasses, only 44% of the reduced total. On the whole, therefore, we may imagine some Monocots to have been late in arrival.

Of the 29 Monocots that reach 112, 18 are *Grasses*, 4 *Carices*, 3 *Juncus*, leaving only one each of *Iris*, *Potamogeton*, *Scilla*, and *Sparganium*, an assortment that perhaps suggests the type of country first available after the ice. Another fact that goes to show that the genera with the 112s are ancient is that among them the Dicots alone have 290 endemic or local species in SPAIN, and 512 in the BALKANS. Of the whole 130 British species reaching 112, 18 are *Compositae*, 18 *Gramineae*, 9 *Scrophulariaceae*, 8 *Caryophyllaceae*, and 7 each *Labiatae*, *Leguminosae*, *Ranunculaceae*, large families, which we shall meet again in various other connections.

The difficulties that the study of distribution brings up for any explanation based upon adaptation are legion, and so long as that hypothesis holds the ground, there can be little but profitless speculation, as HOOKER long ago pointed out. As a species appears to be born at one place and time by a single mutation, its adaptation must evidently be born with it, or it could not survive. Evolution is an independent process, and appears to go on without reference to natural selection, and distribution follows it, as we have seen and shall see, in a largely mechanical way, for which arithmetical rules may be found when one is dealing with large areas and with long periods. In individual cases, on the other hand, ecology comes in to settle, by natural selection, the exact

spots where anything shall succeed and reproduce, while the adaptability with which it must also have been born settles whither and how far it shall travel in the time available.

This sketch must suffice for the present in regard to the British flora and its distribution. It affords ample material for a book, and we have tried to indicate some directions in which it is not impossible that useful work may be done. Geographical distribution ought not to remain in the Cinderella-like position that it has so long occupied. It is as open to inductive reasoning as any other branch of botany, offering a large field for possible labour, as yet little trodden.