

The Sources and Distribution of the New Zealand Flora, with a Reply to Criticism.

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With seven Figures and Map in the Text.

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A NUMBER of reviews and criticisms have lately appeared, supporting or attacking my hypothesis of 'age and area'. Two (11, 12) by Professor Sinnott are of particular interest, and follow lines which he has more fully developed in earlier publications (13, 14). In replying to these criticisms I shall endeavour, as much as possible, to use new facts, or new presentments of facts, about the flora of New Zealand and its surrounding islands, a flora which is of great interest when examined in the light of age and area.

The employment of this hypothesis suggests new methods of attacking the facts of geographical distribution, and has led to the discovery of clear evidence in favour of certain hypotheses which in the past have been the subject of much discussion. It is, for example, as will be seen below, rendered probable that the peopling of New Zealand with plants was by way of land bridges, and that there were at least two of these, one northern, leading to some part of Indo-Malaya, and one southern. By the former the arrivals were mainly trees and shrubs, by the latter herbs. I regret that my reply must to some extent take the form of a criticism of the very interesting hypotheses that Professor Sinnott has brought forward in his various papers, but they are too important in their general bearings upon botanical and evolutionary science to pass without comment, especially as they do not rest upon definite proof, but upon a masterly presentment of probabilities.

Professor Sinnott's chief points, as I understand his papers, are :

- (1) That my hypothesis is an assumption.

(2) That I have not allowed enough for other factors that determine distribution.

(3) That the bulk of endemic species are 'relicts' and not new appearances, i. e. that they are in general older than the wides that are mingled with them; 'very many endemics owe their limited distribution to the circumstance that they are remnants of comparatively unsuccessful types which have been exterminated elsewhere, and which even in these isolated floras are waging a losing fight against more vigorous and adaptable new-comers.'

(4) That trees and shrubs are in general older than herbs.

(5) That age tends to the disappearance of old species. He 'regards isolation as a factor which tends not only to develop new species, but also to modify and extinguish old ones; and hence looks upon species in Ceylon and New Zealand which still maintain specific identity with their co-types on the mainland as the newest arrivals rather than as the most ancient members of the flora'.

(6) That age and area fails to explain the distribution of the New Zealand flora.

(7) Certain minor criticisms near bottom of p. 214.

I must begin by pointing out one or two instances in his papers where Dr. Sinnott shows that he has not quite clearly grasped the exact meaning of my work—no doubt on account of my imperfect presentation of it. In the first paragraph of his paper (11) he quotes my hypothesis without the very important proviso that it be only applied in cases of about twenty allied species, and then goes on to argue as if it were intended to apply in individual cases. He states that 'a highly specialized form, occupying a relatively narrow ecological niche, may in reality be much older than one which from its greater adaptability under diverse environments is able to thrive over a wider area'. Perfectly true, but it is in the highest degree unlikely that he would find twenty allied forms, or even a whole genus of more than five or six species, living in the same ecological niche, and in the rare cases where this does occur, one would not reason as to age.

On p. 215 he quotes the facts upon which I have founded my hypothesis, but omits the very important detail that not only is the area occupied by the wides greater, but they show their maximum number occupying the largest area, and the numbers are graduated down from this. The endemics, on the other hand, usually show the maximum number on the smallest area, and the numbers are graduated in the reverse direction, unless, as in the case of the species endemic to New Zealand and the islands, or the fern endemics, they are also very old. He likewise omits the important detail, which was what led me first to form the hypothesis, that the species of Ceylon and Peninsular India (and the same is true of those of New Zealand and islands) were on the whole intermediate in area occupied between those

of Ceylon only and those of wider distribution than Ceylon and southern India.

Professor Sinnott seems to think that I am propounding age and area as a kind of master-key that is to unlock everything. Naturally I have laid most stress upon it in my papers, for I am trying to get it established as a law. But it would be as reasonable to try to explain everything by it as to try to explain the upward movement of an aeroplane or a balloon by appeal to the law of gravity. What I am endeavouring to make clear is that, though plants (and I am inclined to think that it applies to animals also) are determined in their existing ultimate distribution by the operation of very numerous causes, they all obey as much as possible the law of age and area, which shows quite clearly in the figures of distribution of any group of plants, even though it may not always show in individual cases.

Contentions based upon probabilities cannot weigh so heavily against age and area as the very clear and decisive figures which have appeared weigh in its favour. These figures, it must not be forgotten, do not depend in any way whatsoever upon the acceptance or rejection of the hypothesis, but simply represent the plain unvarnished facts of distribution. They were discovered by aid of age and area, it is true (except the first ones relating to Ceylon, which originally suggested age and area), but that was simply because the hypothesis acted as a guide to directions in which to seek. This alone is a very powerful argument in its favour, that by its use one is able to discover new facts and new methods of looking at them, which may lead to advances in our knowledge of geographical distribution. It is quite impossible to predict by aid of Natural Selection what will be the actual facts of the geographical distribution of any plants in any country. For instance, one cannot predict the distribution in New Zealand of the plants of the Chathams, or that, to quote de Vries, 'the endemics with a small distribution are heaped up in the centre of the country', or again, that an endemic in New Zealand will occupy a greater area than in Ceylon.

Dr. Sinnott is inclined to say that 'so-and-so must be so', but these statements are sometimes rested upon assumptions which are rather difficult to prove. On p. 210, for example, he says, 'a species with means for rapid dispersal will evidently overrun a wider area in a given length of time than will a more slowly moving type', and on p. 214, speaking of new arrivals, he says, 'after its first rapid spread', therein assuming that under untouched natural conditions that spread is rapid. The facts at our disposal do not warrant such assumptions. We have all but no information as to spread under untouched natural conditions; the only material available refers to spread under conditions altered by man, whose interference in a country may rapidly become of supreme importance to dispersal of plants or animals therein.

In my 'Catalogue of Ceylon Plants' (15) is a list of 387 species known to have been introduced and more or less naturalized there, and the rapid spread of some of which, e.g. *Lantana*, has been used by the supporters of Natural Selection as an argument for the greater adaptability of foreign species to local conditions. In a recent paper (20, p. 197), I pointed out that this assumption ignores three important facts, (1) that foreign conditions have also been introduced, (2) that such weeds are also common in continental areas, and (3) that they spread just as much at the expense of the wides already in the country as of the endemics. We may supplement this by a brief analysis of the list. Of the 387, 204 are cultivated only, 47 are semi-wild cultivated plants found only near houses and gardens, and 125 are weeds of open ground, a feature which was almost unknown in Ceylon before the advent of man. This leaves only 11, of which two have only been once recorded, and have not been seen in recent times, and five exist only as clumps of two or three planted trees. There are thus only four left, of which *Passiflora edulis* might almost be added to the semi-wilds, as it is only found fairly near to places where it is or has been cultivated. *Bocconia cordata* and *Sapium sebiferum* have spread a few hundred yards down-stream from Hakgala Botanic Garden, and there remains only *Aloe vera* var. *littoralis*, which is common on the northern coast, and which is quite possibly a real native of Ceylon. The introduced plants of Ceylon are thus plants which are better adapted to the new conditions created by man, but that is all.

Even in the cases recorded of rapid spread of introduced plants, those without special mechanisms have often been dispersed just as rapidly as those with such. None of the Ceylon introductions has spread more quickly than *Tithonia diversifolia* (Compositae), which has no pappus, and has spread largely by vegetative methods. *Elodea* in western Europe was a similar case, and there are several others. It would seem *a priori* probable that the possession of means for dispersal should improve the chances of rapid spread, but there are few facts to support this view. An examination of the 'adaptations' for dispersal shows at once that they are usually confined to very small groups, and are therefore not very old, regarded from the general evolutionary point of view. In Compositae, practically the whole family has the same mechanism, and as it is usually regarded as young, it may be that its wide distribution in the comparatively short time is due to its possession of such a mechanism.

Dr. Sinnott, in bringing up objections to my hypothesis, to which he gives a much wider application than I have yet claimed for it, passes over without mention such extraordinary results as those given in the Tables IV, V, and VI of my New Zealand paper (19). It is perfectly obvious that such results must be explained, and it is almost equally obvious that no explanation other than that they are the result of a mechanical cause will

meet the necessities of the case. If the endemics are dying out, then they are dying out in a purely mechanical way, in 'wheels within wheels', whether they have or have not wides of the same genus beside them.

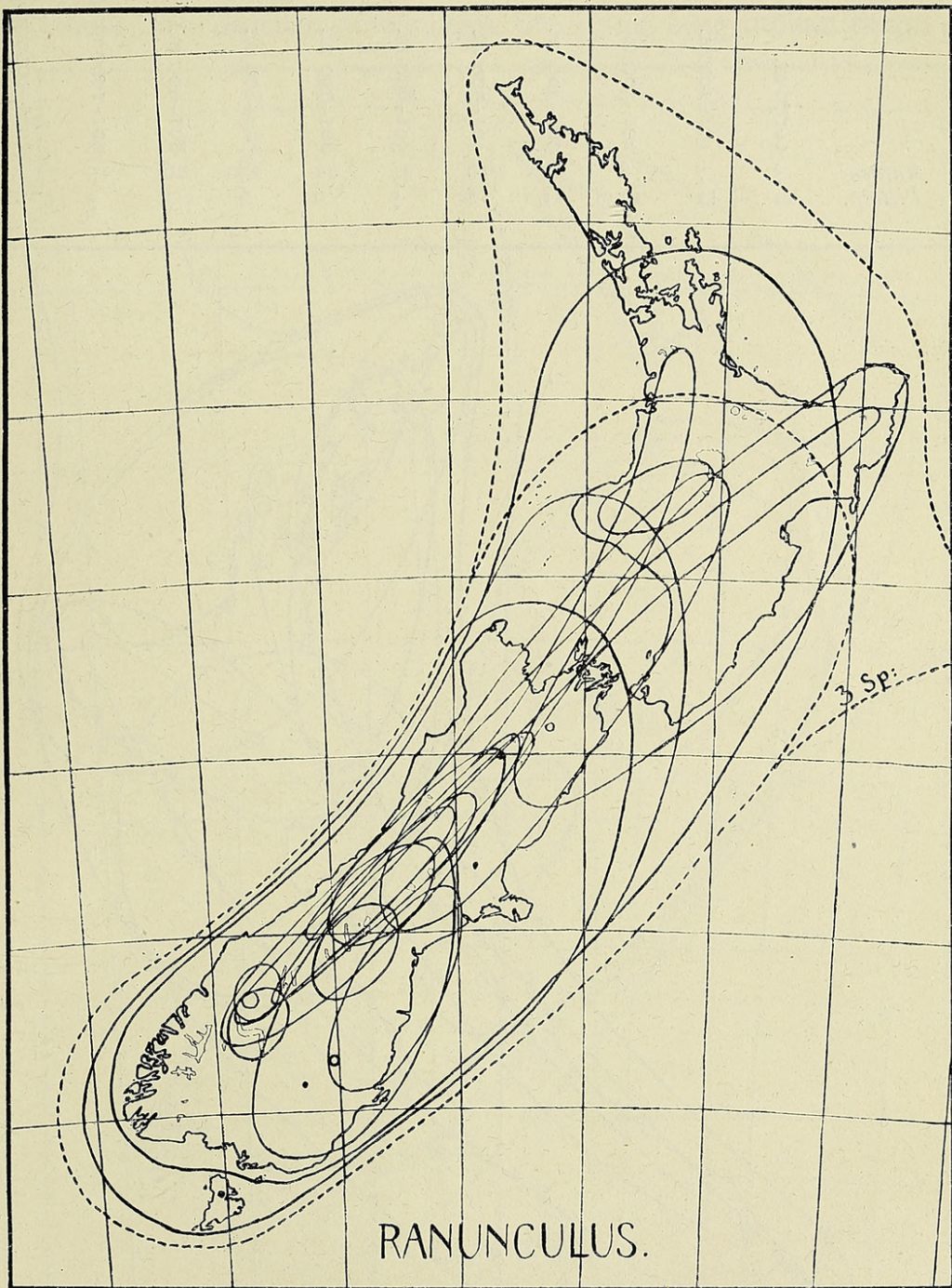


FIG. 1.

Wides dotted ; extension N. includes Kermadecs, E. Chathams.

Every single family and genus in the New Zealand flora shows one of two types of arithmetical arrangement in these tables. Either, as in Ranunculaceae, the endemic species occurring in each successive zone of 100 miles vary from a small figure up to a maximum and then down again,

or, like Pittosporaceae, they begin with their maximum to the north, and decrease southwards.

To save the trouble of reference I quote the figures for these two families :

	1-100 m.	101-200 m.	201-300 m.	301-400 m.	401-500 m.	501-600 m.	601-700 m.	701-800 m.	801-900 m.	901-1000 m.	1001-1080 m.
<i>Ranunc.</i>	3	7	8	13	16	21	21	28	26	15	3
<i>Pittosp.</i>	11	11	11	11	8	7	6	6	5	5	1

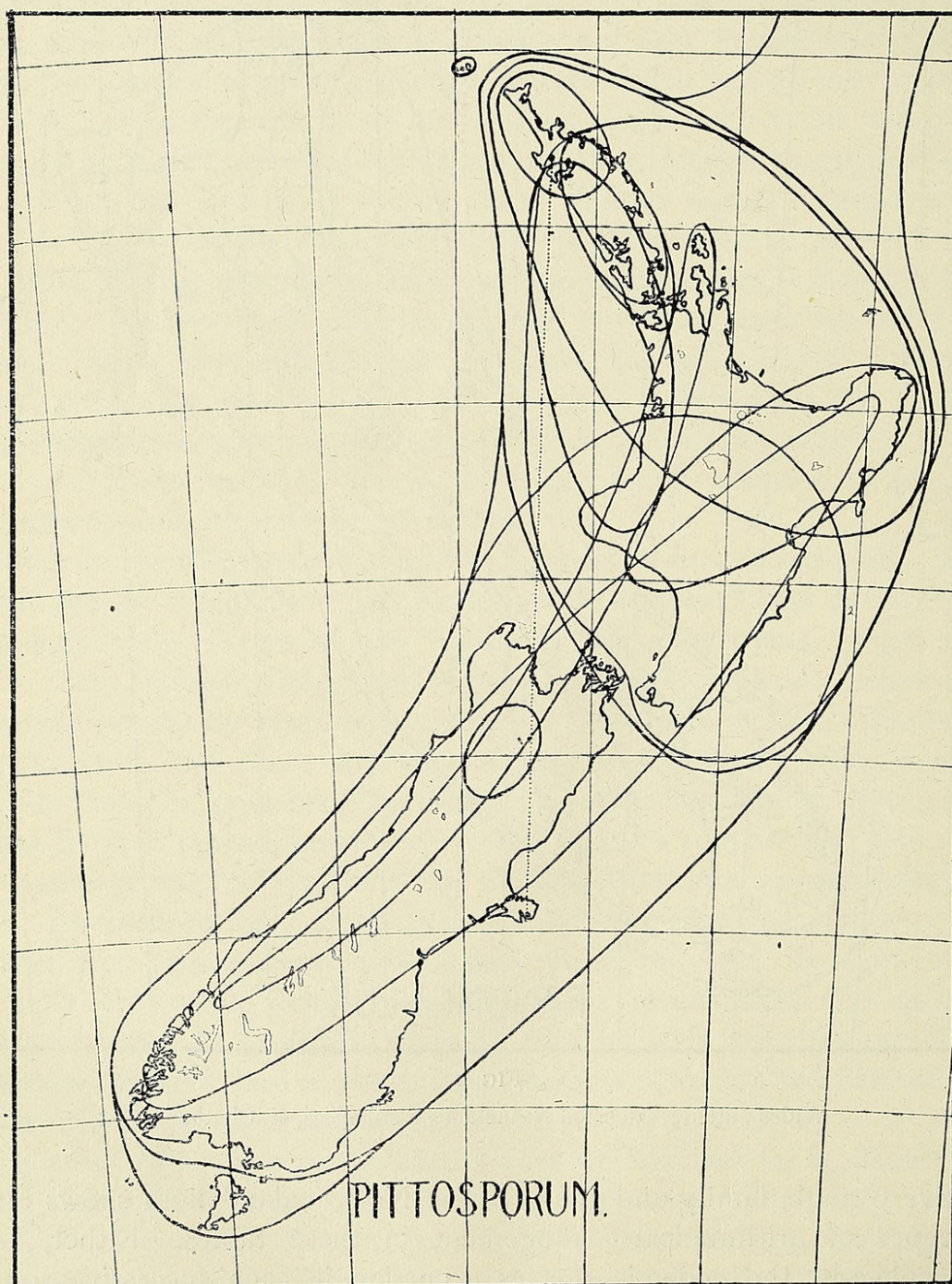


FIG. 2.

As I find that many biologists are not familiar with the method of handling these problems by aid of statistics, so that rows of such figures do not bring the facts clearly before them, I have in the diagrams 1-5 presented the result by a graphic method, showing roughly, by 'circles' drawn round their outermost localities, the actual longitudinal range of the

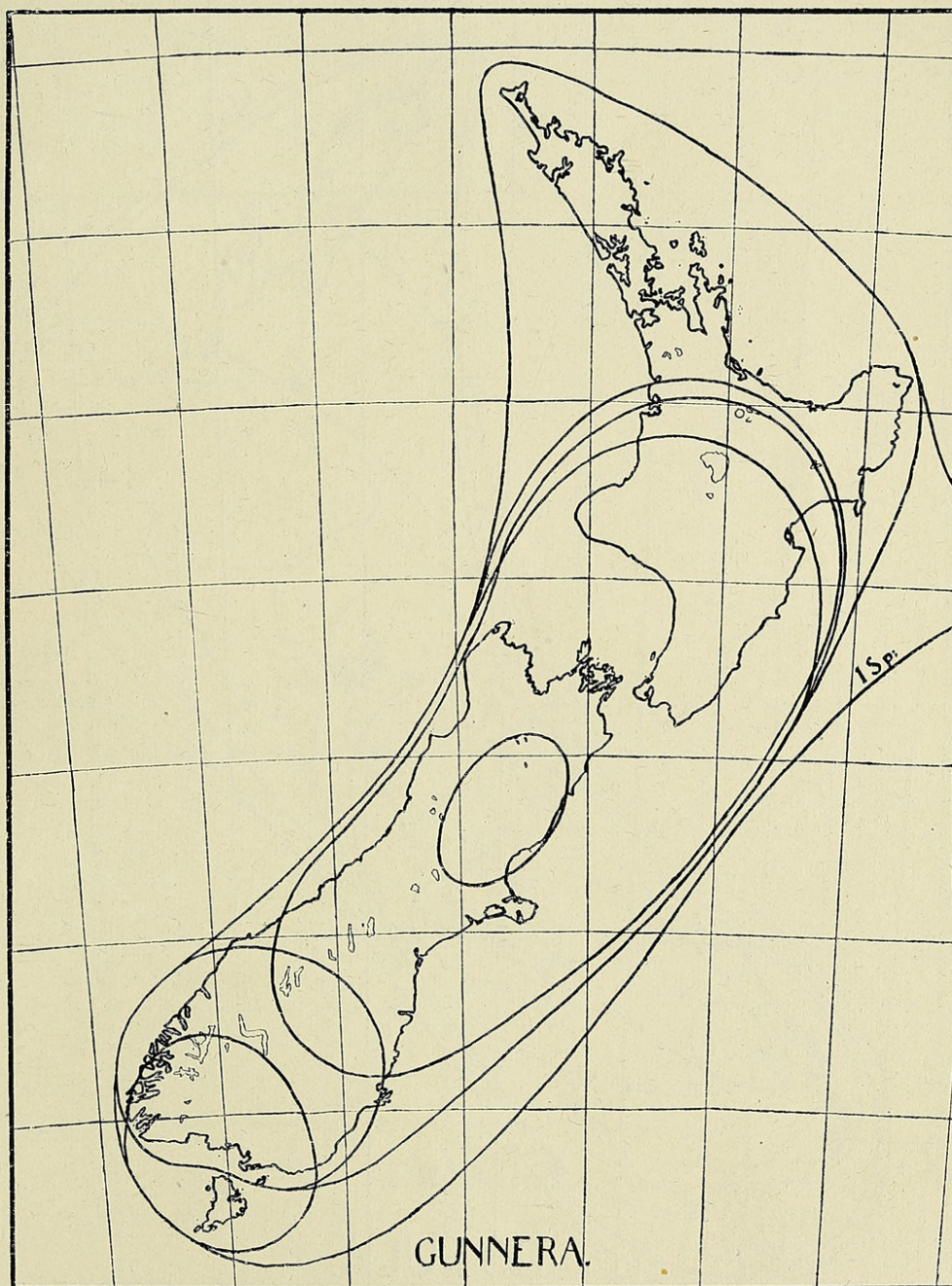


FIG. 3.

species in *Ranunculus* (genus with both wides and endemics, and southern maximum ; herbs), *Pittosporum* (endemics only, northern maximum ; trees and shrubs), *Gunnera* (endemics only, southern maximum ; herbs), and *Cotula* (wides and endemics, southern maximum ; herbs), as well as *Haastia* (endemic genus, southern maximum ; herbs). But it must be

remembered that every single genus in the whole flora would give such a diagram, reminding one of the ripples made by throwing a stone into water, and it seems to me difficult to maintain, in face of such facts, that the distribution of the species is not chiefly determined by a mechanical cause.

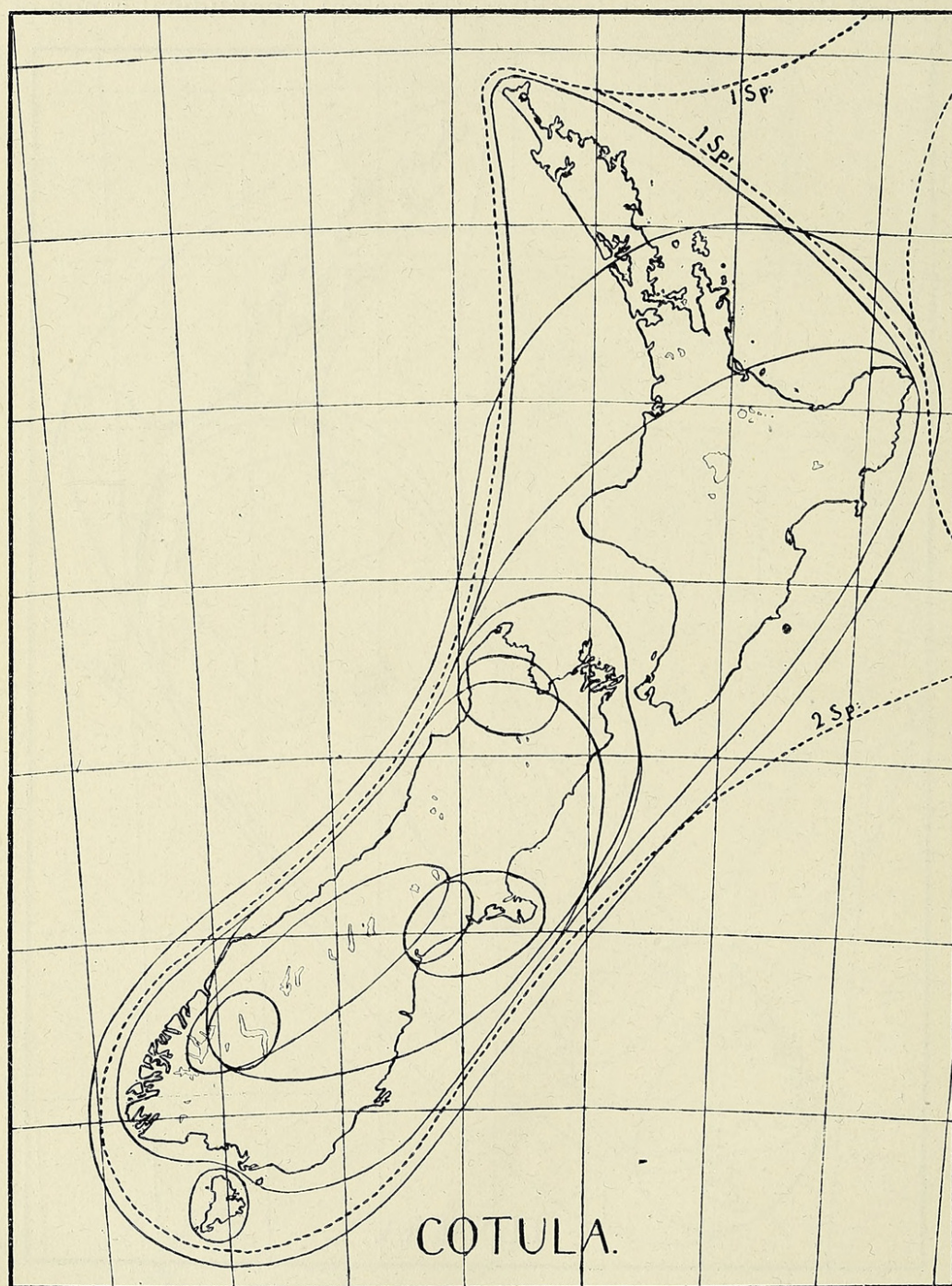


FIG. 4.

This cause I believe to be simply age. Whether the genus be Monocotyledon or Dicotyledon, tree, shrub, or herb, endemic or not, composed of wides and endemic species, or of endemics only, of Indo-Malayan, Australian, or South American affinity, it behaves in the same way.

To turn now to the principal points in Dr. Sinnott's criticisms, as given above, the first is that age and area is an assumption. Perfectly true, but so is Natural Selection, and it is no more improbable that area occupied should increase with age than that a well-equipped plant *A* should beat a less well-equipped *B* in the struggle for existence. Both seem fairly self-

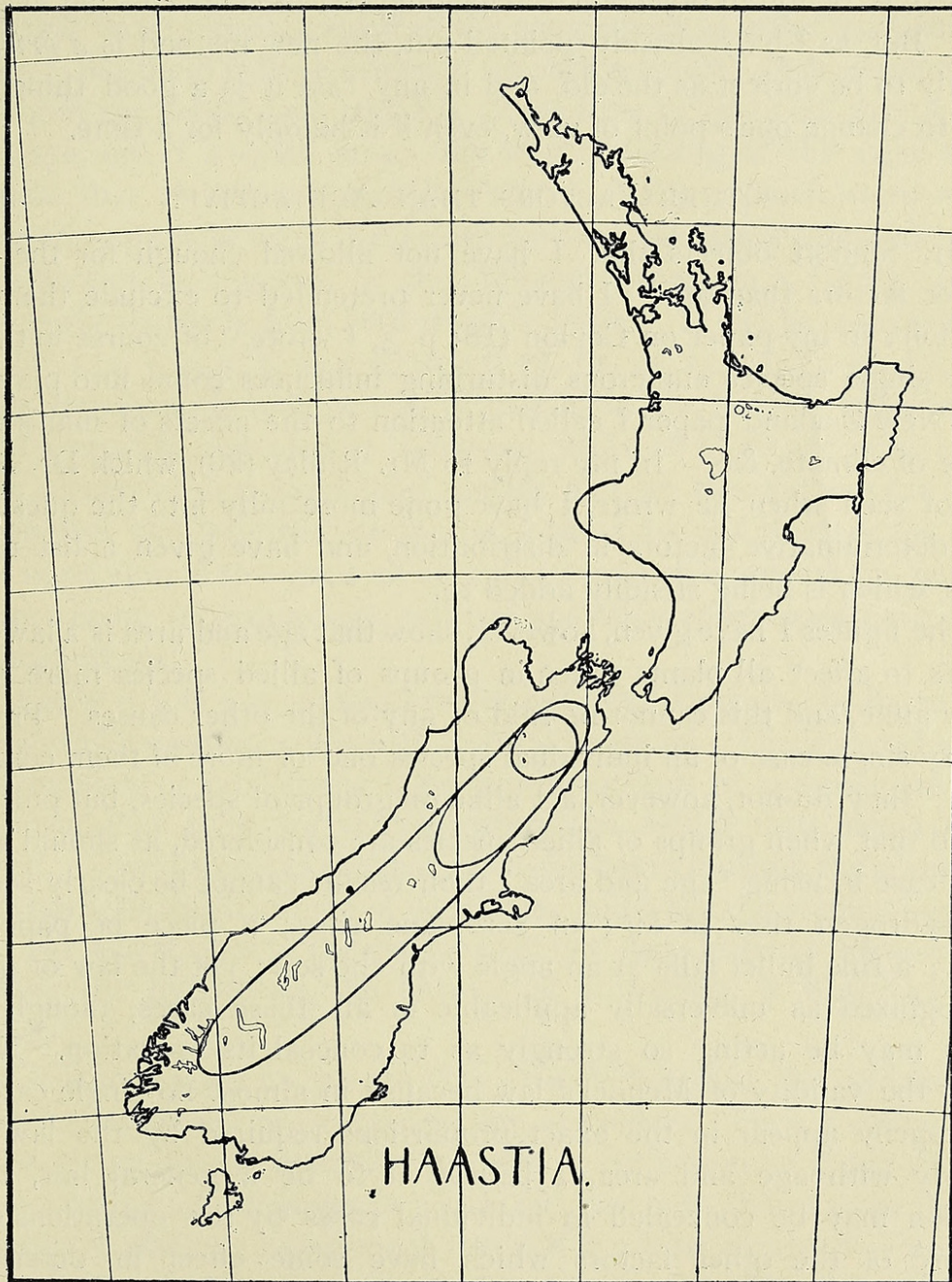


FIG. 5.

evident truths. But for the last fifty years Natural Selection, to the practical exclusion of everything else, has been regarded as the chief operative factor in evolution and geographical distribution. We are still, however, without any proof that it determines the area occupied by species, whereas actual arithmetical results of the clearest kind, which are rapidly accumulating,

speak in favour of age and area. Further, as I have pointed out above, prediction is possible under age and area, and impossible under Natural Selection, and, so far, all predictions made have been verified by the actual facts.

The objection to 'age and area' that many people profess, when analysed, is really an objection to changing the mode of looking at certain facts. But, as I have already pointed out, the new method is *a priori* just as likely to be correct as the old, and in any case it is a good thing sometimes to change one's point of view, even if it be only for a time.

OTHER FACTORS THAN AGE ACTIVE.

Dr. Sinnott objects that I have not allowed enough for the action of other factors than age. I have never pretended to exclude them from operation; in my paper on Ceylon (18), p. 5, I wrote, 'of course in the case of any single species numerous disturbing influences come into play', and in the New Zealand paper I called attention to the effects of man's action, change of climate, &c. In my reply to Mr. Ridley (20), which Dr. Sinnott had not seen when he wrote, I have gone more fully into the question of other determinative factors in distribution, and have given a list of such factors, which is being steadily added to.

The figures I have given, however, show that age and area is a law which appears to affect all plants taken in groups of allied species more or less closely alike, and this cannot be said of any of the other causes. Probably in every single case of an individual species one or more of them come into action; they do not, however, act alike on groups of species, but pull every way, so that when groups of allied species are considered, as should always be the case in using 'age and area', their results cannot be clearly seen.

Hydrogen rises in air; an aeroplane rises; a piece of paper falls slowly; a rifle bullet falls at an angle with the soil; yet the law of gravity is recognized as universally applicable in all these cases, though other factors may be acting so strongly as to conceal its operation. No one doubts the validity of Mendel's law because in almost no single case does the progeny appear in the exact proportions required by the law; and similarly with age and area, I believe it to be a general law, though its action may be concealed in individual cases by the operations of one or more of the other factors which have some effect in determining geographical distribution.

Age and area shows just as clearly in the Ferns as in the Angiosperms, and in both shows family by family and genus by genus, so that it is obviously a very ancient law, whereas the other factors are mostly such as only come into operation in individual cases, or, as in the case of Natural Selection, exert a differentiating action, with results which do not show in the figures for geographical distribution.

ARE ENDEMICS CHIEFLY RELICTS?

Dr. Sinnott takes the popular view, which is based, it must be remembered, upon an assumed efficacy of Natural Selection for which as yet there is little proof, that species with small areas of distribution owe the fact that those areas are small to the competition of other more successful types. But there is little evidence for such a belief. It is simply a way of looking at the actual fact, which is all we have to go upon, that *A* occupies a large and *B* a small area. My way of looking at the same fact is to suppose that *A* is older than *B*. This is really a much more simple explanation, especially when we remember that the areas occupied by the different species in a genus, or the different genera in a family, usually increase fairly regularly from very small to large. If one have areas represented by 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, it seems an unnecessarily oblique way of looking at the facts to say that 1, 2, 3, 4, and 5 must be regarded as dying out, while 16 to 20 are to be looked upon as successful and expanding species, and no two authors can agree about whether the intermediate species 6 to 15 are one thing or the other. It is far more simple to regard all as still in process of expansion, but that some, by reason of greater age and perhaps other advantages, have grown larger than others.

Not only is this explanation simpler, but predictions can be based upon it, a thing which was impossible with Natural Selection. I have already based quite a number of predictions upon my hypothesis of age and area, and have shown that they are verified when the actual facts come to be examined. Now it seems to me that when one has to consider the acceptance of an hypothesis which admits of prediction, and when the predictions made with its aid lead at once to the discovery of new facts hitherto unknown, and confirming the hypothesis, the balance of probability is likely to be in its favour.

Dr. Sinnott says, on p. 212 (11), that I disregard the evidence that many endemics are not of local origin, but are relicts. Here it seems to me that from giving special attention to cases of extinction he is apt to forget that the number of examples in which this has been shown to be likely is comparatively small. I very much doubt if it can be regarded as probable for even 1 per cent. of the endemic species of the world. There are certainly not ten cases in New Zealand, and the islands contain over 900 endemic flowering plants. Age and area simply shows that practically all endemic species in a given country behave in the same way, but cannot easily distinguish between those which were actually formed *de novo* in the country, and those that may have come in from outside over land now submerged. But if these species are endemic, then they must have originated, if not within

the country, at least not very far away. And often the local distribution enables one to decide.

The same criticism applies to the remark lower down on the same page, that 'we are familiar with many species, the range of which is widely discontinuous'. Here, again, the total number, though in itself considerable, is really very small when compared to those with continuous ranges. Again he says, dealing with the species of Ceylon (wides) which have discontinuous ranges and have co-types in Assam, and New Zealand wides which have co-types in South America, that a little more dying out would result in the production of forms definitely endemic in one of their present areas. Quite true, but he has to show that such a thing as *dying* out without change of conditions can occur. On my view a species may be *killed* out by submergence, great climatic change, or other catastrophe, but will continue to spread (following age and area) in the regions where it survives, so long as conditions there remain unaltered. In the case of the New Zealand species, the antarctic land that once connected them to South America has either disappeared or become incapable of supporting plant-life, and in the case of Ceylon and Assam there is good reason to suppose that the two were for some time separated by an arm of the sea, while in recent times, at any rate, the intermediate country has been dry, Ceylon and Assam being both wet. Though cut off from their co-types, the species of Ceylon and New Zealand behave in those countries exactly like the other species found there, and are arranged in graduated series in 'wheels within wheels'. It is impossible to reconcile the idea that *many* endemics are dying out with the regular graduation of species shown by my figures. One cannot conceive of species dying out in such a regular way, whether they have or have not wides beside them, whether they are endemic species in wide genera, or endemic genera, whether endemic with large or with small area, and the rest (cf. the distribution map of *Doona* (18, p. 14) and those given above).

Can Dr. Sinnott produce, on the hypothesis of Natural Selection, any shadow of a reason why *Ranunculus Lyallii*, perhaps the finest of the Ranunculi, should be confined to South and Stewart Islands in New Zealand, while *R. acaulis* and *R. rivularis* (wides) range New Zealand from end to end and reach the Chathams, and several endemics range into the North Island also? Other reason, that is, than the mere fact that such is the case. The natural selectionists assume, without facts to go upon, that this and other endemic species are dying out by reason of unsuitability. But in no single case can they say with certainty that a species is really dying out under unchanged conditions. In this particular case, for example, some would probably maintain that it was dying out, others would vehemently deny it. They cannot in the least define a size of area above which species are to be regarded as growing, or below which as dying out, and would apparently prefer to see the subject of the distributional areas

remain as incomprehensible, just as the special creationists considered was the case with the fact that such and such species occurred in one country, such and such in another.

The position of the natural selectionists is based upon assumption, whereas age and area is already supported by numerous incontrovertible facts, which are being rapidly increased by new work, and every prediction as yet made by its aid has been verified. Why does not *Ranunculus Lyallii* occur in the North Island, where there are fewer Ranunculi to compete with, fewer species of every kind, a less strenuous competition generally. Natural Selection cannot hope to explain this fact, but can only accept it as a fact, whereas age and area simply explains it as being so because it was not evolved in time to reach the North Island before the formation of Cook's Strait.

In many cases, no doubt, but in few compared to those in which it is not so, there is a certain amount of geological evidence of former greater spread, but that is no evidence that the species is dying out where it now exists, unless man has altered the conditions. It is almost impossible at the present juncture to lay too much stress upon the influence of man, for Natural Selection has been so largely supported upon evidence of what has happened under that influence, without any evidence that it would happen under unchanged conditions.

I have already been very fully into this question, but as it is the principal argument brought forward by those who are opposed to age and area, it may be as well to bring up other points in this connexion. I may commence by enumerating the chief points of a recent paper (20).

(1) The regular arrangement of my figures demands that youth be substituted in detail for age in my hypothesis, if endemics are to be regarded as older. This may be youth within the country, or absolute youth.

(2) Absolute youth is somewhat discredited by the fact that range within the country does not depend upon range outside.

(3) Youth within the country—the logical reversal of age and area—has no conceivable connexion with area occupied, and leads to various absurdities, besides involving much rising and falling in the scale of commonness (area of distribution) for which we have no warrant.

(4) The dying out (assuming that it is occurring) of the endemics is purely mechanical, every family and genus behaving in the same way, whether it has or has not wides, and whatever its habit of growth, its origin (local or foreign), or its distribution generally. The usual type of distribution is that shown in the distribution map of *Doona* (18, p. 14), or in that of *Haastia*, &c., above.

(5) The wides of New Zealand take no notice of Cook's Strait in their distribution, while the endemics do.

(6) The maximum of the wides coincides with that of the endemics, and both decrease together from that point, the endemics much the more rapidly.

(7) The specialized (later) and highly modified genera of Podostemaceae and Tristichaceae are all strictly localized; those that resemble ordinary water plants are widely scattered, and are just as common everywhere.

To these one may add the following notes and queries, which if not successfully answered, are very fatal to the view that endemics are chiefly relicts:

(a) How, on the view that endemics are relicts, is it possible successfully to predict what has already been successfully predicted by the aid of age and area?

(b) How are the facts of the regular graduation of species, of narrowly localized endemics up, and of wides down, to be explained at all?

(c) Why is there no difference in behaviour between endemic genera and species?

(d) Why does a genus behave in just the same way in New Zealand (for example), whether endemic with small area, endemic with large, endemic in New Zealand, endemic in New Zealand and islands, endemic in New Zealand and Australia, or endemic in New Zealand and the rest of the world?

(e) Why do all endemics show graduated maps like those given above?

(f) Why are the endemics of the same order of rarity in all families and genera?

(g) Why are the endemics of the same order of rarity whether there are or are not wides in the same genera?

(h) Why is an endemic genus the rarer the more species it has (17, p. 323)?

(i) Why should the islands round New Zealand have more endemics the more wides they have (21, p. 332)?

(k) Why are the endemics of New Zealand least numerous at the ends of the islands and not in the middle, and the wides the same (20, p. 201)?

(l) Why do the endemics that reach the ends of New Zealand range on the average so much farther than those in the middle (19, p. 448)?

(m) Why are the endemics still less numerous in proportion on the islands surrounding New Zealand than on New Zealand itself, and the wides more numerous? (N.Z. Wides/Endemics 301/902, Kermadecs 45/25, Chathams 69/76, Aucklands 27/72).

(n) Why do the endemics of both northern and southern invasions (cf. this paper, below) taper down in number with the wides, but much more

rapidly, so that in the case of the southern forms they are actually less numerous than the wides in five zones?

(o) Why, if endemics are being driven in by the wides, do their areas almost invariably overlap?

(p) Why are there practically no broken areas among them?

(q) Why do the Ceylon-Peninsular India species show a range on the average intermediate between the Ceylon endemics and the wides?

(r) Why are the species endemic to New Zealand and the islands so common in New Zealand, more so than the average of the wides in that country (21, p. 331), and why are the wides that also reach the islands yet more common again? What is there in ranging to these little groups of islands to make plants so well suited to New Zealand?

(s) Why should youth make a species more capable of spreading?

(t) Why should a species get to more islands the younger it is (21, p. 330).

(u) Why do endemics occupy so much larger an area in New Zealand than in Ceylon, even proportionately to the size of the country (19, p. 454)?

(v) Why do fern endemics, which must on the average be older, show greater distribution areas than Angiosperm endemics (22, p. 340)?

(w) If the wides are the younger, there is no reason why they should be specially closely related to the endemics, and why should they show the same arithmetical relationships throughout?

(x) Why do endemics and wides, in the majority of cases, belong to the same genera?

(y) Why do the wides give flatter curves for local distribution than the endemics?

(z) Why are the endemics so often on mountain-tops?

(aa) Why do separate species of endemics occur for different mountains near together (16, p. 132)?

(bb) Why do the endemics belong almost entirely to widely spread and successful genera, and this even more on the very isolated islands like the Chathams?¹

(cc) Why does the area covered in New Zealand go, not with that covered in the world in general, but with that covered in what I have called the New Zealand archipelago (21, p. 331)? This seems to me to exclude both Natural Selection and absolute youth.

¹ The Chatham endemics belong to *Geranium*, *Aciphylla*, *Pseudopanax*, *Corokia*, *Coprosma*, *Olearia*, *Cotula*, *Senecio*, *Sonchus*, *Cyathodes*, *Myrsine*, *Gentiana*, *Veronica*, *Carex*, *Poa*, *Festuca*. The Auckland endemics belong to *Ranunculus*, *Stellaria*, *Colobanthus*, *Geum*, *Azorella*, *Ligusticum*, *Coprosma*, *Olearia*, *Celmisia*, *Cotula*, *Abrotanella*, *Gentiana*, *Veronica*, *Plantago*, *Urtica*, *Bulbinella*, *Hierochloe*, *Deschampsia*, *Poa*.

THE RELATIVE AGE OF TREES, SHRUBS, AND HERBS, AND THE
SOURCES OF THE NEW ZEALAND FLORA.

Relative age is a very large question indeed, and I may be pardoned if I point out that for the present, at any rate, age and area is quite incompetent to solve it, though Prof. Sinnott so far extends the application of my hypothesis as to include that point among its possibilities. I have nowhere committed myself, so far as I can find, to an expression of opinion upon this question. These groups are ecological, not systematic, and nothing is more clear than that they are extremely polyphyletic, a fact which makes determination of relative age difficult. There are very few families composed entirely of trees or herbs, and even among genera there are many containing two or more forms. In Ceylon 87 show this, in New Zealand 12: these include such well-known genera as *Polygala*, *Hypericum* (in both countries), *Abutilon*, *Hibiscus* (in both), *Helichrysum*, *Senecio* (in both), *Dracophyllum*, *Solanum* (in both), *Euphorbia*, *Phyllanthus*, *Ficus*, *Urtica*, and many more. Even in such a markedly herbaceous family as Cyperaceae there is one tree, occurring in West Africa. Does Dr. Sinnott regard this as a solitary prehistoric Cyperacea now dying out?

Except in the case of genera, whose members are systematically allied, and where (17, p. 337) it appeared to me probable that their distribution 'in wheels within wheels', exactly like the species in any one country, was easily explicable on the hypothesis of age and area, I have only applied this hypothesis to groups of twenty allied forms within a given country. It might perhaps be possible to prove, by careful application of the hypothesis, that within New Zealand trees were older than herbs, but that would prove nothing as to the absolute age of either group, except that the trees were the first comers. Only if it could be shown that they were the first comers to most countries would it be possible to say that they were in reality the older group.

I have nowhere committed myself, so far as I can find, to the view that all plants occupying equal areas are of the same age, though I maintain that all are governed alike by the law of age and area. I have not attempted to decide, for instance, which of two genera or species, one a tree, the other a herb, is the older, when both occupy the same area in the same country. But in any case my figures show that each group is ruled by age and area, and a Dipterocarp (tree) with a radius of 200 miles in all probability bears the same relationship in age to one with a radius of 100 miles as does a Composite (herb) with a radius of 200 to one with one of 100. *A priori* it would seem probable that the herb would spread the more rapidly, but one must remember another complication, that some herbs are of open

ground, and cannot spread in forest, others are forest herbs and cannot spread in open ground.

Dr. Sinnott argues as if herbs could of themselves, without outside assistance of some kind, supersede and replace forest. There is little evidence for this, though the fact that trees can replace herbs is familiar to every one who has lived in the midst of forest vegetation. So far as I am aware, some extraneous assistance is needed for the reverse to happen, such for instance as the operations of man, or a desiccation of the climate.

So far as age and area is concerned, trees, shrubs, and herbs all behave in exactly the same manner. Except in the position of the maximum there is no difference to be seen in the figures quoted for the genera in Tables V and VI (19, p. 446). All show a gradual increase to a maximum, usually in the South Island, and a falling away again, or an increase to a maximum at the north, as in *Pittosporum*. Yet *Clematis* is shrubby, *Ranunculus* and *Lepidium* herbaceous, *Pittosporum* is composed of trees and shrubs, *Carmichaelia* is shrubby, *Tillaea* herbaceous, and so on.

Another point that Dr. Sinnott is apt to forget is that trees, shrubs, and herbs may come to a country from different sources, so that the tracing of their relative ages is rendered still more difficult. In this connexion it is worth while to see what can be learnt about New Zealand from a consideration of Tables IV, V, VI of my paper (19). Though the discovery of the facts contained in these tables was the result of a prophecy made by aid of age and area, the tables themselves contain nothing but bald facts. One of the first points that one notes is that whilst the majority of the families (and genera) show figures leading up to a maximum in the south, and falling away again (and that quite regularly for every family and genus in the flora), a very fair number, e. g. Pittosporaceae or Myrtaceae, commence with their maximum to the north, and taper away towards the south. Whatever be one's views as to age and area, it is quite clear from the tables that the previous distributional history of these families was different from that of the others. Table IV gives only endemic species, but if we add to them all the families with northern maxima, we get the result shown in Table I, below.

The first glance shows that all these families are markedly Indo-Malayan, though they contain in New Zealand a few genera whose southern location indicates a southern derivation, and indeed some of them, like *Laurelia* in Monimiaceae and *Donatia* in Saxifragaceae, are South American genera. But the overwhelming majority are Indo-Malayan.

TABLE I.

Family.	Shrubs and Trees.			Herbs.		
	Wide.	N.Z. and Islands.	N.Z. only.	Wide.	N.Z. and Islands.	N.Z. only.
1. Pittosporaceae	—	1 (K.)	18	—	—	—
2. Rutaceae	—	1 (K.)	2	—	—	—
3. Meliaceae	—	—	1	—	—	—
4. Olacineae	—	—	1	—	—	—
5. Rhamnaceae	3 (1 Ch.)	—	2	—	—	—
6. Sapindaceae	1	—	1	—	—	—
7. Anacardiaceae	—	1 (K., Ch.)	—	—	—	—
8. Saxifragaceae	—	—	7	1 ¹	—	—
9. Myrtaceae	1 (Ch.)	1 (Au., Cpl.)	16	—	—	—
10. Passifloraceae	—	—	1	—	—	—
11. Cucurbitaceae	—	—	—	1 (K.)	—	—
12. Araliaceae	—	2 (K., Au.)	12	—	1 (Snares)	—
13. Cornaceae	—	—	4	—	—	—
14. Caprifoliaceae	—	—	4	—	—	—
15. Sapotaceae	1	—	—	—	—	—
16. Oleaceae	—	—	4	—	—	—
17. Apocynaceae	—	—	2	—	—	—
18. Lentibulariaceae	—	—	—	1 ²	—	5
19. Gesneriaceae	—	—	1	—	—	—
20. Myoporaceae	—	1 (K., Ch.)	—	—	—	—
21. Verbenaceae	1	—	2	—	—	—
22. Nyctaginaceae	1	—	—	—	—	—
23. Amarantaceae	—	—	—	1	—	—
24. Piperaceae	1 (K. Ch.)	—	—	2 (1K.)	—	—
25. Monimiaceae	—	—	2	—	—	—
26. Lauraceae	—	—	3	1 ³	—	—
27. Proteaceae	—	—	2	—	—	—
28. Santalaceae?	—	—	2	—	—	—
29. Balanophoraceae	—	—	—	—	—	1
30. Urticaceae	—	1 (Ch., Au., Ant.)	4	3 (1K.)	—	1
31. Palmae	1 (Ch.)	—	—	—	—	—
32. Pandanaceae	—	—	1	—	—	—
33. Typhaceae	—	—	—	2 (1K.)	—	—
Total	10	8	92	12	1	7

The islands reached by some of the species (K., Ch., Au., &c.) are shown in brackets.

To these may probably be added Magnoliaceae, Ficoideae, Convolvulaceae, Solanaceae, and Chenopodiaceae, as well as parts of such families as Malvaceae, Tiliaceae, Orchidaceae, Liliaceae, Cyperaceae, Gramineae, &c., and many single genera in other families.

From this table one may at once draw an important conclusion. If one mark the zones in which the different species occur, one gets the result :

TABLE II.

	1-100 m.	101-200 m.	201-300 m.	301-400 m.	401-500 m.	501-600 m.	601-700 m.	701-800 m.	801-900 m.	901-1000 m.	1001-1080 m.
Wides	13	11	12	10	8	8	7	7	6	5	3
Endem.	84	89	87	78	64	62	50	40	35	32	14

¹ *Donatia Novae Zelandiae* : range 480-1080 m. and Tasmania ; S. American genus.

² *Utricularia monanthos* : range 380-1080 m. and Tasmania ; probably arrived from south.

³ *Cassythia paniculata*, perhaps an introduction, but cf. Guppy, *Nat. in Pacific*, p. 56, &c.

The falling off from north to south is extremely regular. If we plot these figures in a curve we get the result shown in Fig. 6. Both fall off from north to south, but the endemics fall off much more rapidly; both have maxima and minima at the same points, or practically the same. Nothing as yet proposed but age and area will explain such curves as these. The wides are older, and have mostly spread so far down New Zealand that their curve is nearly flat: the endemics are younger, and have only spread to varying distances down the islands, so that their curve rapidly falls off. In face of a curve like this one cannot maintain that the wides are killing out the endemics.

Now if these families had arrived in New Zealand by casual transport across the sea, it is very difficult to believe that their arrangement would

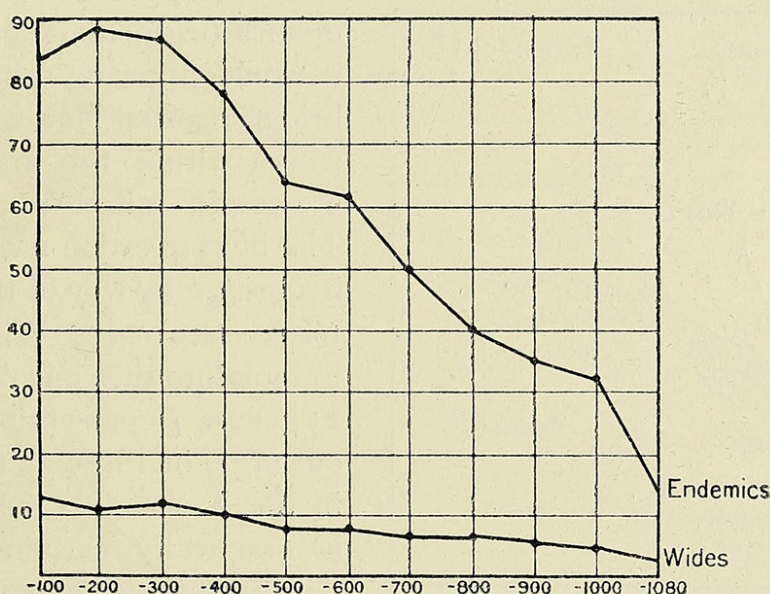
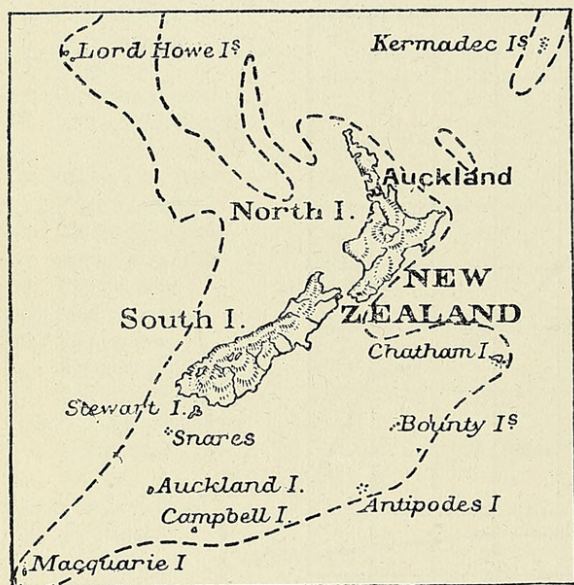


FIG. 6.

have shown such symmetry. It would seem much more probable that they arrived at some comparatively narrow point of entry in the north. The diagram on p. 442 (19) gives an idea of what may happen under age and area, and shows that the maximum of endemics is to be expected at or near the point of entry. In connexion with this diagram, as Dr. Sinnott and others say that my whole argument about New Zealand hinges on the fact that I commence with an hypothetical entrance of the flora at the centre, it may be worth while to point out that the result will be similar wherever be the point of entry, the maximum of the endemics always being near to that point. Further, it is not absolutely necessary that it be a *point* of entry; the result would be similar if it were a belt of entry. If, for example, the entry were by the whole belt from 300 to 700 miles, above E 2 and 3, we should get a zoning

0 2 4 7 8 7 6 2 1 1

The curves for the species of this northern invasion give one to imagine that the point of entry was comparatively narrow, perhaps not very much wider than one or two of the zones of 100 miles into which I have divided the islands. As New Zealand is mountainous throughout, it is possible that birds, which would be likely usually to land in the same hills, might have brought the plants, but many of them have seeds very much unsuited to bird transport. It would therefore seem probable that they must have arrived by some *land* bridge, and the same applies to the remainder of the flora, which shows a southern maximum. This is not denying that casual transport may occur, and indeed there are cases, like *Ipomoea palmata* on the northern coast, whose limited or peculiar distribution is more readily explained in this way than by a land bridge. As after 300 miles from



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

North Cape both wides and endemics begin markedly to fall off, it would appear probable that the bridge reached New Zealand somewhere within the first 300, or at most 400 miles from the north. The next question naturally is, was it a bridge by way of the Kermadec Islands (see map)? When one comes to look into this, one finds that only 11 genera (representing 10 families) out of 60 in these 33 families occur in the Kermadecs, and of these it is practically certain that some, e. g. *Sicyos*, are genera which really entered by way of those islands.¹ It would therefore seem probable that

the connexion by which these families entered was not that way. But as they are all represented in tropical Australia, which is part of Indo-Malaya, it would seem likely that one of the two strips of shallow water shown in the map as running down from NE. Australia represents the remains of the bridge by whose means they arrived.

Passing on now to the constitutional habit of these plants, which is given in the table, one notices at once that they are nearly all shrubs and trees, only 20 out of 130 being herbs. The proportion of trees and shrubs is no less than 84 per cent. And of the 110 no fewer than 46 are trees, out of a total of 72 trees in New Zealand. If we add the other families of probable northern origin, we get a total of 48 trees. In any case it is clear that the bulk of the trees in New Zealand arrived from the north, or were evolved from or in genera that arrived in this way.

¹ The question of the union of New Zealand and the islands will be discussed in later papers.

When we examine the zoning of these species, given above, it is clear that on the whole they are very old in New Zealand, for they take no notice of Cook's Strait, between the fifth and sixth figures, and comparatively little of Foveaux Strait, between the tenth and eleventh. But this is no proof, without much confirmatory evidence from other countries, that they are absolutely very old.

If from the list of families we exclude these which have just been considered, it will be noticed that all the rest have their maximum of species to the south, sometimes towards the north end, sometimes towards the south end, of the South Island. If we take only those families which have a maximum in the zone 701-800 miles¹ (south of North Cape), or to the south of that, we get the following list of families :

TABLE III.

Family.	Shrubs and Trees.			Herbs.		
	Wide.	End. N.Z. and Islands.	N.Z. only.	Wide.	N.Z. and Islands.	N.Z. only.
1. Ranunculaceae	—	—	9 ²	6	—	30
2. Cruciferae	—	—	—	4	2	16
3. Caryophyllaceae	—	—	—	5	2	8
4. Portulacaceae	—	—	—	2	—	1
5. Rosaceae	—	—	4 ³	5	—	7
6. Droseraceae	—	—	—	5	1	—
7. Haloragidaceae	—	—	—	9	1	9
8. Onagraceae	—	—	3 ⁴	4	7	17
9. Umbelliferae	—	—	—	10	1	43
10. Stylidiaceae	—	—	—	—	1	6
11. Campanulaceae	—	—	—	2	2	7
12. Gentianaceae	—	—	—	2	—	13
13. Scrophulariaceae	1	1	65 ⁵	9	—	33
14. Plantaginaceae	—	—	—	—	1	5
15. Juncaceae	—	—	—	15	2	7
16. Naiadaceae	—	—	—	12	—	1
17. Centrolepidaceae	—	—	—	1	2	3
18. Gramineae	—	—	—	35	9	53
Total	1	1	81	126	31	259

Now if we zone these families from north to south, as we did with the northern group, we get the result :

TABLE IV.

	1-100 m.	101-200 m.	201-300 m.	301-400 m.	401-500 m.	501-600 m.	601-700 m.	701-800 m.	801-900 m.	901-1000 m.	1001-1080 m.
Wides	83	87	100	97	101	105	104	102	100	91	51
End., N.Z. and Islands	16	17	19	21	24	27	28	28	29	29	18
End., N.Z.	33	55	76	95	115	189	205	220	228	166	46

Both wides and endemics taper off from south to north, but, as in the case of the northern families, the endemics taper down far more rapidly.

¹ The 800-mile line passes a trifle south of Raleigh and Timaru.

² *Clematis*.

³ *Rubus*.

⁴ *Fuchsia*.

⁵ *Veronica*.

The tapering is especially shown in the last 400 miles at the northern end of New Zealand, where the endemics actually fall below the wides. When plotted into curves, as in Fig. 7, it is clear that these families exactly reverse the behaviour of the northern families just dealt with.

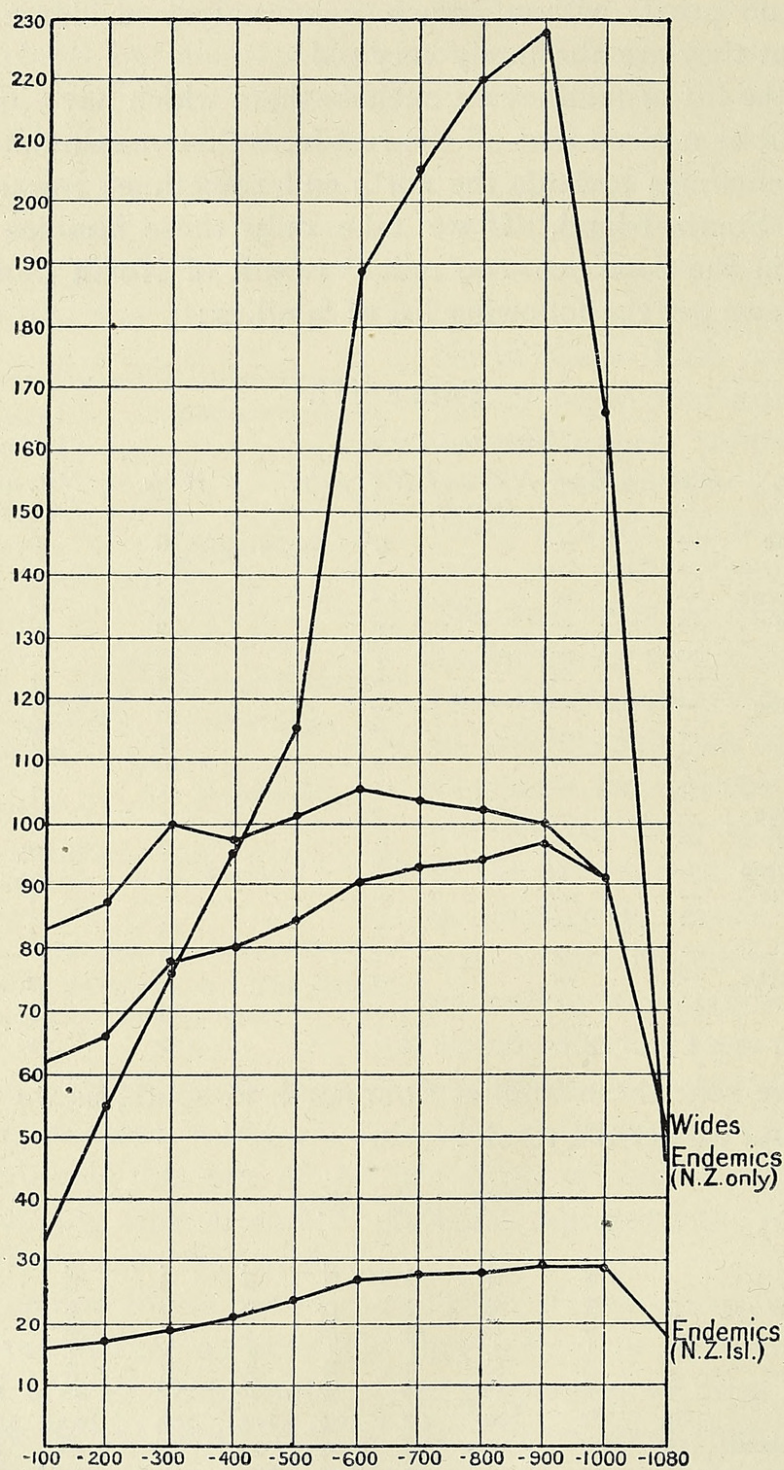


FIG. 7.

In Gramineae and one or two other families, there are quite a number of wides beginning at the North Cape and ending somewhere to the south, e. g. *Paspalum scrobiculatum* ranges as far as East Cape, *P. Digitaria* as far

as Coromandel, *P. distichum* as far as Waikato River, all at distances not over 430 miles from North Cape. It is clear that these are northern types, and that some of these families invaded New Zealand at both ends. If we subtract them, we get for the wides the result:

	83	87	100	97	101	105	104	102	100	91	51
less	21	21	23	17	17	14	11	8	3	—	—
	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>
	62	66	77	80	84	91	93	94	97	91	51

a result which brings the wides exactly into line with the endemics, and with the maximum at the same zone (see lower of two curves for wides).

Many will perhaps object to my treatment of these families, and say that if one pick out the families with a maximum at a certain point, and add them up, it is not surprising if they show great regularity in the curve. True, but the surprising thing has already been pointed out (19, p. 444), in giving these curves for the individual families, that *all* of them show such curves, and similar curves, rising to a maximum and then falling off again—a result quite unsuspected until I had applied to the New Zealand flora the ideas suggested by age and area, and had added up for each zone the actual plants that occurred therein.

It seems probable that these families, or a great part of them, which show as great symmetry in their curves as did the northern families, arrived in New Zealand by a southern route, which perhaps reached New Zealand with its central part about the middle of the southern half of the South Island. The maxima are at 800–900 miles, or a little north of Dunedin, which lies on the 900-mile line. Whence this southern bridge came is a more complex question that must be left for the present unanswered.

Passing on now to deal with the constitutional habit of these plants, the first thing that one notices is that not only are they much more numerous (though of fewer families) than the northern invasion, but they are nearly all herbs, there being only 83 shrubs and no trees in 499 species. Of the shrubs 67 are Veronicas. The proportion of herbs is 83 per cent., almost exactly equal to the percentage of trees and shrubs in the northern families that we first dealt with. Now as these herbs are mostly types of the Northern Hemisphere, it is clear that herbs must be very ancient, but as to whether they are older or younger than the trees and shrubs, the flora of New Zealand gives little clue. On the whole, one imagines, these southern types perhaps arrived in New Zealand later than the northern, for they do take some notice of Cook's Strait, quite a number being held up there, and they take about as much notice of Foveaux Strait as the northern forms, though they must have started so much nearer to it. Their curve of zoning of endemics, also, is rather more sharp, which would tend to show that the endemics were younger than the northern endemics. But it is clear that New Zealand alone will not permit of drawing any conclusion with the aid of age and area as to the relative ages of the different habits of growth.

Of the remaining families of the New Zealand flora, nine at least are composed of so few species, and range so uniformly along the whole length of the islands, that age and area will not permit of any deductions as to their source. There thus remain twenty-six families. Of these several, e.g. Orchidaceae, can be easily separated into two well-marked groups, one commencing at the North Cape and ranging to a greater or less distance southwards in New Zealand, and the other commencing at the south end and ranging northwards, so that it seems justifiable to infer that these families have invaded New Zealand both from the north and from the south. But when these have been taken out, there still remain a few families like Stackhousiaceae, Epacridaceae, and Myrsinaceae (Australian families) which have a fairly marked maximum in the middle of New Zealand, and range from that to the north and to the south. There is little or no evidence to show by which (if either) of the two routes already discussed these plants arrived.

From what has been said above, it will be clear that whilst the application of age and area to the problem may lead to fairly good evidence as to what has happened in the past in New Zealand itself, the hypothesis cannot be used in its present early stages to give evidence for or against the question of the relative age of trees, shrubs, and herbs. This question is really a very large one, and rendered much more complex by such questions as polyphyletic origin, &c.

AGE TENDS TO EXTINGUISH OLD SPECIES?

Like the question of the greater age of woody vegetation, this is a very large problem, and I shall simply endeavour to show that it is a somewhat complex one, not easily to be solved off-hand. Dr. Sinnott proposes an hypothesis to the effect that 'the longer a successfully invading species remains in an isolated area . . . the less common it tends to become until it is actually "swamped" out of existence—quite the reverse of the "age and area" idea'. He suggests that 'some may simply be exterminated outright, and some by continual crossing with new forms may ultimately lose their specific identity'.

There is no doubt that the fact that genera are common in these floras with endemics only, and no wides, is a feature which requires explanation; but as the genera with endemics only behave exactly like those which also contain wides, or like the endemic genera, the fact that it cannot at the moment be explained does not in the least militate against the hypothesis of age and area. Age and area may not agree with other views as to this or that, but it must be remembered that it is based upon very clear and definite figures, which must either be controverted or explained in some other way—they are far too striking to go without any explanation. It is somewhat difficult to controvert figures which simply represent bald facts, and if age and area be not accepted, it is consequently necessary to have

some other hypothesis, which must be mechanical, owing to the fact that the figures show such mechanical regularity.

Dr. Sinnott bases his views largely on the undoubted fact that the proportion of 'swamped' genera is larger in the more outlying of the big islands—in New Zealand than in Ceylon, in the Hawaiian islands than in New Zealand. But that mere isolation is not sufficient as an explanation would seem to show in the fact that in the very isolated islands round New Zealand the proportion is not so high as in New Zealand itself. In New Zealand 151 genera out of 316 show it, in the Kermadecs only 8 out of 62, in the Chathams the same, and in the Aucklands 12 out of 64. In none of the islands is the proportion anything like so high as in New Zealand, and it is highest in the Aucklands, which were probably nearest to the incoming stream of plants. On the other hand, the number of genera which are swamped in *New Zealand* is 13 in the Kermadecs, 33 in the Chathams (the most isolated), and 26 in the Aucklands, facts tending to show that the swamped genera were in existence fairly early opposite to the Chathams, and therefore were rather old in comparison to some of the rest, though even in the Chathams the unswamped genera are almost as numerous (29).

Another test that we may apply is to find the proportion of 'swamped' genera in the northern and southern invasions of plants above discussed. The northern shows 45 out of 75 or 60 per cent., while the southern shows 36 out of 108 or 33 per cent. We have seen that probability is in favour of the greater age in New Zealand of the northern invasion, so that to some extent this speaks in favour of Dr. Sinnott's views, in a general and purely local sense. But as only one herb (*Elatostema*) is swamped in the northern invasion, and all the shrubs but one (*Veronica*) in the southern, it is, it seems to me, equally possible that swamping may go with woody habit, and further tests are necessary.

Of the 151 'swamped' genera, 45 Dicotyledons and 30 Monocotyledons are herbs, or 50 per cent., while of the 165 unswamped, 75 Dicotyledons and 63 Monocotyledons are herbs, or 83 per cent. Of these unswamped genera 99 have no endemics, and of these 85, or 85 per cent., are herbs, while of the 66 with endemics 53, or 80 per cent., are herbs. From these figures it would seem that the evidence is just as good for the connexion of swamping and woody nature as of swamping and age.

The Coniferae are probably older than the flowering plants, and as they have no wides at all in New Zealand, this speaks in favour of age, but they are also all woody plants. The Ferns, on the other hand, which are probably older again, show very little 'swamping', only 5 genera out of 31 exhibiting this phenomenon. Of these it may be noted that three are the only tree-ferns in New Zealand. The remaining two, and all the unswamped genera, are herbaceous. It is evident that the question of swamping must be first disentangled from the question of the relatively greater

age of woody vegetation, and that, as in that case, the investigation of any one or two floras is quite insufficient to provide a solution.

If, as Dr. Sinnott suggests, the absence of wides in a genus had anything to do with the age of the genus, one would rather expect to see some difference in the figures of distribution of the two classes, especially in the zonal figures, in which Cook's Strait may interfere with the younger forms. But in actual fact the figures for the two classes show the most extraordinary similarity:

TABLE V.

Southern genera.											
Swamped	83	110	139	158	179	236	240	242	232	186	75
Not	45	64	82	99	112	188	193	202	189	152	48
Northern genera.											
Swamped	77	78	76	72	58	56	50	37	32	31	12
Not	11	11	11	7	7	7	6	6	4	3	3

The parallelism is most remarkable, and both groups show the holding up at Cook's Strait almost equally in the southern genera, and not at all in the northern.

A very interesting comparison, which does not harmonize very well with the hypothesis of swamping, may be made among the various classes of wides. There are 66 genera containing both wides and endemics, 99 with wides only. Of the 66, 35 genera have a second wide species, and 22 more than one, and of the 99, 24 genera have at least one extra species, and 5 more than one. This alone would go to show that it was mainly the older wides which gave rise to the endemics. But now if we pick out first the commonest (most widespread) wide in each genus, next the second commonest (for the 35), and the others (for the 22), but, as the numbers are small, lump together all the others for the 24 genera with no endemics and more than one wide, we get:

TABLE VI.

Class.	<i>Wides with endemics.</i>			<i>Wides without endemics.</i>	
	<i>First.</i>	<i>Second.</i>	<i>Others.</i>	<i>First.</i>	<i>Others.</i>
1	37 (56 %)	13 (37 %)	7 (10 %)	21 (21 %)	4 (12 %)
2	9	5	9	27	13
3	3	3	14	9	—
4	4	4	11	8	2
5	5	1	6	8	1
6	3	3	4	9	—
7	1	—	7	7	2
8	1	5	3	5	3
9	—	—	3	5	2
10	3	1	5	—	5
	—	—	—	—	—
	66	35	69	99	32
Rarity	2.5	3.4	4.5	3.6	4.6

It will be seen at a glance that the commonest wides in the genera with endemics are much more widespread than those in the genera without,

ranging on the average 132 more miles (difference 1.1, each 0.1 representing 12 miles).

When one comes to examine these figures a little more closely, one notices in the first column that 37 wides (56 per cent.) cross Foveaux Strait, ranging the entire length of New Zealand, while only 9 range the two main islands without crossing the Strait. In the second column only 37 per cent. cross the Strait, and in the third only 10 per cent. This is as one would expect from species picked in order of commonness. But when one goes on to the wides without endemics, one finds that even the first column shows only 21 per cent. crossing the Strait, and 27 per cent. held up there. It is clear that on the average these wides arrived in New Zealand as late as, or rather later than, the second wides in the genera which have endemics, and in the same way their later species (column 5), though 19 out of 24 are second arrivals, are rather later than the third (and later) arrivals of the first lot of wides, those with endemics. This table shows, in a very clear manner, that the wides with endemics are on the whole earlier arrivals than those without.

One may examine these tables in another way. The 46 wide genera with endemics that occur in classes 1 and 2 have altogether 304 endemics, those in classes 3, 4, 5, and 6 have 148,¹ and those in classes 7, 8, 9, and 10 have 7 only; again age is indicated as being more likely to 'involve' endemics. The 151 swamped genera have between them only 481 endemics, against 421 for those 66 genera which also contain wides. These facts go to show that on the whole it is the older wides which are accompanied by endemics, not the younger, as might be expected upon the hypothesis of swamping.

Dr. Sinnott's objection that age and area will not explain the New Zealand flora because it is based (cf. my diagram in 19, p. 442) on a central point of arrival of the flora, and it is generally agreed that the flora arrived in two or more directions, seems to me due to misunderstanding of my tables, which show with great clearness that there were at least two sources. I have already been into this question, but may just call attention to the fact that though there is a very clear northern invasion, the southern is so much larger that the *total* figures show practically the same result as the southern only—the northern are lost in them.

I am much indebted to my daughter Margaret for drawing the diagrams here reproduced, and to Dr. H. B. Guppy, F.R.S., for criticisms.

¹ Including 77 Veronicas and 22 Myosotises.

SUMMARY.

The paper is a reply to criticism, and brings up new facts about the distribution of plants in New Zealand. It is shown that age and area now occupies a strong position, because by its aid numerous prophecies as to geographical distribution of plants have already been made, and have proved to be correct upon examination of the facts.

Incidentally the flora of introductions into Ceylon is analysed, and it is shown that there is practically no evidence of large spread without the aid of man.

To make more clear the true meaning of the tables of figures that have been published, diagrams are given, showing the range in New Zealand of the species of *Ranunculus* and other genera. Their resemblance to the rings made by throwing a stone into a pool will at once be noticed, and is a strong argument against any but a mechanical explanation of these ranges. The widest range farthest, the endemics successively less.

A section is devoted to the activity of other factors than age, which have already been considered in detail in other papers. The question whether endemics are chiefly relicts is then discussed, and it is shown that for the vast majority the evidence is much against such being the case. Explanation by age and area is simpler and more convincing. Natural Selection cannot explain such cases as *Ranunculus Lyallii*, which are very numerous. Finally, there is given a list of twenty-eight awkward questions for the supporters of the dying-out hypothesis, questions which if not successfully answered are very damaging to that hypothesis.

The relative age of herbs, shrubs, and trees is then dealt with by showing that this question is really very complex, and at present far beyond the capacity of age and area to answer. The figures already given for distribution in New Zealand are analysed, and it is shown that thirty-three or more families have their maximum at the far north, and taper down steadily to the south. This goes to show that there must probably have been a northern land bridge reaching New Zealand from some part of Indo-Malaya (probably N. Australia), and similarly there are eighteen or more families which must probably have reached New Zealand by a southern bridge from some region abroad. The northern families are mainly trees and shrubs, the southern herbs. This alone shows how difficult is the question of relative age, and it is also pointed out that I have not claimed the same age for two plants occupying the same area, unless systematically related. Nor, it seems to me, are age and area and greater age of trees incompatible hypotheses.

Dr. Sinnott's hypothesis of swamping is considered, and it is shown that while it may have certain probabilities in its favour, the evidence is very conflicting. It is more common on the whole in genera of very ancient arrival in New Zealand, but it is also much more common in trees and

shrubs than in herbs. 'Swamped' and unswamped genera behave alike in their distribution through New Zealand. Swamping is rare in the Ferns, which on the whole must be old.

Finally, it is shown that the wides with endemics are on the whole probably older than those without.

LITERATURE QUOTED.

1. BERRY, E. W. : A Note on the Age and Area Hypothesis. *Science*, vol. xlvi, 1917, p. 539.
2. COPELAND, E. B. : Natural Selection and the Dispersal of Species. *Phil. Journ. Sci.*, vol. xi, 1916, p. 147.
3. COULTER, M. C. : Review in *Bot. Gaz.*, May, 1917, p. 419.
4. DE VRIES, H. : L'évolution des êtres organisés, par sauts brusques. *Scientia*, vol. xix, 1916, No. 1.
5. ——— : The Origin by Mutation of the Endemic Plants of Ceylon. *Science*, vol. xliii, 1916, p. 785.
6. ——— : The Distribution of Endemic Species in New Zealand. *Science*, vol. xlv, 1917, p. 641.
7. LOTSY, J. P. : Die endemischen Pflanzen von Ceylon, und die Mutationshypothese. *Biol. Centr.*, vol. xxxvi, 1916, p. 207.
8. MACDOUGAL, D. T. : Review in *Plant World*, 1916, p. 79.
9. SMALL, J. : The Age and Area Law. *Sci. Progr.*, Jan. 1918, p. 439.
10. SINNOTT, E. W. : Comparative Rapidity of Evolution in various Plant Types. *American Naturalist*, vol. 1, 1916, p. 466.
11. ——— : The Age and Area Hypothesis and the Problem of Endemism. *Ann. of Bot.*, vol. xxxi, 1917, p. 209.
12. ——— : The Age and Area Hypothesis of Willis. *Science*, vol. xlvi, 1917, p. 457.
13. ——— and BAILEY, I. W. : The Origin and Dispersal of Herbaceous Angiosperms. *Ann. of Bot.*, vol. xxviii, 1914, p. 547.
14. ——— : Foliar Evidence as to the Ancestry and Climatic Environment of the Angiosperms. *Amer. Journ. Bot.*, vol. ii, 1915, p. 1.
15. WILLIS, J. C. : Catalogue of Ceylon Plants. London, 1911.
16. ——— : The Floras of Hill-tops in Ceylon. *Ann. R. B. G. Perad.*, vol. iv, 1908, p. 131.
17. ——— : The Endemic Flora of Ceylon. *Phil. Trans., B.*, vol. ccvi, 1915, p. 307 (and correction in *Proc. Roy. Soc., B.*, vol. lxxxix, 1916).
18. ——— : The Evolution of Species in Ceylon. *Ann. of Bot.*, vol. xxx, 1916, p. 1.
19. ——— : The Distribution of Species in New Zealand. *Ann. of Bot.*, vol. xxx, 1916, p. 437.
20. ——— : The Relative Age of Endemic Species, &c. *Ann. of Bot.*, vol. xxxi, 1917, p. 189.
21. ——— : The Distribution of the Plants of the Outlying Islands of New Zealand. *Ann. of Bot.*, vol. xxxi, 1917, p. 327.
22. ——— : Further Evidence for Age and Area ; its Applicability to the Ferns, &c. *Ann. of Bot.*, vol. xxxi, 1917, p. 335.



Willis, J. C. 1918. "The sources and distribution of the New Zealand flora, with a reply to criticism." *Annals of botany* 32, 339–367.

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