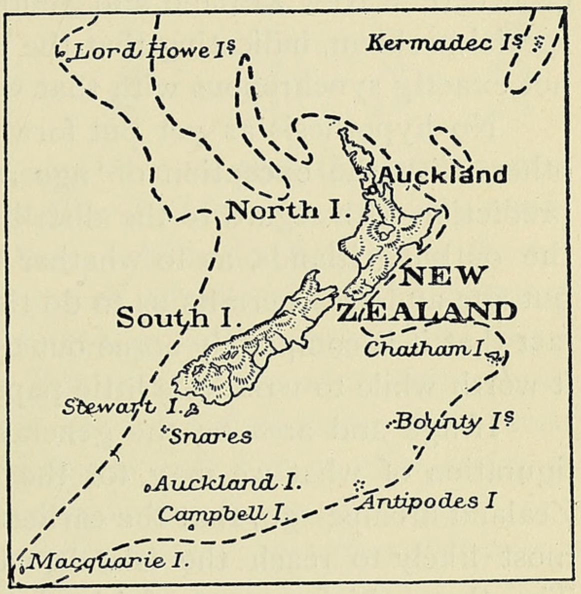
The Distribution of the Plants of the Outlying Islands of New Zealand.

BY

J. C. WILLIS, M.A., Sc.D.

With one Diagram in the Text.

IN a paper[1] upon the distribution of plants in New Zealand, I mentioned that the distribution of the plants in the outlying islands bore out in a very complete manner the hypothesis of age and area which was originally based upon the estimates given in Trimen's Ceylon Flora, and which was confirmed to the point of reasonable certainty by the distribution of the New Zealand flora, where estimates were replaced by actual measurements of longitudinal range in the islands.



New Zealand and outlying islands. The dotted line is the 1,000 fathom limit.

On the submarine plateau which soundings (given roughly in the accompanying diagram) show to exist around New Zealand, there are quite a number of islands or groups of islands, viz. to the north the Kermadecs (420 miles away), to the east the Chathams (375 m.), to the south the Snares (60 m.), Aucklands (190 m.), and Campbells (330 m.), to the south-east the Antipodes (490 m.), and to the south-west Macquarie (570 m.). It is fairly certain that at one time or another—it need not have been the same for all—all these were connected directly with New Zealand. East of them the Pacific Ocean descends to enormous depths, only exceeded at one spot upon the globe. It is therefore practically certain that the flora common to these islands and Australia must usually have passed through or near to, or have been evolved in or near to, New Zealand.

[1] Annals of Botany, vol. xxx, 1916, p. 437.

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The Kermadec Islands, it will be noticed, are divided from New Zealand by a greater depth than 1,000 fathoms at one part of the intervening sea. The ridge on which they stand leads to the Tongas and Fiji. Now the distribution of their plants in New Zealand does not exactly agree with that of the plants of the other islands, which are not divided from New Zealand by so great a depth of water. It agrees perfectly with my age and area hypothesis, but it shows several very special and interesting features, which tend to indicate that the period when the Kermadecs were united to New Zealand was not quite coincident with that of the union with the other islands. To work out the matter in detail requires geological aid, but my figures come out with such astonishing simplicity and accuracy that it is becoming increasingly clear that evidence based upon 'age and area' cannot be altogether neglected, even in dealing with geological problems.

We shall deal principally with the species common to these islands and New Zealand, or New Zealand and Australia, leaving out those only found elsewhere in New Zealand and South America, which again present a very special problem, indicating that the union with South America was perhaps not exactly synchronous with that with Australia.

No hypothesis as yet put forward, whether Natural Selection or any other, with the exception of 'age and area', will enable us to make any prediction with regard to the distribution *in New Zealand* of the plants of the outlying islands, as to whether they are or are not widespread there; but age and area permits us to do this. The prophecy is obvious, and the fact that it is completely borne out by the actual state of the case has made it worth while to write this little paper.

If age and area be the general rule, then it is evident from the configuration of what we may, for the purposes of this paper, term the New Zealand archipelago, that the earliest arrivals in New Zealand would be the most likely to reach the islands, whilst the later ones would not do so. The three chief groups of islands, which bear enough plants to make argument from their floras by age and area fairly safe, are the Kermadecs, Chathams, and Aucklands. Examination of the little map showing the soundings will show that they lie at more or less the same distances from the narrow strip of less than 1,000 fathoms which runs down from Australia, and which, in the absence of any evidence to the contrary, one must look upon as probably the centre of the line of immigration. It is safe to prophesy, however, that those plants which reach the islands will have been the first to reach New Zealand, and should therefore be more widespread there than those that do not reach them.

Let us now examine the Australian wides of New Zealand which also reach the islands, and classify them according to their range in New Zealand, as was done in Table VIII of the previous paper on that country, In that table (l. c. p. 449) the total of wides was given as 399. From this we have first to subtract the 98 species which are endemic to New Zealand and the islands only (dealt with below), as is done in Table X (l. c., p. 450), and then further to subtract the wides which reach New Zealand and the islands as well as Australia, 78 in all, and those going only to South America, 10 in number. The remaining 213 species, common to New Zealand and Australia but not reaching the islands, are given in the table.

Table I.

Class.	*Range in N. Z.*	*Kerm. Chath. Auckl.*	*Kerm. Chath.*	*Chath. Auckl.*	*Chath. only.*	*Auckl. only.*	*Kerm. only.*	*N. Z. only.*
1	1001–1080 m.	4	10	6	21	—	4	35
2	881–1000	—	4	—	10	—	5	39
3	761–880	—	—	—	2	1	—	26
4	641–760	—	—	—	1	1	1	28
5	521–640	—	—	—	—	—	1	19
6	401–520	—	—	—	—	—	1	17
7	281–400	—	—	—	—	—	3	12
8	161–280	—	—	1	—	—	—	14
9	41–160	—	—	—	1	—	1	7
10	1–40	—	—	—	—	—	—	16
Total		4	14	7	35	2	16	213
Rarity		1·0	1·2	2·0	1·7	3·5	3·6	4·3

An examination of this table discloses at once that the species that reach any of the islands are commoner in New Zealand—usually very much commoner—than those in the last column which do not reach them.[1] Those which reach all three chief groups of islands show the greatest commonness possible; those which reach two groups show less, and those that reach only one group less again. But there is one exception: those reaching the Chathams and Aucklands show greater rarity than those reaching the Chathams only. But the first are only 7 in number, which is rather few to be at all safe for deduction, especially as the single conspicuous exception in class 8 doubles the rarity without any other assistance; were it left out the rarity would be only 1·0.

This leads us to examine the exceptions, which are mostly very conspicuous in the table, and we shall find several points of interest. There are none in the first two columns, but in the third we find one in class 8. This plant, which instead of ranging the whole of New Zealand ranges only over Stewart Island and the south end of the South Island, is given in Cheeseman's Flora as *Carex appressa*, R. Br., and reference to that work shows at once that there is some doubt about the identification, both in New Zealand and in the Chathams. Incidentally it may be noticed, as a very strong argument in favour of my hypothesis, that when a species is found to behave very exceptionally in regard to its distribution—as

[1] Each unit of rarity represents a range of 120 miles, e.g. if 2·0 represents a range of 940 miles, 3·0 represents one of 820.

regarded from the 'age and area' point of view—it is almost always found to be one about whose identification or true nativity there is a doubt. This was well shown in the case of the exceptional number of 21 species found in the last class of the flora in place of the expected 5 or 6 (l. c., p. 452).

In the next column, the plants reaching the Chathams only, there is a conspicuous exception in class 9, *Pomaderris apetala*, which is of such interest that I have devoted to it the last paragraph of this paper. The 16 species in class 10 in the last column have already been dealt with in the preceding paper, as mentioned above. Nos. 2, 3, 4, 9, and 14 of that list range to the islands and are omitted here.

Now if we omit these exceptional cases, the order of rarity comes exactly into line with my hypothesis, the lowest being for the plants of two or three islands and New Zealand, the next for the plants of one group and New Zealand, and the highest for New Zealand only. But in any case, the plants which go to the islands are far commoner (more widespread) in New Zealand than the plants which do not. Now there is no conceivable reason why ranging also to a few little islands should make a species more widespread in New Zealand, unless it be age, which has given them time to spread in New Zealand to the maximum degree. The reverse hypothesis, that dispersal goes with youth, will be rather hardly pressed to explain why youth should ensure that a species should reach more islands. Nor, to go back to yet older views, is there any reason why great dispersal in New Zealand should ensure reaching the islands. If it were so, why were only 45 wides of class 1 selected, and the other 35 left behind, and why 19 of class 2 (instead of any of these 35), leaving 39 behind? It is evident that those which reached the islands were on the whole the first comers to New Zealand. The intermediate position of the species which range only to one group of islands renders the older explanations impossible.

Further consideration of what has been said brings out a very important point which may easily be lost sight of. Twenty species ranged the entire length of New Zealand, and got to two or more island groups; 25 to one island group; and 35 did not reach the islands at all. It is therefore evident that many of these last 60 once ranged to greater or less distances across land which is now submerged. In other words, *submergence may overtake spread*, and greatly reduce, even to extinction, the area occupied by a species. New species, therefore, have probably the best chance of survival and wide dispersal if they arise in the middle of a large continental area, and those that have the best chance of long survival are those which have been fortunate enough to disperse into areas so large that the chance of extermination by submergence or other catastrophe is least.

Other points of interest come out from an examination of Table I. The number of wides which reach two or more islands is 25, reaching one group only is 53, and not reaching any is 213. This indicates age as the chief factor. Further, in the last column, it will be noticed that though the numbers increase upwards, the highest is not in class 1, which reach Stewart Island, but in class 2, which range only the two main islands. This goes to indicate comparative youth, Stewart having been cut off before many of the plants could reach it.

It is thus clearly evident that the distribution in New Zealand of the Australian wides goes, not with the area covered in the world in general, but with that covered in the New Zealand archipelago, which was entered probably by a comparatively narrow connexion with Australia. This, it seems to me, completely excludes any explanation based on Natural Selection, whilst youth and area can only be made to explain it with the aid of supplementary hypotheses. It excludes the idea of absolute youth, and youth within the country is too far-fetched an idea to be tenable.

We may now go on to the species endemic to New Zealand and the islands, which in the previous paper were treated as wides. They occur nowhere else in the world. They, on my hypothesis, are younger than the wides already dealt with, and should be fewer in proportion to the endemics of New Zealand proper than was the case with those wides. In actual fact they are 98 to 902, against 78 to 213. None of them reach all three of the chief island groups, and only 19 reach two (8 the Kermadecs and Chathams, 11 the Chathams and Aucklands). It is therefore safer to reason from them as a whole, and they give the following table :

TABLE II.

Class.	*Range in N. Z.*	*Species.*
1	1001–1080 m.	41
2	881–1000	21
3	761–880	8
4	641–760	7
5	521–640	5
6	401–520	6
7	281–400	2
8	161–280	3
9	41–160	—
10	1–40	5

This gives an average rarity of 2·9 ; that is to say that, though confined to New Zealand and the islands only, they are far more common in New Zealand than the average of *all the wides* (3·5). The difference of 0·6 represents a range of 72 miles per species more than the mean range of the wides (760 m.). But in actual fact they should rather be compared with the 301 wides that are left after their removal, and these have an average range of 24 miles less, or 736 m. The dispersal of these endemics, however, as is required by my hypothesis, is less widespread than that of the wides which also go to the islands, which, if all be added together, gives a rarity of 1·9, or 120 miles more than the endemics (2·9).

Now, on the hypothesis of Natural Selection, or of youth and area, what conceivable reason can be given to explain why these endemics, which only range to a few small groups of little islands outside New Zealand, are yet more widespread in that country than the great group of 'wides'. Are these endemics younger than the wides as a whole, but older than the wides which reach the islands? If they are older, why did they not reach more islands? And why are they more widespread than the wides which reach to Australia, Asia, or South America, but do not reach to the islands? Nothing but age and area will explain these facts simply and reasonably.

Of the five endemics in class 10, four range far to the south through the Aucklands, only reaching Stewart Island of New Zealand proper, and the fifth, *Lepyrodia Traversii*, is a species as to whose correct identification with the one upon the Chathams I feel some doubt (see Cheeseman's Flora).

Now let us take the case of the species endemic to the islands only, and which do not occur in New Zealand. These, eighty in all, were omitted in my previous paper. None are endemic to the Kermadecs and Chathams, or to the Chathams and Aucklands, but a good many to more than one of the southern groups, which are not so far apart. This would be expected if they are the younger, for the wides would only reach the islands comparatively late. If we take those which are confined to the three principal groups, we obtain the following table:

TABLE III.

Islands.	*Wides.*	*Endemic to these islands only, and N. Z.*	*Endemic to these islands only.*
Chathams	72	50	25
Kermadecs	36	14	13
Aucklands	24	12	9

Twenty species are endemic to the Aucklands with the Campbells or other southern groups, but all but about three or four belong to South American genera. It will be noticed at once that, as in New Zealand itself, the larger the number of wides, the larger that of endemics, a fact very difficult to reconcile with the hypothesis of Natural Selection, or with the dying out of endemics on account of the competition of the wides.

It is thus clear that the floras of the outlying islands of New Zealand, and their distribution, give very conclusive evidence in favour of my hypothesis of age and area. In a later paper I hope to discuss the peculiar features shown by the species common, not to New Zealand and Australia, but to New Zealand and South America.

In conclusion, it may be noted that this work throws a side-light upon the much-discussed problem of the original home of the Maoris. It was mentioned above that *Pomaderris apetala* was a very conspicuous exception in the grouping of the flora common to New Zealand and the Chathams. It only occurs near to Kawhia, on the west coast of the North Island. Cheeseman remarks that 'the Maoris assert that it sprang from the rollers or skids that were brought in the canoe *Tainui* when they first colonized New Zealand'. It is fairly evident, from the figures, that this legend is quite probably correct, and therefore, as this tree only occurs elsewhere in Australia and the Chatham Islands,[1] that the Maoris came immediately from one or other of these places, perhaps most probably the former, as Kawhia is on the west coast. The origin of the Maoris remains a problem, but their route is perhaps made a little more clear.

Summary.

The distribution in New Zealand of the plants which also reach the outlying islands is here dealt with. Starting from my hypothesis of age and area, the prediction is made that the most widespread plants in New Zealand will be those that reach the islands also, and that those which do not reach them will be less widespread. This is confirmed by the facts in the most striking way, both in the case of wides and endemics.

The endemics which reach the islands are more widespread in New Zealand than the average of all the wides, a fact impossible of explanation by Natural Selection; the hypothesis of youth and area is placed in a difficult position to explain why the younger a species is, the more islands it should reach. The species endemic to the islands only are also grouped in a way very difficult of explanation on any other hypothesis than age and area—the more wides, the more endemics. Other facts are also brought up which render these hypotheses untenable.

It is shown that submergence may overtake spread, even to the extent of killing out a species.

Incidentally, a strong point in favour of my hypothesis is the almost certain way in which it picks out those species where there is doubt about identification or nativity.

[1] Eleven 'wide' species only occur on the islands without occurring in New Zealand, and of these four are Kerguelen species occurring only on the southern islands, and six are tropical forms only found in the Kermadecs. One only, *Leucopogon Richei*, occurs in the Chathams and Australia, and may be classed with *Pomaderris* as a case for which there must be some special explanation.