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## CHAPTER II

# Some continental and other floras

Leaving BRITAIN to east or south, one soon comes upon unfamiliar plants, at first almost always of British genera, and as most British species go beyond the boundaries of EUROPE, the genera become better and better represented as more new species appear. *Centaurea* is the most striking, with 12 species in BRITAIN, 22 in FRANCE, 87 in SPAIN, and 171 in the BALKANS. Of the Spanish species, 49 are local to SPAIN, or *endemic* there, and 112 are endemic in the BALKANS. This fact, which on a smaller scale and with a less steep rise is shown by all important British genera, offers an insoluble problem to the supporters of selection, or of distribution by adaptation only. As it is the large genera that show it, this adaptation must be generic. Why, too, are there over 1200 endemics in the BALKANS, and another 1200 in SPAIN, with practically none north of the ALPS? Endemics used to be regarded, and still are, as the relics of things that were once more widespread and are now dying out, defeated in the struggle for existence by plants better adapted to conditions. So numerous, however, are they in most large genera, like Centaurea above, that when they finally die out, the genera will become quite small, and one begins to wonder what is the proper criterion of "success" (cf. Testcase I, Evol., p. 90), and also how small a dispersal is necessary that a species should be a relic.

Going on with our journey, we come upon genera new to BRITAIN, like the soapwort (*Saponaria*) or the chalk-plant (*Gypsophila*), both *Caryophyllaceae*, and familiar in British gardens, where they are quite at home. One usually meets one new species first, and others gradually, and every now and then one meets members of tribes, sub-families, or families that do not occur in BRITAIN. About 32 new subdivisions of families are met with in FRANCE, represented by such things as the paeony, the rosemary, or the lavender, while the rue of the south belongs to a new family, the *Rutaceae*. One meets about 25 new families before reaching GIBRALTAR, and it is of special interest to note that in 17 cases one first encounters the largest genus in the family in the world (cf. p. 27), while in two more it is the second, and only in *Acanthaceae* and in *Gesneraceae*, tropical families with little overlap into colder zones, is the genus a small one. In the far south, too, we come upon many genera that are localised or endemic.

The current theories, that evolution was by gradual structural adaptation. and that wide distribution was due to the possession of "superior adaptation", are evidently helpless to explain such facts. But now that we know that distribution is largely governed by the laws of ASA, whereas previously we knew of few cases where it obeyed any law, it is clear that the explanation must be rather mechanical than Most of the actual work of distribution of the indivivital. dual plants into their most suitable situations is of course done by vital factors operating upon the plants in accordance with whatever may be the local conditions, which will differ from one place to another. But age, size, and area or space always influence things in the same direction, and working without reference to any vital consideration, they determine almost entirely what shall happen in large areas and in long time. The larger the area, and the longer the time, the more will their effects override the local and temporary results due to the vital factors. Only when we know what is due to the simple ASA factors, can we disentangle with any hope of success the effects of the vital factors upon ultimate dispersal, and the study of distribution will cease to be so much a matter of speculation as it is at present. It is for this reason that we have been so careful about laying down the rule about comparison only in groups, and with closely allied forms, so that all compared may be likely to resemble one another in habit, in mode of life, and in reaction to outside influences.

*Barriers.* The effects of age and of area are positive and cumulative, but they are always accompanied by the negative

effects produced by barriers of different kinds, especially physical, climatic, and ecological. There is no need to repeat what we have already said in Age and Area, pp. 12, 20, 32-45. Two well marked barriers occur in going southwards from BRITAIN, the CHANNEL and the PYRENEES. Conditions do not appreciably change in crossing the channel, yet one finds a number of new species soon after landing in FRANCE; the presence of the sea has prevented them from crossing, though since its formation they have become frequent upon the French side. In the same way, there is a marked change in crossing the PYRENEES. Even the passes are so high that much functional adjustment would be required in order to cross, first in the direction of colder later in that of warmer, conditions, an adjustment that is apparently beyond the range of most lowland species in the time that has been available.

The things that are left behind at any barrier tend to be the smaller and more localised genera, and what corresponds to them in species—the more recently born, and therefore much localised species, which as we have seen are much more numerous in the larger genera. A comparison of the *Labiatae* in SPAIN, FRANCE, and BRITAIN shows :

Genera	Species	Average per gen.	% of Span. gen.	of Sp. spp.
Spain 34 France 29 Britain 19	$\begin{array}{c} 235\\ 108\\ 57\end{array}$	$\frac{7}{3.7}$	$100\% \\ 85\% \\ 56\%$	$100\%\ 46\%\ 26\%$

a marked decrease at each stage, especially, as we should expect, among the species. The Spanish genera left behind in crossing into FRANCE have 4, 1, 1, 1, and 1 species, and the same kind of thing shows at every stage, even including the change from the flora of BRITAIN to that of IRELAND, or other islands outlying, and again to the smaller islands outlying from these.

We may now compare the floras of BRITAIN, FRANCE, SPAIN and the BALKANS, dividing the plants into British and non-British, and we get the table on p. 47, in which the floras are taken just as they stand, with no attempt at equation, so that the British flora includes all the small *Rubi* and *Hieracia*, which fact goes to reduce the difference. The figures given in this book are mostly too emphatic to suffer from lack of equation.

Proportions of British and non-British genera in the floras of Britain, France, Spain, and the Balkans

Total Genera	and S	pecies		Britis	h gen.		Non-Brit	-	
			% Dicots		S	pp. per gen.		S	pp. per gen.
-	Brita	in (a)				Bour			Bon.
$\operatorname{Dicot}$	347	$15\dot{2}\dot{1}$	77%	347	1521	4.3		-	
$\operatorname{Monocot}$	128	<b>435</b>		128	<b>435</b>	3.4		-	
$\mathbf{Total}$	475	1956		475	1956				
	Fran	.ce (b)							
$\operatorname{Dicot}$	640	2494	79%	354	2019	5.7	<b>286</b>	475	1.6
Monocot	184	651	-100,000	108	<b>548</b>	5.0	76	103	1.3
			•						
$\operatorname{Total}$	824	3145		462	2567		362	578	
	Spai	n (c)							
$\operatorname{Dicot}$	748	4143	83%	<b>343</b>	3153	9.2	405	990	2.4
Monocot	179	806		101	666	6.6	<b>78</b>	<b>140</b>	1.8
				. <u> </u>					
$\operatorname{Total}$	927	<b>4949</b>		444	3819		483	1130	
	Balk	ans (d	1)						
$\operatorname{Dicot}$	739	5449	84%	337	<b>4184</b>	12.4	402	1258	3.1
Monocot	209	1038	, ,	119	838		90	200	2.2
	·			•					
$\mathbf{Total}$	948	6487		456	5022		492	1458	

(a) London Catalogue, 11th ed., including all Rubi and Hieracia.

(b) BONNIER, Flore de France, Suisse et Belgique, Paris (1911-35).

(c) WILLKOMM and LANGE, Prodromus Florae Hispanicae, Leipzig (1861-1880; and Suppl. 1893).

(d) TURRILL, Plant Life of the Balkan Peninsula, London (1929).

Slightly greater numbers for British genera abroad, and other irregularities, are due to different conceptions of genera by different authorities.

Alike in all, nearly all the British genera occur, but while in BRITAIN the Dicots have only 1521 species, the same genera have 2019 in FRANCE, 3153 in SPAIN, 4184 in the BALKANS, the average number per genus being nearly trebled there. The same happens in the Monocots, but the number of species per genus is lower throughout, perhaps indicating greater youth. Their increase in proportion westwards perhaps suggests that the climate in BRITAIN is more favourable at any rate to that portion of them which consists so largely of grasses, sedges, rushes, &c.

The increased size of the continental flora is largely shown by an increase in species of the British genera, which are much larger than the non-British, though the increase of the latter in similar proportion indicates that they are not inferior in adaptation, as was formerly supposed. The Dicots increase more than the Monocots, again suggesting greater age in EUROPE. Their non-British genera do not outnumber the British, and their proportion of small genera is greater, both confirmatory points. British species are supposed to be specially well suited to BRITAIN, but it is clear that they got their adaptation to it in BRITAIN, for they are just as well suited to the other countries, often with very different conditions.

It is clear that it is in general the larger genera rather than the smaller that pass the barriers, and each successive flora is a reduced copy of the one before. That of BRITAIN is in general a reduced French flora, and in the same way the Scottish or the Irish is a reduced English flora, that of the ORKNEYS or the SHETLANDS a reduced Scottish, and so on (cf. PALMGREN, and my work on STEWART, CHATHAMS, &c). In such islands as NEW ZEALAND itself, or the HAWAHANS, however, it is not so easy to determine the origin or origins of the flora, for there must evidently have been different continental connections at different times. The help of geology becomes more and more necessary and important, as we shall see, the further back in time that one goes.

Land transport usual. GUPPY, who spent many years at this work, has shown (44, and cf. Age and Area, p. 17) that in the islands of the PACIFIC 90% of the plants have fruit that is not buoyant, and that could only be carried by sea under some accidental concurrence of circumstances. "DE CANDOLLE was quite right in minimising the effect of currents on the distribution of plants". "One can scarcely controvert KERNER's opinion that the dispersal of plants as a whole is not appreciably affected by this process." The writer and Prof. STANLEY GARDINER'S work upon the flora of the MALDIVES (162), a group of atolls about 400 miles from CEYLON, showed that the flora was simply a miscellaneous assortment of things that could be carried by water or otherwise, and as far as its composition went, might have come from any palaeotropical country.

Carriage by water could not but exert a selective action, for all seeds are not alike. But there is not the faintest evidence to show that this selection would on the whole pick out the genera with most species as those that ought to be carried, other than the fact that on the whole they are rather commoner. But the selection of the larger genera in any flora is somewhat too pronounced for this to be at all likely. And why is the change from FRANCE to BRITAIN, across water, like that from SPAIN to FRANCE, across mountains? Only land transport can explain such facts, and it is also not improbable that some mountains, like some straits, were at one time less of a barrier than they now are.

We have seen that the largest (oldest) genus of a family is the most likely to reach any given country, but there are many hazards that come in the track, and if conditions change rather rapidly, as in coming north, it probably puts a great strain on plants coming from the south, while genera born in the north will not have to encounter so much. Because a plant is not found (like *Hibiscus*, the largest Malvaceous genus), further north than the south of FRANCE, while *Malva* is common in BRITAIN, is no proof that *Hibiscus* cannot reach BRITAIN, given time enough for acclimatisation (cf. Age and Area, p. 29).

I have used as a working hypothesis for 40 years the supposition that such strains are probably the chief reason why new species and genera are developed, species with a moderate strain, genera with a greater.

Let us now look at the French Ranunculaceae, taking the facts from BONNIER (14). If, as we have suggested on p. 27, the oldest (largest) genera of a family are those most likely to be found near the outer edge of its distribution, we shall expect to find many of them in the British flora, while younger and smaller ones will gradually appear as we go southwards. In BRITAIN there are the first genus in the world (Ranunculus), second (Clematis), fourth (Anemone), fifth (Aconitum), sixth (Thalictrum), seventh (Aquilegia), eighth (Caltha), twelfth (Helleborus), fourteenth (Actaea), fifteenth (Trollius), and also the small genus Myosurus. Of the missing five, *Delphinium* (third) soon appears in FRANCE with one species, and has six more in the south of FRANCE, and a dozen in SPAIN; Isopyrum (ninth) has one species in FRANCE and SPAIN, Viorna (tenth, Clematis p. p.) occurs only in N. AMERICA, Nigella (eleventh) has three in FRANCE and five in SPAIN, and *Paeonia* (thirteenth), with three rather rare French species, is the first representative of the hitherto missing third subgroup Paeonieae, which, as has been pointed out in Evol., pp. 80-87, is a group of lower rank than the other two, arising rather from a secondary than a primary shoot of the family. The original parent of the family, Ranunculus, belongs to subgroup III, Anemoneae, hitherto regarded as the highest representation of the family, although headed by such very old genera. It is just possible that *Clematis*, which is of slower growth and travel, and seems more southern in origin, may be an original parent; cf. Evol. pp. 70, 135. Under the theories that we are here bringing forward, there is no absolute necessity for it to belong to the same genetic line as the rest.

It is clear that the laws of ASA have had much more to do with the distribution of the *Ranunculaceae* than have questions of adaptation, selection, or relicdom, and the same may be said of most families. It will be shown later that there is evidence of a general kind to show that these latter factors have also had a hand in the matter, though not a very important one.

While the "British" genera found in FRANCE average there about seven species each, the new genera found only average three, and their average world size is only 47 against 88. The nearer one goes towards the centre of distribution of a family, the more do the smaller genera in world size—the relics upon the older views—come into the picture, so that the average size becomes less and less. We may therefore predict that in any family the genera that occur in BRITAIN will average more in size in the world than do those in FRANCE, including in the latter those that also reach BRITAIN. The same thing will be repeated at the PYRENEES. Taking the *Cruciferae* as an example we find : — World size of genera of French Cruciferae, showing the differences between British and non-British genera

Brit. Not	$\begin{array}{c} 240 \\ 60 \end{array}$								
					j.			0	
Brit. Not	$20 \\ 6$		$20 \\ 5$						1
British to Non-Briti		$\frac{1282}{463}$							

The prediction is completely borne out, every "British" genus being larger than its corresponding non-British one. We may go on to predict that the latter (the younger) will have fewer species in FRANCE, and arranging the genera as above, we get : —

# Numbers of species in France of British and non-British genera of Cruciferae, added up in groups of five

Brit. 6 17 11 7 4; 9 4 4 3 5; 9 3 4 1 4; 1 2 2 4 3; 1 1 1 1 1Not 10 2 2 3 4; 1 3 3 2 1; 1 1 1 2 1; 1 1 1 1 1; 1 1 1 1; 1Totals of fives45/2125/1021/612/55/5

The 25 British genera average 4.3, while the 26 non-British only average 1.8. Again the prediction is borne out, and it can be seen how on the whole the number of the species diminishes with the size of the genera (in the *world*). Individual variation is great, probably showing, among other things, the local effects of the vital factors, but disappears when they are taken in fives. The same kind of variation, cancelling out in grouping, is shown almost everywhere, and goes to show that the action of vital factors in dispersal is too local and too variable to overwhelm that of the mechanical factors like time.

The Umbelliferae, taken in another way, may form a further illustration:

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	Britain	France	Spain	Balkans
British Genera/Species	34/59	34/102	34/148	34/218
Average size of genus (local)	1.7	3.0	4.3	6.4
Non-British		32/43	40/69	48/116
Average size		1.3	1.7	2.4
Percentage of non-Brit.				
genera		48%	54%	58%
Percentage of non-Brit.				
$\operatorname{spp}$ .		30%	32%	34%

British and non-British Umbelliferae in Europe

In this connection it is of interest to divide the Balkan flora into Dicots and Monocots, and these again into British and non-British : -

Balkan	flora	to	show	behaviour	of	genera	of	different s	sizes

Size of Genu	IS	Dico	ts		Monocots			
(species)	Brit.	Non-Brit.	Proport	tion	Brit. N	Ion-Brit.	Pro	$\mathbf{p^n}$
1	67	210	10 to 3	31	<b>42</b>	<b>56</b>	10 to	13
2	<b>36</b>	63	]	17	15	17		11
3-5	66	70	]	10	<b>23</b>	9		4
6-10	60	36		6	21	<b>5</b>		<b>2</b>
11-20	<b>55</b>	18		3	8			<u> </u>
21 - 30	20	<b>2</b>		1	8			
Over	33	3		0.9	• 4			

The proportion of non-British genera, high at first, especially in Dicots, rapidly shrinks, and most of the large genera are British. Most of the non-British genera are evidently recent arrivals in the BALKANS as compared with those that reach BRITAIN. The proportion of British Monocots is greater in the small genera.

As we have been pointing out for 40 years, all these statements are statistical, and must always be qualified by "on the whole", and not applied to single cases if one expect reliable results. It is still needful to remember a comparison I made many years ago. Statistics show that on the average, or on the whole, the Scot is  $1\frac{1}{2}$  inches taller, and 10 lbs. heavier, than the Englishman, but many people imagine that fact disproved by the subordinate fact that the English John Matthews is taller and heavier than William Ferguson. This latter fact is cancelled out by the superiority of James Howie to Ernest Lowe, and as many more Scots in proportion to the total are superior, the statistics show the superiority of the Scot.

To return to the figures of French distribution (p. 47), as all the genera behave in much the same way, we may devote our attention to *Ranunculus* itself, which in species makes up about half the family in northern EUROPE. We shall see that the species found in BRITAIN have a very wide dispersal indeed, as on the whole they were the oldest and the first to arrive. By the same law, those that only reach FRANCE will probably have less dispersal in the world. If we place the French species in the approximate order of their dispersal in FRANCE, we get:

Dispersal	of	French	spec	cies	of	Ra	inu	nculus,	in	approximate
		order	of	disj	perse	al	in	France		

Species	France (14)	Britain	Aver.	World
+aquatilis +repens +bulbosus +acris	Very common Very common Very common Very common	112	112	N. temp., Austr. N. temp. Europe, W. Asia N. palaeotemp.
+fluitans	Common	75		Most of Eur., W. As.
+divaricatus	Common	76		Eur., W. As.
+Flammula	Common	112	ų	N. temp.
+ Philonotis	Common	87	94	Eur., except far N.
+sceleratus	Common	104		N. palaeotemp.
+auricomus	Common	97		N. palaeotemp.
+Ficaria	Common	112		Eur., W. As., N.
		,		$\mathbf{Afr.}$

Species	France (14)	Britain	Aver.	World
+Lingua arvensis nemorosus	Rather common Rather common Rather common	l	93	N. palaeotemp. C. Eur. and Medit. Europe, except far N.
+ hederaceus + parviflorus	Here and there Here and there	$\left. \begin{array}{c} 112 \\ 62 \end{array} \right\}$	50	Eur., W. and N. Eur. W. and S., Medit.
+tripartitus nodiflorus macrophyllus muricatus falcatus	Here and there Here and there Here and there Here and there Here and there	3 J		W. Europe SW. Eur. Medit. Medit. C. Eur. and Medit.
+Lenormandi W +ophioglossifoliu		$\left. \begin{array}{c} r. 71 \\ 3 \end{array} \right\}$	37	W. Europe Medit.

Species found in BRITAIN are marked +.

and also eighteen other species, none of which occur in BRITAIN, described as Rather rare, Rare, Very rare, or in the case of the last twelve, mountain species, the actual locality given. None are endemic in, or confined to, FRANCE.

Roughly speaking, the dispersal of the French species, like that of the British, goes with their dispersal in the world, and all those above rather common, which show great dispersal in the world, occur in BRITAIN, while only two below the middle of the list have done so. The last dozen or so are very local, and chiefly montane. But as there is often a large gap between the mountains, as between the ALPS and the PYRENEES, they frequently show a dispersal that we call discontinuous, whereas we rarely apply this term to things far apart in BRITAIN. There is so great a difference in climate between the high mountains and the plains in FRANCE that the things of high levels could not cross, except under special circumstances, like colder climate.

When the species are taken in groups, the average dispersal in BRITAIN goes with the average dispersal in FRANCE, so that it is fairly evident that in large areas and in long time, the vital factors and the local conditions, so important in ecological and local dispersal, have but little to do with the general result which is the subject of geographical distribution, properly so called. It is clear that they treat alike no two individual cases.

Though the dispersal of the lower half of the species is small, none are actually confined to FRANCE itself, though in a few alpine species there is little overlap. Other members of the family, however, are very local; *Thalictrum macrocarpum* and *Adonis pyrenaica* are confined (*endemic*) to small areas in the PYRENEES, *Delphinium Requienii* to the little island of PORQUEROLLES, off HYERES, where it was probably formed by a recent mutation, and had not time for further dispersal before the island was cut off.

On the south side of the PYRENEES we find about 30 new Ranunculi, about half of which are endemic to SPAIN, while many others do not go very far beyond it. The term endemic is very loosely applied, and most people, being more or less politically minded, allow a Spanish species as an endemic, while refusing the title to one found in the smaller area of CEYLON and the southern end of INDIA, these being politically different. When one traces species about the world, as we have done for 40 years, and sees how they may be found on every size of area in the same genus, it is evident that a local endemic is, in the great majority of cases, a young beginner as a species. There is no evidence that these Spanish Ranunculi are relics of a previous vegetation, while it is possible that the widely dispersed species may be so in some cases, where some of the widely dispersed species may perhaps be able to survive a serious catastrophe, and go on again afterwards (cf. 57).

There is a regular progression in going northwards through EUROPE. In SPAIN there are species of enormous distribution like *acris* or *repens*, down to species of extremely local dispersal. In FRANCE there are less of these latter, so that the average dispersal there is greater, and in BRITAIN there are left practically only species of very wide dispersal indeed, which, by the law of age and area, are those that were also old enough to reach BRITAIN before the land connection was severed. The Spanish endemics, it may be noted, all occur in broken and especially in mountainous country.

Let us now follow the 15 largest genera of *Ranunculaceae* into many different parts of the world, to get an idea of their relative importance.

### J. C. WILLIS

## Occurrence of the 15 leading Ranunculaceae in 33 floras of different parts of the world

The object being merely to get an idea of the relative importance of the genera, any convenient and not too old flora has been used, the countries selected being LAPLAND, RUSSIA, BRITAIN, SPAIN, BALEARICS, SARDINIA, ITALY, BALKANS, CRETE, ASIA MINOR &c (BOISSIER), EGYPT, ALGE-RIA, AZORES, CANARIES, INDIA, CEYLON, MALAY PENINSULA, INDO-CHINA, HAWAHAN IS., NORTH AMERICA, BRITISH WEST INDIES, tropical AFRICA, NATAL, SOUTH AFRICA, MAURITIUS, AUSTRALIA, TASMANIA, NEW CALEDONIA, NEW ZEALAND, AUCKLANDS, CHATHAMS, CHILE, JUAN FERNANDEZ. The numbers of species of any one of the 15 genera in each of these floras are added together into total occurrences for each genus : —

	Genus	Floras in which it occurs o	Total ccurrences		Genus	Floras	Occurrences
1.	Ranunculu	ıs 28	743	9.	Isopyrum	7	13
2.	Clematis	<b>26</b>	181	10.	Viorna	1 (la	arge) 14
3.	Delphiniu	m 13	186	11.	Nigella	10	50
4.	Anemone	<b>21</b>	<b>148</b>	12.	Helleborus	9	42
5.	Aconitum	10	81	13.	Paeonia	9	31
6.	Thalictrun	n 15	133	14.	Actaea	9	11
7.	Aquilegia	12	47	15.	$\operatorname{Trollius}$	8	20
8.	Caltha	13	<b>29</b>				

The floras for Anemoneae (genera 1, 2, 4, 6, 10) add to 91, the occurrences to 1219; for Helleboreae (3, 5, 7, 8, 9, 11, 12, 14, 15) the floras are the same in number, but for nine genera instead of five, the occurrences only 479; for Paeonieae 9 with 31 only. Ranunculus has an overwhelming preponderance, with 743 out of 1729 occurrences in 28 out of 33 floras, missing only the MALAY PENINSULA, NEW CALEDONIA, the WEST INDIES, MAURITIUS, and JUAN FERNANDEZ, in all of which but the last, where Anemone alone appears, its place is taken by Clematis.

While the leading Anemoneae are more or less cosmopolitan, though their greatest concentration is in the northern temperate regions, the *Helleboreae* are almost confined to these, and the *Paeonieae* completely so. *Ranunculus* and *Clematis*, more particularly, are very widely spread, and it is clear that the genetic relationship between them needs further investigation, for *Clematis* (supposing that it is really a member of the same genetic series) is a more southern genus which looks as if it had been overtaken and passed by the herbaceous buttercups, and may really be the original parent of the family. *Ranunculus* is the only representative in the HAWAHANS and some other outlying islands, and is well over 60% in NEW ZEALAND, the CANARIES, LAPLAND, and CHILE, over 50% in BRITAIN, TASMANIA, SPAIN, and SARDINIA. The greater the isolation of the region, the greater the share that *Ranunculus* takes in the flora.

The Helleboreae centre in the eastern Mediterranean region, and *Delphinium*, their leader, though next in size after the two just mentioned, has only a small area of distribution in comparison with them, though it may have had more at some time. If there were an early catastrophe, as some people think, that only left Ranunculus and Clematis at a few widely separated places, from which they have since filled in the blank spaces, it may have reduced Delphinium -which as younger would probably cover less area-to its central part. It is quite possible that many fossils are really relics of such catastrophes that killed out the local things altogether, but left the old genera, which covered large areas, unharmed in some of their stations. It is to such occurrences that we owe the present wide, but discontinuous, distribution of so many of the large genera that are found in both worlds, with a vast expanse of sea dividing them.

We may take the Umbelliferae as another example. While BRITAIN has 34 genera with only 59 species, the proportion per genus increases as one crosses the continent, and BOISSIER's great Flora Orientalis, which covers the region of the eastern Mediterranean where the Umbelliferae are most common, shows 123/629, or over five per genus. The 34 British genera, just over a quarter of the genera in BOISSIER, have there 305 species, or nearly half the total, five times as many as in BRITAIN. Eight of the eleven genera in BOISSIER with more than 15 species are British. Even in NATAL, ten out of the 14 genera are British, and all seven of the CEYLON genera, and all the genera upon the HAWAIIAN IS. (4), JUAN FERNANDEZ (4), GALAPAGOS (2); and *Hydrocotyle* is the only genus in MAURITIUS and the SEYCHELLES. Six British genera in NEW ZEALAND have 35 species, while the other five have only 26. The British genera, evidently old, are well represented all over the world. The large Monocot families give similar figures, and we need not labour the point in this book, which is only a sketch.

Contour lines. What is evidently happening in thus traversing EUROPE is that we are crossing contour lines in the way familiar to all who know how to read and use a good map of hilly country, the contour lines being the outer boundaries of the areas occupied by the various species (cf. the map of Beta in Nat. Pfl. 16 c, p. 461, 1934). If there be not some boundary like sea or high mountains, which may stop at the same place various species arriving there at different times, one generally meets a genus one species at a time, and as one approaches the other side of its area, the species fall off again in the same way, as one may see the species of a genus diminish in going northwards through EUROPE. On the whole, the genera found in northern BRITAIN go as far as any European genera, and some of them, like Senecio, Ranunculus, Juncus, or Carex, are cosmopolitan or nearly so, and usually have a great many species, though this varies with the affinities and the habit, water plants, for example, usually going much further with fewer species, and herbs of open ground than trees. The 39 British genera marked in my Dictionary as cosmopolitan average 312 species each. Why, incidentally, should a cosmopolitan genus, which must, upon the Darwinian theory, have a good adaptation, need so many species, and why should related genera, but with fewer species, have smaller distributions?

When a species or genus is small, like the monospecific genera of Umbelliferae of the PYRENEES (Dethawia, Endressia, and Xatardia) or like the local species of other and larger genera found there, its area is clearly enough marked out by a line drawn though its outer localities. But as it slowly increases its area, it may go across, or more likely around, areas with unfavourable conditions, such as those with communities in which it cannot find a place. Deserts, seas, lakes, mountain chains, obstacles of all kinds, interfere with direct expansion from the original birthplace, so that the area ultimately reached may be very irregular, as is so often the case in the broken and hilly country of western EUROPE. A plant already established may be killed out somewhere by some change of conditions or other happening, unless this be slow enough to allow of functional adjustment. Or when a plant travels a long way it may come to some place whose conditions suit it admirably, and may there extend and multiply, perhaps giving rise to an unusual number of new forms. *Compositae* are especially common, not only around the Mediterranean, but also in places like CALIFORNIA or CHILE.

For most of its plants, BRITAIN is at the edge of the contour maps. But this is far from saying that the edges of all the contours reach the outer edge of the BRITISH IS.; comparatively few actually do so. Roughly half of its genera, and half of those of NEW ZEALAND, which occupies a somewhat similar place in the south, have only one species, the numbers of species increasing as one goes more inland and towards the equator. This of course means that the oldest, and therefore largest, genera in any circle of affinity will be near the edge of its distribution, as we have already Yet the conditions in BRITAIN are at least as varied as seen. in other European countries, so that it is evidently a very weak contention that is sometimes brought forward, that the great numbers of species at the centres of generic contour maps are due to the great variety of conditions there. This is especially emphasised when one finds that these centres are scattered all over the world, though they are rare in the colder parts, and tend to aggregate in such regions as the MEDITERRANEAN, (BOISSIER'S Flora Orientalis has 54/1 in 123 genera of Umbelliferae), or CHILE. In any such centre of genera (centre of creation in the pre-Darwinian expression), genera of one species (only) tend to be very numerous, which is a very remarkable fact if we accept the Darwinian view that such genera are relics; why should they be common at the very centre of prosperity? Some NEW ZEALAND contour maps are given in Age and Area, pp. 154-6-8, and one in Evol., Testcase XXVII, p. 151, and on p. 65 below.

Effect of climate. As the climate alters more rapidly to the south than to the east of BRITAIN, at any rate in warmth, it has long been, and still is, customary to put down the greater alteration of the flora in that direction to the greater alteration of the climate. But there are several factors concerned in these results, and they must be disentangled before we can feel safe in any assertion. Darwinism considers the structural alterations to be adaptational, but they are not so gradual as the changes of conditions, being rather mutational, with definite steps, small or even large, appearing at long intervals of time and of space. There is little or no evidence to show that they are in any way adaptational, except in a very few possible cases. But the alteration in the flora from one country to another is at bottom structural. Were it not for the structural differences, we should not see any change in the vegetation at all, except for such things as density upon the ground. One flora usually changes gradually to another by the disappearance of some species and the appearance of others, thus altering the ecological make-up of the flora, but there are few characters in the plants of a family that show any adaptation to the conditions. The small proportional difference as compared with the general mechanical progression shows how small a part is played by adaptation as compared with that of mere time.

There are a number of things that go together in this connection, and the difficulty is to make out which is cause and which effect, or whether any one of them is really cause, and there is not some as yet unknown factor behind it. Structural alterations are the only thing to show that evolution has gone on at all, and as Darwinism set out to explain evolution upon an adaptational basis, adaptational value was necessarily given to these changes of structure-a value which has very rarely indeed been shown to exist, in spite of all the desperate efforts made to prove it. A leaf probably assimilates equally well whether ovate or cordate, palmate or pinnate, and so on, to say nothing of the fact, brought out in Testcase X, Evol., p. 114, that the urge to improvement would fall off more and more the nearer the improvement came to perfection. Yet in actual fact, characters are usually shown in a perfect stage.

Adaptation under selection must be acquired gradually, but a great proportion of the structural changes are so distinct and widely separated from one another that they could only be acquired suddenly, and it is upon such prominent facts as these, and facts so universal, that we have based our theory that evolution was by sudden mutations, giving rise to new species, genera, or families at one operation. Structural differences thus acquired can hardly be looked upon as adaptational, but rather as incidents due to the mutation, for unless the new form is at once, upon birth, sufficiently adapted to its place to be able to survive there, it will at once be killed out by the action of natural selection. All survivors (with rare accidental exceptions) *must* be adapted and the adaptation is presumably functional rather than structural.

What chiefly changes the look of a flora in travelling through a country is the ecological alterations of local distribution that are to be seen, and which of course are mainly dependent upon changes of climate, soil, and other conditions. Compared to these, the actual changes in the composition of the flora are of much less importance, and we have seen how far one must go in order to find a great difference in taxonomic composition. Even in SPAIN or in the BALKANS about 80% of the flora still belongs to genera native in BRITAIN, and even in NEW ZEALAND about 46%. One might have to travel a long way to find a greater change in the botanical landscape than one may see in the short journey from the DERBYSHIRE moors to the LINCOLNSHIRE fens.

There is, however, a fairly sudden structural change between one species and the next, and only rarely does one find any kind of zone of hybridisation between them. It is probable, as we have tried to show in *Evol*., that the structural differences that distinguish one species from another have nothing directly to do with the climate or other conditions, and may be susceptible of a completely different explanation. Upon what interpretation of climatic effects can one explain the contour maps given by genera, with their centres scattered in all parts of the world, though principally in the warmer ones?

It is clear that to put down the increasing number and variety of species, in crossing EUROPE, and that especially in the British genera, to increasing differences in the conditions and climate, is to confuse the issue, for it is not to be supposed that the conditions in SPAIN should be two or three times as complex as in BRITAIN, nor those in the BALKANS still more so. Why should SPAIN need 499 *Leguminosae*, when BRITAIN is content with 90, and FRANCE with 287? Why should the BALKANS need 548? And why, incidentally, should *Leguminosae*, an obviously "successful" family, fall oft so quickly in numbers towards the north, as compared with some other families? The total number of them in BRITAIN is smaller than that of their endemics in SPAIN. It is worth notice that there are, in Mrs REID's list on p. 36, no Leguminosae, Cruciferae, Ericaceae, Chenopodiaceae, Polygonaceae, Liliaceae, &c. On the theories that we are bringing forward, a greater number of species at any one point is mainly due to the genus having been there for a longer time.

The conditional differences between area A and area B cause differences in the ecological make up of their floras, but flora A and flora B are both made up, by the work of natural selection, from the total flora that is available in that neighbourhood, and one can hardly doubt that if the total flora were larger, or if the dates of arrival of the species in the existing total flora had been different, the composition of the floras A or B might have been somewhat different. Ecology studies the flora A and its local dispersal, but distribution proper studies the whole flora X, of which A forms a part, and the movements of X and its members about the world in secular periods, and it is thus necessary to know how and when these members came into existence, or in other words to study their evolution in connection with their distribution.

To attempt to explain things that occur in large areas and in long time upon an adaptational basis, for which after all there is little evidence but wishful thinking, is to overstrain the capacity of any adaptational hypothesis, suitable as it is to local occurrences. The facts that we have described are quite inconsistent with any theory of gradual adaptation other than simply functional, but are easily explained by the laws of ASA, especially when supplemented by the theory of divergent mutation.