The Distribution of Plants in Perthshire in Relation to 'Age and Area'.

BY

J. R. MATTHEWS, M.A., F.L.S.,

Royal Botanic Garden, Edinburgh.

With two Figures in the Text.

A RECENT series of papers from the pen of Dr. Willis has made familiar to students of plant-distribution the theory which its author has styled 'Age and Area'. The principle has been fully worked out by Willis from the study of numerous floras, and the chief contention, that, *on the average*, the older a species is within a given country the greater area it will occupy, is one which is now generally accepted. A review of the hypothesis and of its manifest limitations has been given by Willis (1921).

The applicability of the theory to the flora of Britain may appear doubtful, since the effects of man's occupation are only too well known, the action of man being one of the modifying factors emphasized by Willis. Nevertheless, an analysis of certain portions of the British flora was undertaken by the present writer. The work resolved itself into a cartographic study, since the possibility of examining invasions became the chief point of interest. From this standpoint, a short paper, illustrated by maps, was communicated to Section K at the Edinburgh meeting of the British Association for the Advancement of Science, and abstracts have appeared in the 'Naturalist' (November 1921) and in the 'Journal of Botany' (January 1922).

A recent communication by Willis and Yule (1922) indicates that the distribution of certain *local* floras and certain groups of British animals agrees perfectly with the 'Age and Area' principle. When this paper appeared, I had just completed an examination of the distribution of plants in Perthshire, and since the facts are available they may serve to illustrate how far the hypothesis is applicable to a particularly interesting local flora and, at the same time, emphasize the complexity of the problem in so far as certain constituents of our flora are concerned. I have not sought to deal with size of genera within and without Perthshire. The facts which

I wish to present deal with the range of dispersal in Perthshire as determined by the number of districts occupied.

For botanical purposes Dr. White (1898) divided the county of Perth first into two primary regions, Highland and Lowland, the area of the former being a little more than twice that of the latter. A convenient boundary was found in the line of the 'Great Fault' which runs across the county in a south-westerly direction (Fig. 1). The Lowland area is further subdivided into five, the Highland region into eight districts, the boundaries being largely determined by the chief river systems. Within the Lowland

FIG. 1.

region, with an area of 842 square miles, only 91 square miles are over 1,000 ft. The Highland region extends to 1,747 square miles, embracing 1,346 square miles over 1,000 ft., 314 over 2,000 ft., and 17 over 3,000 ft., including 89 peaks which each exceed 3,000 ft., the highest being Ben Lawers (3984 ft.) in Breadalbane. We are thus dealing with a region presenting a very varied topography, with edaphic and epedaphic conditions which differ according to whether the Lowlands or the Highlands are concerned, and whose rivers and mountains present a succession of barriers to the migration of plants from one district to the next. If the application of the 'Age and Area' hypothesis throws any light on the distribution and migration of plants within this region, it may also prove a useful aid

in the search for a solution to the much-debated problem of the origin and distribution of the British flora as a whole.

So far as Perthshire is concerned, the following quotation from White's 'Flora' (1898) gives fair expression to the problem: 'I have been speaking of the British flora and Britain, but with the object of attempting to show that what concerned these in remote ages may have a more modern application to the Perthshire flora and to Perthshire. The various contrivances for the dispersion of plants, to which we have alluded, clearly indicate that the extension of the area of plants is for the benefit of the species. Perthshire is not cut off by the sea from the rest of Britain, therefore the methods by which the British flora reached Britain, when there was a land connexion, may have always been, and still be, operative as regards Perthshire in relation to the rest of Britain provided that climatic conditions are favourable, and that there is room.' It is clear that Dr. White held the view so consistently advocated by Mr. Clement Reid regarding the destruction of Britain's pre-glacial flora during the period of maximum glaciation, and on this view, that the Perthshire flora re-immigrated during post-glacial times, we may, without lengthy discussion on a debated question, proceed to examine the facts of present distribution.

There are 738 flowering plants admitted as 'native species' in the county, and their range of distribution, in terms of the number of districts they occupy, is shown in the following table:

TABLE I.

Occupying.	Number of species in Perthshire.	Percentage.	Same species in Britain.	Percentage.
1. Thirteen districts	190	25.7	258	35.0
2. Twelve "	113	15.3	72	9.8
3. Eleven "	42	5.7	77	10.4
4. Ten "	30	4.1	52	7.1
5. Nine "	34	4.6	58	7.9
6. Eight "	35	4.7	29	3.9
7. Seven "	41	5.6	30	4.1
8. Six "	36	4.9	18	2.4
9. Five "	27	3.7	18	2.4
10. Four "	31	4.2	32	4.3
11. Three "	43	5.8	31	4.2
12. Two "	41	5.6	28	3.8
13. One district	75	10.1	35	4.7

If we mark the rarity of these groups from one to thirteen simply, to avoid awkward fractions, the average rarity for the total number of species is 5.6, while for the same species in Britain, calculated on the same basis from vice-comital distributional data, the rarity is 4.4. Thus, within the limits of Perthshire, species are, on the average, not so widely distributed as they are in Britain. This might be expected from general considerations of geographical position, topographic, climatic, and edaphic factors. But

doubtless, also, the time factor is concerned, since, in general, species will have spread over a great part of Britain before they penetrate far into Perthshire.

Although a large proportion (46·7 per cent.) of the Perthshire flora possesses a wide range; occupying 11–13 districts, a not inconsiderable number of species (159, or 21·5 per cent.) is limited to one, two, or three districts. The numbers, as they stand, do not illustrate that regular descending series, from many of wide distribution to few of restricted distribution, which characterizes the ‘wides’ of Willis’s investigations. The figures do not give an entirely satisfactory ‘hollow curve pattern’. For we have, in fact, in Perthshire a flora comprising both the common and the rare, and the interesting question is how far this rarity may be due to recent arrival (we are not concerned with endemics) or to other causes.

Now, it is well known that many of the rare species in Perthshire are arctic-alpines, plants of the Highland region essentially. But a larger number of uncommon species belong, in fact, to the Lowland region, while a considerable number overlap, some being predominantly Highland, others chiefly Lowland. Along these lines a further analysis of the flora has been undertaken, the results being set out in Table II.

TABLE II.

<i>Occupying.</i>	<i>Widely distributed.</i>	<i>Chiefly Lowland.</i>	<i>Entirely Lowland.</i>	<i>Chiefly Highland.</i>	<i>Entirely Highland.</i>	<i>Totals.</i>
1. Thirteen districts	190	...	...	...	...	190
2. Twelve „	113	...	...	...	...	113
3. Eleven „	42	...	...	...	...	42
4. Ten „	30	...	...	...	...	30
5. Nine „	27	...	...	7	...	34
6. Eight „	20	...	...	6	9	35
7. Seven „	...	23	...	10	8	41
8. Six „	...	19	...	8	9	36
9. Five „	...	15	7	2	3	27
10. Four „	...	13	11	3	4	31
11. Three „	...	7	18	8	10	43
12. Two „	...	3	27	0	11	41
13. One district	...	0	40	0	35	75
Totals	422	80	103	44	89	738
Rarity	2·2	8·6	11·8	7·7	10·6	5·6
		4·7		9·6		
Rarity in Britain	2·2	5·2	5·9	7·0	11·3	4·4
		3·2		9·9		

In discriminating between common and rarer species it is only the number of districts occupied that is considered, and, for purposes of general discussion, widely distributed species are taken as those occupying eight or more districts. The division of the county into five Lowland and eight Highland districts has rendered necessary an extension of the analysis of the rarer Highland element beyond the limits imposed by the smaller number of Lowland districts.

The 'Age and Area' hypothesis is so well known that it is here unnecessary to do more than point out that at least certain of the results obtained above agree perfectly with the general aspects of the theory. The widely distributed species in Perthshire prove to be common species in Britain. In both the rarity is 2.2. Chiefly Lowland plants show a higher degree of rarity both in Perthshire and in Britain, and these, taken together with the widely-distributed species (i. e. 502 species out of a total of 738), exhibit a remarkably striking descending series, quite comparable with the 'wides' of Willis. But Perthshire possesses 103 rare, entirely Lowland species, as many as 40 of these being limited to a single district. The numbers run in the opposite direction from the 'wides'. Since these species are not endemics, their great rarity cannot be due to recent origin, but, on the view of 'Age and Area', to recent arrival within the county. They are confined very largely to Gowrie and Lowland Earn, where the bulk of the Perthshire flora seems to have entered, and they are thus possibly at an early stage of invasion.

These three groups, widely distributed, chiefly Lowland, and entirely Lowland elements, form the bulk (605 species, or 82 per cent.) of the county flora. They constitute an assemblage of temperate plants and their mass distribution suggests migration from the east, since this temperate flora is concentrated in the Lowlands, as many as 553 species occurring in the small area of Gowrie, while the average number for the five Lowland districts is 518, or 86 per cent. In the Highland region, Highland Isla possesses the largest number, 454 species, but the average number in the Highland districts is 380, or 63 per cent., only. There is thus indicated a pronounced thinning out of the temperate flora towards the interior and mountainous parts of the county, although it is true that many species have spread often far into the Highland valleys. In general, then, this portion of the county flora affords further evidence in favour of 'Age and Area', although the occurrence of an entirely Lowland group, of very marked rarity, may mean that other more vital factors result in certain species lagging behind the steady march of the main body. This is, of course, admitted, and will be due, generally, to ecological barriers, into the details of which in Perthshire we cannot here enter.

Another aspect of the problem arises when the Highland element of the flora is considered. This is largely composed of species which are the recognized arctic-alpine or, at least, boreal members of the British flora. There is no evidence from the facts of present distribution that these plants follow the law of 'Age and Area'. Nor shall we seek to apply it, since if the Highland species have a high degree of rarity, it is not because they are, in general, of recent introduction. We know from geological evidence that arctic-alpine species were formerly more widespread, an arctic flora occurring not only generally throughout Scotland in early post-glacial

times, but extending far south into England during late Pleistocene (Bennie (1896), Lewis (1911), Reid (1911), Chandler (1921)).

It has been estimated that about 13,000 years have elapsed since the beginning of emergence of Scotland and Scandinavia from the ice cap of the last glacial period. Since then an arctic flora has almost disappeared. Numerous species once occurring in Britain are now extinct. Those that remain are confined to our higher hills, and while they may not be visibly

FIG. 2.

disappearing, except from the extravagance of collectors, they must, on a long view, be regarded as relics of an outgoing flora. They are members of that palaearctic flora which once girdled the globe in high latitudes, and which, I believe, will be found to provide a greater number of relics than occurs in a tropical flora. The bulk of the returning, incoming temperate flora, which has replaced the earlier more arctic assemblage, I regard as of comparatively recent date. Much of it is due to and depends upon man's occupation of the country. But as man's migrations and operations must have been determined broadly by the time factor, so would the migration

of those plants which were directly or indirectly affected by human activity. Thus, the mass of the flora, a recent temperate assemblage, fits in, generally speaking, with the ideas expressed in the 'Age and Area' theory. Since the Highland plants are relics, their range will not depend upon age but upon other factors, and their curve of distribution may be, and in Britain is likely to be, irregular. The curve for the species in Perthshire is shown in Fig. 2, and above it is placed the curve for the temperate or general lowland flora. Further comparisons between the outgoing and incoming floras suggest themselves, but these are left for another paper which will deal with the entire Scottish flora.

SUMMARY.

The native flowering plants in Perthshire number 738, of which 605 (or 82 per cent.) belong to a lowland or temperate flora. This element is concentrated in the Lowland districts of the county and thins out in the Highland districts. The distributional data relating to these species, arranged according to number of districts occupied, furnish evidence to show that the general principle expressed in the recent theory of distribution termed 'Age and Area' is applicable to a county flora. Exception to the general bearing of the hypothesis is not unexpectedly found in the distribution of the remaining 133 species, which are essentially arctic-alpine or boreal plants. These, as proved by the fossil record, are relics of a northern flora formerly more widespread, and a gradual elimination since glacial times has produced their present discontinuity of distribution.

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