Age and Area :

A Reply to Criticism, with Further Evidence.

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With five Figures in the Text.

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GENERAL.

WITH a paper in October, 1921 (10), I began a second series of communications, of wider scope than the first ten, though also based upon Age and Area. My first intention was to continue the series in logical order until I had published the whole theory of Age and Area and its many implications, but when I fully realized that to do this would take perhaps six or seven years, I determined to bring out a book dealing chiefly with Age and Area, and incidentally with its further implications. To this course I was also strongly urged by various friends. The book (11) has now appeared, and contains original matter that would have sufficed for at least another dozen papers. A gap is thus made between this paper and the last, which I must ask my readers to regard as filled by the publication of the book.

At a joint session of the Zoological and Botanical Sections at the meeting of the British Association at Hull in 1922, there was a discussion upon 'The Present Position of Darwinism', understanding thereby the theory of Natural Selection. At the meeting I continued the attack upon Natural Selection which I have persistently carried on since 1902 (cf. 5.

pp. 441-4, and especially 7, 12). Papers based upon Age and Area were read by Mr. G. Udny Yule and myself, the title of mine being 'On the Inadequacy of the Theory of Natural Selection as an Explanation of the Facts of Geographical Distribution and Evolution'. We had read papers upon somewhat similar lines at a meeting of the Linnean Society in February (abstract, 13), and the change of view-point of the biologists since that meeting was clearly marked. Many of the speakers were concerned less with defending Natural Selection than with attacking Age and Area, which was variously described, then or in subsequent newspaper articles, as 'worth less than nothing', 'utter balderdash', 'a few well-known facts distorted', and 'a theory whose career has already ended', with more to this effect.

As usual the objections were mostly due to a misunderstanding of the hypothesis. In spite of the fact that throughout I have made clear that it must not be applied to less than ten species at once, and those allied, and that these must only be compared with other groups allied to the first, persistent and somewhat pathetic attempts are made to apply it to individual cases, or to unrelated forms. As an instance of the kind of argument employed, I may quote from the second review of my book in 'The Times' the sentence (which falls into both errors) 'Is the barn-owl, almost world-wide, more ancient than the three-toed ostrich, found only in South America?'. In my book, upon p. 62, I have given an illustration of the way in which, though only dealing with fives instead of tens (as should always be the case), Age and Area is inapplicable to three out of five cases, although all species are following the law with complete exactness, a thing that is somewhat improbable in real life. In chapter ix I have devoted much attention to this difficulty, and I have repeatedly pointed out, there and elsewhere, that inapplicability to single cases does not in the very slightest degree invalidate the theory.

The single-species difficulty seems a stumbling-block to a very great number of people, and it is needful once more to emphasize the fact that one cannot reduce statistics to individual cases—the very name statistics indicates this. To take an illustrative case from ordinary life: no amount of study of individual members of the Goddard family would tell us much about the origin of the family, and it might be very difficult to make out anything, so far as I know, from history (corresponding to palaeobotany). We might ultimately know every detail about their anatomy and physiology, and even about their genetics, but none of these would be likely to give a clue. But supposing that we add up the numbers of Goddards in every county, in the more slowly-moving section of the population, the farmers, we obtain in this way *statistics* which show that they form 0.55 per cent. of the farmers in Berkshire, and no more than 0.31 in the adjacent counties, whilst they almost disappear beyond Dorset, Derby, and Norfolk. Con-

sequently one may infer with fair probability that Berkshire was the first original home of the name (2), for not even the most enthusiastic supporter of Natural Selection and adaptation would contend that a Goddard was especially adapted to Berkshire. The biologist fights shy of statistics, except when he wants to prove something in his own work, and at other times is apt to believe in the old gibe that statistics can be made to prove anything—a gibe which really refers to statistical fallacies, into which the untrained experimenter with statistics is very apt to fall. But in the case of the statistics upon which Age and Area is based, the fact that the work has been taken up *con amore* by a statistician of Mr. Udny Yule's reputation should be sufficient to show that there is no fallacy involved, as one or two speakers at Hull seemed to imply. There are very many problems, and those often problems of wide range, which can only be solved by means of statistics, but from their very nature these statistics cannot be applied to individual cases. Statistics show that the average Scot is about 20 lb. heavier than the average Englishman, and it does not in the very slightest degree affect this result to say, 'Oh, but Smith weighs 13 st. and MacPherson only 10'. And the bulk of the single-species arguments against Age and Area are almost exactly similar to, and equally as valid as this.

It is probable enough that *no two species*, allied or not, travel at exactly the same speed in their diffusion over the surface of the earth. But each will, on the average of long periods, travel at more or less of an average rate, so that in twice the time it will cover twice the distance. A species *A* may travel at the rate of 50 miles per 10,000 years, say, and in 20,000 will cover a distance of 100 miles, while *B* may only travel 5 miles in the 10,000 years, and 10 in 20,000, requiring therefore 200,000 years to cover a distance traversed by *A* in 20,000. The area covered will be the same, yet *B* will be ten times as old as *A*. But both fall in with the Age and Area theory, and with equal exactness.

If one were to take a group of closely allied species, e.g. species of similar habit belonging to the same genus, it would seem probable that as they will all have much the same mechanism for dispersal, and somewhat the same type of reactions to surrounding circumstances, they will spread at rates not very widely different. And taking at least ten will do away with the small differences that will occur between them, so that one group of ten will give much the same result as another group of ten allied to the first. One group, for example, might show rates of spread represented by 1, 3, 2, 1, 4, 3, 2, 1, 2, 3, and another by 3, 2, 1, 4, 2, 4, 1, 3, 2, 1. On adding these up one finds the first to give an average of $22/10 = 2.2$, and the second of $23/10 = 2.3$, a very small difference. If one deal with species always in *groups* of at least *ten allied forms*, and compare only with similar *groups allied to the first*, one will find that Age and Area is closely followed.

That it *is* closely followed is shown by the extraordinary success of

predictions based upon it and upon it only, of which further examples are given below. It is necessary to make once more clear that the success of prediction upon so large a scale as has now been effected proves the supposition of Age and Area so completely that it can only be displaced by finding some other hypothesis that will also explain the facts and make the predictions—a thing that no one has as yet attempted.

The general principle of Age and Area, when once grasped, seems almost axiomatic, as I have already pointed out on various occasions, and would probably be accepted with little difficulty were it not, among other reasons, for the lingering influence of Natural Selection, which has always insisted that competition was the chief agent in determining the areas occupied. In fact, it has been predicted by two of my supporters, and various reviews, letters, and notices have led me to expect the same, that within a short time Natural Selection will be quietly dropped, and people will say that Age and Area has long been obvious to the meanest intelligence, and that there was no need to make such a fuss over a simple axiom.

Another objection which was strongly urged at Hull was that endemics must be regarded as chiefly relics. I have already devoted much attention to this point, e.g. in my book, p. 88, but it evidently requires further emphasis. People who work in much detail with individual species, and come across many which are obviously of relic nature, are apt, more or less unconsciously, to exaggerate the number and importance of these cases, while they do not properly realize that the number of local species to which no stretch of imagination can apply the term relics is enormous. There are in Brazil alone 240 local species of *Eugenia* and 200 of *Paepalanthus*, to take merely a couple of genera. Five or six such genera would equal the whole number of species that are usually regarded as relics. It cannot be made too clear that the relics are outnumbered by about 60 or 70 to 1, so that when dealing with large numbers, as in statistical work, they are quite lost in the crowd. The objection is really a single-species objection in another form. It has been pointed out in the book, e.g. on pp. 94, 243, that in dealing with such forms from an Age and Area point of view, one must obviously include the 'fossil' area.

As I pointed out at Hull, no one has attempted to answer the many queries that I have propounded upon this subject in (8), p. 349, in the book, p. 89, and elsewhere, though one speaker said that time enough (four years) had not yet been allowed. If in four years no one can answer one of these questions, which could now be multiplied if required to a hundred or more, the chance of any serious reply seems but a small one.

A paper in the July number of the Annals (3) gives a striking illustration of the kind of work that will probably mark the next stage in the development of Age and Area. There Mr. J. R. Matthews takes the flora of Perthshire. At first glance it seems as if it had been distributed quite

independently of Age and Area, but when analysed it appears that 82 per cent. of the flora belongs to the more recent 'lowland' type, and has closely followed Age and Area in its distribution, while the remaining 18 per cent. '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.' But if one were able to determine the whole fossil record of these species, one would find, I have not the slightest doubt, that in their time of spreading they also followed Age and Area. Mrs. Reid, our leading palaeobotanist of the Tertiary, wrote to me about this paper, and allows me to quote the following sentence: 'Mr. Matthews . . . has proved that, though Age and Area on the surface appears not to hold particularly well, it is not because it really fails, but because it is masked by a disturbing cause, and when that cause is discriminated and eliminated, there stands the law fully evidenced.'

In actual fact, the results of the Age and Area law may be seen even on this receding highland flora, by working with larger areas, as is done below in dealing with the flora of Dublin, where it is shown that the plants of this highland flora that occur in Dublin and Wexford can be mainly predicted from determining those that occur in Wales at corresponding distances from Duncansby Head.

The general proposition put forward in Age and Area—that the area (sum of individual areas) covered by a group of ten or more allied species depends upon its age (sum of individual ages), whether within the country concerned, or (taking the whole world) from the time of its first evolution—is now being accepted by many biologists, but the further deductions which logically follow from its acceptance are still a bugbear to many, and I have myself come across two or three who say that they would accept Age and Area were it not for these inevitable sequels.

The general standpoint taken up with regard to the relations of Age and Area to the theory of Natural Selection, which was set forth in very limited time at Hull, has been more fully elaborated in a paper in the 'Nineteenth Century' (12), to which reference may be made by those who desire a simple statement of the chief points of difficulty that Age and Area has brought up for the latter theory to surmount if it can. It has long been recognized that Natural Selection has only been repelling attack with greater and greater difficulty, and that it is hopelessly unable to explain the results of work upon Mendelian lines. Age and Area, which has opened a range of facts as widespread as those of Mendelism, and as inexplicable by Natural Selection, has thus brought a formidable attack to bear from a new quarter and with new forces.

The acceptance of Age and Area, with its allied proposition of Size and Space, makes easily comprehensible many phenomena which have long

been regarded as insoluble problems in geographical distribution. No theory based upon adaptation to conditions could hope to explain why the genera and species were distributed as they are—why, for example, they overlapped one another in such a casual way, some occupying large, some small, areas, and no two coinciding. It was almost impossible to conceive that conditions should overlap in this extraordinary way (cf. the map of the distribution of *Ranunculus* in New Zealand in 8, p. 343, and in 11, p. 156), and perhaps even more impossible was it to understand why, as a rule, a genus retained its area unbroken, except by large barriers like expanses of sea. If there were much killing out of species by competition, one would expect a good many genera to show broken areas.

So utterly hopeless did it seem to be ever to find explanation of the simplest facts of distribution upon the theory of Natural Selection, that for many years work upon general distribution had been practically abandoned, or confined to speculation with little fact to back it (cf. Hooker's remark, 11, p. 104). Practically the only important work of the last twenty years has been that of Guppy, which has led him to conclusions diametrically opposed to the Darwinian theory. Even so simple a fact as that *Coleus elongatus* is confined to the summit of Ritigala in Ceylon, while *C. barbatus* occurs there and also ranges tropical Asia and Africa—a fact which can be matched from almost any large genus of animal or plant—is quite incapable of explanation by the theory of Natural Selection.

If one adopts the very simple theory of Age and Area, which has been placed in a position of great strength by the fact that it can be, and has been, so successfully employed in making predictions, all this is made clear. If we start with a hypothesis *A*, and from it deduce that *B* must therefore occur, and then find, upon examining the facts, that *B does* occur, we get a very strong argument indeed in favour of *A*. When a hypothesis *A* has been successfully used in this way on many occasions, it can only be disproved by producing a new hypothesis *X*, which will explain what *A* explains, and allow at least the same predictions, or as many, to be made. Successful prediction goes a long way in proof of the correctness of the hypothesis with which we set out, when carried out many times, without failure, as has been the case with Age and Area. This method of proof, however, is as yet somewhat new and unfamiliar to most biologists, having been only rarely employed, and then mostly in connexion with work upon breeding on Mendelian lines. Age and Area has now been used to make more than a hundred predictions about geographical distribution and endemism. As every one of these has proved correct, within comparatively small limits, very strong evidence—not *a priori*, but in support of a rival hypothesis—is now required to displace it.

Age and Area imagines that species spread, under the pull of the many and various factors acting upon them, at a rate which over long periods of

time is slow and uniform, or fairly so, and which thus allows acclimatization to go on at the same time. Age thus becomes a measure of dispersal, or vice versa, but, as already explained, the measure probably differs for every species, though all will spread, if unimpeded, about twice as far in 100,000 years as in 50,000. The spread is everywhere impeded by ecological and physical barriers, and will ultimately be stopped in one or more, or all directions, by one of these barriers, perhaps most often by a physical barrier, or by a sudden change of climate. There seems no reason to suppose, however, when one looks at such a map as that of the species of *Ranunculus* in New Zealand, that most species have reached their limits of dispersal.

Age and Area, then, implies that, on the whole, area occupied increases with age, and that as a general rule the very localized species are not the failures, as used to be imagined, but the young beginners. Whether the increase with age is in direct proportion or not, we do not yet know. There seems reason to believe that at first, when a species is probably represented by few individuals on a small area, the rate of dispersal will be much slower than when it becomes more common, but when once it has reached reasonable commonness on a considerable area it would seem probable that further dispersal will be at a more or less uniform rate.

The study of the localized species (cf. maps in 8, p. 343, or 11, p. 156) shows that they appear within, or very close to, the boundaries then occupied by the genus, but in what to us at present appears a casual way. A consideration of the map of the New Zealand species of *Ranunculus* upon p. 156 of my book, and of the diagram upon p. 76, will make this clear. Even in the case of the most localized species of all, confined to a mere spot of ground (cf. p. 151), where the conditions now existing must be practically the same as those under which it arose, one can see no special reason for its appearance, nor anything of special local adaptation in the characters that distinguish it (cf. pp. 225-7).

Now, as has been shown in the book, chaps. xvi, xx, genera appear to obey the same rules as species, also appearing in this casual manner; and they spread in the same way with age, increasing their number of species on the whole as they do so. As has already been frequently pointed out, no two genera or species will spread at the same rate, though all will follow the law of Age and Area. The result will therefore be what we actually see in nature—a vast multitude of more or less rounded areas, overlapping one another in every conceivable way, and of every possible size.

One of the most essential differences between this and the Natural Selection position is that under Age and Area one need no longer engage in the hopeless task of finding differences between species in characters that are of importance in the struggle for existence. If they exist, well and

good; but obviously they rarely exist in any marked degree, or the figures for distribution would not come out in such definite agreement with those that would be expected were Age and Area alone operative. Under the latter supposition we regard most species as not yet having necessarily reached their limit possible of dispersal.

Under Age and Area species are supposed to owe their differences in distribution not primarily to differences between *themselves*, but to differences in the time at which they were first evolved, or first appeared in the country under consideration, and secondarily to differences in the average rate at which they are dispersed. Into this latter factor there, of course, enter all those differences due to dissimilarities between the species themselves. Trees, for example, will spread at a slower average rate than herbs, Cruciferae probably more slowly than Compositae, and so on. By taking the species always in groups of ten, and comparing these with other tens allied to the first, chance differences between them will have their effect reduced to a minimum.

It will be seen that this method of looking at species and their distribution substitutes for the essentially 'vital' character of distribution under Natural Selection a much more 'mechanical' conception, that species owe their distribution primarily to their age, a distribution checked only by barriers, mechanical or ecological. On the old theory species were regarded in general as having reached their limit of possible distribution; on the new they are regarded as usually in process of expanding their areas, and generally with extreme slowness. On the old theory species of very limited area were looked upon as owing that smallness to the competition of other more successful types, and therefore as the failures in the struggle for existence; on the new, they usually owe it to the circumstance that they are still comparatively young, and have not had time to occupy larger areas.

Now the relative values of these two theories can be quickly tested by putting them to the proof, and using them to make predictions as to distribution. If only one of them can be thus used, and at the same time proves to be successful in its predictions, then it is clear that the evidence in favour of that theory becomes very strong. This is exactly what happens in the present case. No one has ever suggested that Natural Selection can be used for prediction, whereas Age and Area has already been used over a hundred times with success. So easy is it to make predictions, and so regularly are they successful, that it is almost literally true to say that one may at the present time 'shovel' in results in the study of distribution. The criticism that has been directed against Age and Area is of the arm-chair *a priori* type; but if the critics would take the trouble to try the methods for themselves, I feel certain that they would not long decry them. In the present paper I make some predictions of larger range

than hitherto, and it will be seen that they are successful, and that their results have bearings upon many problems of distribution.

There were many minor criticisms brought up at Hull, and in reviews of my book and elsewhere, and some of these will be dealt with in later papers.

THE CRITICISMS OF MR. C. TATE REGAN (WITH A NOTE ON
DISTRIBUTION OF FAMILY NAMES).

According to the very careful report of the papers and discussions made by my friend Mr. G. Udny Yule, and according also to my own notes, Mr. Tate Regan 'questioned whether areas gave a true hollow curve; he thought that the curve was probably modal, and appeared J-shaped owing to the grouping of the lower portion. He did not consider that hollow curves had any particular significance; you could obtain them from all sorts of data, e.g. from the numbers of occurrences of surnames in the London Telephone Directory. He emphasized the importance of sterility and of isolation in evolution. Dr. Willis's views did not explain adaptation, which could only be explained by selection of slight favourable variations.'

It will be seen that this is much less a defence of Natural Selection and the other features of the Darwinian theory than an attack upon Age and Area. That Mr. Tate Regan himself holds the general principle propounded in Age and Area is clear from the following extract from the chapter on Geographical Distribution in his book (4) upon 'The Fresh-water Fishes of the British Islands', 1911, p. 271: 'The fact that species which have a very wide and a very similar distribution on the mainland of Europe and Asia have very dissimilar distributions in the British Islands can only be explained by supposing that our islands were connected with each other and with continental Europe comparatively recently, when our eastern, and probably our southern, streams were tributaries of continental rivers and received from them the fishes which they contained; only nine or ten of these had reached Ireland before it became a separate island, and the distribution of the rest in Britain at varying rates according to circumstances has not yet proceeded long enough to spread them all over the island.'

This paragraph (which I threw upon the screen at the meeting of the British Association at Hull) is so clear a statement of Age and Area that, had I not made a brief preliminary statement four years earlier, I should feel inclined to ascribe priority to Mr. Tate Regan. His phrase 'at varying rates according to circumstances' so clearly expresses what I have tried once again to make clear above—that no two species travel at the same rate, but that all follow as closely as possible Age and Area, spreading twice as far in twice the time (when the time is long)—that I should like to have Mr. Tate Regan's permission to adopt the phrase for future use. The sentence that concludes the quotation gives the rest of the proposition of

Age and Area—‘has not yet proceeded long enough to spread them all over the island.’ There is no suggestion here of competition, of adaptation, or of any of the other outstanding features of the Darwinian theory.

The author of this paragraph explained that he imagined all the fishes to arrive at the same time, or in other words that they were all at the same time at the line of junction with the Continent. This of course means that though in Britain they might be distributed ‘at varying rates according to circumstances’, this was not so upon the mainland, where they all simultaneously reached the same line. Or if this interpretation be rejected, then we must suppose that those fishes that first reached the line of division must have waited there until all had arrived, so as to effect a kind of Norman conquest of the English rivers. And this although England was attached to the Continent for a very long period.

The only reasonable explanation of the distribution of the freshwater fishes, as of the plants, is that they came over so soon as they reached sufficiently far down the Seine and the Rhine, &c., each one spreading at its own average rate, when long periods are considered, and that the dispersal in Britain has been mainly determined by the time factor, so that, in the words of Mr. Tate Regan, ‘Ireland has only ten of the twenty-two species. . . . In Britain there is a considerable diminution in the number of species towards the north . . . in the Northern Highlands, as in the outlying islands, there seem to be no indigenous true freshwater fishes . . . a similar decrease . . . takes place from east to west. . . . Quite a number . . . are absent from Wales west of the Severn system. . . .’

With regard to the question whether areas give a true hollow curve, the matter seems to me one of comparatively small importance. It is really a matter of the size of the units of area employed. Taking fairly large units, as I have done, there can be no question that the greatest number of species are found, in any genus of reasonable size, upon the smallest areas. But if one try to divide these units into smaller ones, one finds only a very few genera with a sufficient number of species to enable such a thing to be done. It is obviously unfair to divide the smallest area into yet smaller without at the same time doing the same thing to the larger areas, and there are so few in these larger areas that one may often find many of the smaller units without any species in them at all. Suppose, for the sake of example, that we divide the flora of New Zealand by smaller areas than at present (cf. 11, pp. 64, 77, &c.). To take the first large genus, *Ranunculus*, one finds the endemic species to have the following ranges:

830, 670, 580, 570, 540, 460, 420, 340, 340, 320, 310, 280, 260, 220, 180, 170, 90, 60, 60, 20, 20, 20, 10, 10, 10, 10, 10 (miles of the length of New Zealand).

It is clear that the smallest unit, ten miles of longitudinal range in

New Zealand, contains five species, the second (20) three, while the whole 100 miles from 101 to 200, or any of the higher hundreds, never contains more than four. The areas are obviously concentrated towards the bottom. If one made the unit one mile instead of ten, it is clear that there would still be five species in the first ten classes, while in the one hundred classes from 601 to 700 there would only be one species. I think that one may say that the curve is not modal, but hollow, but to get a curve at all one must work with units of appreciable size. If one take all the genera in the New Zealand flora that have over 20 species, and add up their endemics, one gets the result that while the endemic species with a range of 100 miles or less are no less than 105, those with a range from 101 to 200 miles or any of the other hundreds never exceed 38. Splitting up the 105, one finds that 43 have a range of ten miles or less; more, that is, than in any hundred above the first. Of these 43 I feel confident that more will be near to the unit of one than to ten miles of range, but much more detailed study is yet needful before a definite decision can be given on this point. The flora of New Zealand is too small for a proper decision, and one requires that of a continent.

The importance of the question lies in the fact that if the curve be shown to have a mode at, say, five miles, with diminishing numbers below that (when large numbers are taken), it will mean that that is the probable size of area upon which species commenced, and that those with smaller areas are perhaps dying out. Even so, however, the area is too small to have allowed of Natural Selection of infinitesimal variations. Judging from the great numbers of species that are confined to very small areas indeed, I should imagine, however, that a smaller unit than five miles of range will be found to show the maximum.

Mr. Tate Regan did not think that the hollow curves had any particular significance. Such a statement can only be attributed to an insufficient consideration of the matter. Can it for a moment be supposed that all the first fifteen families of flowering plants should give such a series of curves for sizes of genera as those in Fig. 1, without a *very* definite reason? In no single instance does the curve for one family even approach closely the curve for another, though the points of origin are only five squares apart upon the tracing-paper. Why should every family, animals and plants alike, show such a large proportion of monotypes? Why should they all turn the corner between the threes and the fives? These curves would not show such an exact similarity, and, for animals and plants alike, always turning the corner between the figure for three species and the figure for five, unless there were some overmastering reason for it.

Not only are these curves hollow curves, but they are all hollow curves of the *same mathematical type*, and when plotted logarithmically they give straight lines or close approximations thereto, which is a thing that does

not necessarily happen with a hollow curve. The fact that the logarithmic curve is a straight line (Figs. 2, 3) indicates that the genera have been formed by a close approximation to the rule of compound interest, a conclusion which has very important consequences, to which I shall refer in later publications.

FIG. 1. Hollow curves exhibited by the grouping into sizes of the genera in the first fifteen largest families of flowering plants. Each curve is diagonally above the preceding one, as indicated by the heavy black dots (points of origin). Note that the curve almost always turns the corner between the point marking the number of genera with 3 species, and that marking the number with 5 (indicated by the dotted lines). The number after the name of the family shows the number of genera in it.¹

Mr. Tate Regan quoted the case of the names in the London Telephone Directory as giving a hollow curve like the plants, evidently thinking that there was no rule which governs the origin of names, and that they showed no distribution like plants. The answer to this criticism has been made very easy by the existence of a book of which Mr. Tate Regan was evidently

¹ Fig. 1 is reproduced by permission from Willis (11); the block kindly lent by the Syndics of the Cambridge University Press.

ignorant, and which was written by our leading distributionist, Dr. H. B.

FIG. 2. Logarithm curve for Rubiaceae (from Willis, 'Dictionary') with corresponding curve for all flowering plants beside it (from Willis, 'Age and Area').¹

FIG. 3. Logarithm curve for Chrysomelid beetles, with corresponding curve for all flowering plants beside it (from Willis, 'Age and Area').¹

Guppy—the 'Homes of Family Names.' The names in the Telephone Directory were found to give a hollow curve, the great bulk of the names

¹ Figs. 2 and 3 are reproduced by permission from Willis and Yule (13); the blocks kindly lent by the Syndics of the Cambridge University Press.

being rare, but a few, like Smith, Brown, Jones, and Robinson, being very numerous. But the reason for their distribution is evidently the same as in the case of plants. Some names are older than others, and will thus be more widely distributed and common, whilst, just as in plants, the large ones will tend to gain upon the small at an accelerated rate (cf. book, p. 34). Further, polyphyly, or multiple origin, is more likely to occur with names than with species.

The most slowly moving class of people in Britain is undoubtedly the class of farmers, many of them yeomen of very ancient descent upon the same spot. Guppy has made a special study of the distribution of their names in England and Wales, with statistical figures of frequency. Taking all names that occur in any county to a frequency (in the class of farmers) of 7 per 10,000, or more, he finds 3,925 names represented. When tabulated by frequency, these show :

<i>Reaching a commonness of 7 per 10,000 in</i>		<i>Number of names.</i>
1 county		2,441
2 counties		650
3 "		268
4 "		130
5 "		83
6 "		69
7 "		45
8 "		36
9 "		28
10 "		15

The numbers afterwards show a few trifling irregularities, but show some for every number of counties up to 36 (8 for 15 counties, 4 for 20, 5 for 25, 3 for 30, 1 for 35), and there is also one each for 39, 40, and 41 counties.

In other words, the distribution of these names is closely similar to the distribution of the species of a genus (cf. many examples in my book in ch. xvi), beginning with a great many on the smallest unit of area, and diminishing rapidly at first and more slowly later. The same general rule has evidently guided both distributions. Take, for example, opening the book at random, the name Halfacre. It reaches a frequency of 20 per 10,000 in Berkshire, but does not reach 7 anywhere else. It therefore may be presumed with good probability that the name originated in or near Berkshire. In the same way Hadfield (frequency 52) occurs in Derbyshire, Haffenden (18) in Sussex, Hadley (22) in Worcester, Haggett (9) in Somerset, none of these reaching a commonness of 7 anywhere else. But if one take such a name as Smith, one finds it common in nearly all counties, though varying from 300 in Worcester to 22 in Somerset.

Now let us look at the figures in another way. For each name and each county Guppy gives the proportion per 10,000 when it is above six. Let us begin with the names that are given for one county only. These

show an average proportion of 15.8 per 10,000 names (of farmers) in the county. But if we split up the 2,443 into ten groups we find:

<i>Names beginning with</i>		<i>Average proportion per name per 10,000 names of farmers.</i>
A, B	326 names	15.4
C	208 "	15.7
D, E, F	262 "	15.9
G, H	329 "	16.9 (maximum)
I, J, K, L	241 "	15.8
M, N, O	225 "	16.6
P, Q, R	255 "	14.9 (minimum)
S	237 "	15.4
T, U, V	191 "	15.5
W, Y	169 "	15.0

A most extraordinary resemblance is thus to be seen among these ten groups whose individual size is given in the table. The whole range of average occurrence is only from 14.9 to 16.9 per 10,000. The larger figure for G and H is due to the occurrence there of unusually large proportions of 'stay-at-home' names. These are, however, well distributed over the country, the only regions in which there are none being Wales and some of the Eastern Counties.

If we go on to the names which are above a density of six in two counties, we find, taking the larger number of the two in each case, that the proportions vary in the same ten groups from 18.5 to 25.6, with an average of 21.9. Thus the minimum here is a good deal higher than the maximum for the names of one county only. In the same way the 'threes' show a range yet larger again (corresponding to the diminishing numbers) with an average of 27.1.

It will be noticed that the average proportion in the county with the largest representation shows an increase with the number of counties covered by the name, and when we tabulate the figures we get the following interesting result:

<i>Number of counties in which a commonness of 7 per 10,000 is reached.</i>		<i>Average commonness per 10,000 in the county with the maximum.</i>
1	2,443 names	15.8
2	650 "	21.9
3	268 "	27.1
4, 5	213 "	35.8 ¹
6, 7, 8	150 "	40.8
9-12	72 "	64.6
13-20	78 "	90.2
Over 20	53 "	144.1

¹ The fours show a maximum proportion of 33.8.

" fives " " " 38.8.

In other words, the more widely distributed over the country the name has become, the more common is it in the region where it appears to have started (what was said above about polyphyly being borne in mind). This is exactly parallel to what is seen in plants and animals, just as was the

other phenomenon described above, and seems to me completely to answer Mr. Tate Regan.

Mr. Tate Regan then went on to emphasize the importance of sterility and of isolation in evolution—points to which there will be few dissentients. It may be pointed out that the large mutations postulated by my supposi-

FIG. 4. Hollow curves exhibited by the grouping into sizes of the genera in ten British Floras, 1782-1908.

tions (11, p. 215) will be much more likely to be mutually sterile with their ancestors than would smaller ones.

Finally Mr. Tate Regan objected to Age and Area because it did not explain adaptation. This, however, no theory since the older theories of Darwin and Lamarck has attempted to do. Personally I do not think that adaptation is nearly so well marked as is often supposed (cf. 6), and it has often been pointed out, e.g. by de Vries on p. 224 in my book, and by

Mr. J. T. Cunningham at Hull, that it shows chiefly in generic and family groups, rather than in species, so that any theory of evolution that begins with the species, as does the Darwinian, must fail in its explanation. But a separate paper is required to deal with so large a subject.

SOME STATISTICS OF THE BRITISH FLORA, TO SHOW THE TRIFLING DIFFERENCES DUE TO 'LUMPING' AND 'SPLITTING', OR TO CONTINUED WORK UPON THE SAME FLORA.

An objection often brought up (cf. 11, p. 98) is that my figures, if not indeed accidental, depend upon the fact that the floras used are by a particular type of systematist. It is contended, in other words, that the flora of a 'lumper' will give a very different result from that of a 'splitter'. Others contend (cf. 11, p. 84) that the figures will be vitiated by further work upon the floras concerned.

I have already mentioned that in fact neither of these objections can be supported when the actual facts are examined, but in order to show their inapplicability in a striking way, I have taken at random ten British floras which I found in the University Library in Cambridge, ranging from 1782 to 1908, or over a period of 126 years during which much work has been done, and including the work of such 'lumpers' as Bentham, and such 'splitters' as Babington and the editor of the London Catalogue.

Though in some cases hardly a genus or a species has the same limitation in two of these floras, it will be seen at once that the general result is one of the most extraordinary similarity. There cannot be the slightest doubt that the curve is the same curve in all cases, with only unimportant variations. All the floras show the same hollow curve. And from this I think that one may assume that a similar result would follow in any other case, as indeed I have found to be the case in other instances.

The actual figures for the distribution of the genera in these various floras into sizes are given below, commencing with the flora that shows the greatest number of genera represented in Britain by one species only.

Flora.	Genera of 1.	2.	3.	4.	5.	10.	Larger.	Largest.
A. Lindley, 1859	271	102	52	25	18	5	3/14	1/65
B. W. J. Hooker, 1830	254	83	50	27	21	6	3/14	1/66
C. Bentham, 1878	252	84	49	22	23	4	4/15	1/47
D. Babington, 9th ed., 1904	249	92	43	37	20	5	2/14	1/97
E. J. D. Hooker, 1870	228	90	53	27	18	6	3/15	1/69
F. London Catalogue, 10th ed., 1908	227	83	42	27	20	7	4/14	1/130
G. London Catalogue, 8th ed., 1890	223	90	35	32	16	3	8/11	1/72
H. Hudson, 1798	198	76	44	20	18	4	2/16	1/35
J. Sowerby (Smith), 1814	191	74	44	38	18	6	3/15	1/57
K. Enchiridion Botanicum, 1782	177	82	54	26	11	3	3/15	1/38

It is clear that though the 'splitter' pours contempt upon the 'lumper',

and vice versa, both really work upon what are essentially the same principles, and that they produce results of the most extraordinary parallelism.

THE DISTRIBUTION OF GENERA BY SIZES IN DEFINITE AREAS;
A DIFFICULTY FOR THE SUPPORTER OF RELICDOM.

A commencement has been made with this subject in my book, upon p. 189, where it is shown that in South America, to take one instance, there exist, confined to this continent, 18 per cent. of the world's monotypes, but only 16 per cent. of the ditypes, 13 per cent. of the genera with five species, 11 per cent. of those with ten, and so on, the proportions steadily diminishing. To explain this by Natural Selection appears to me an impossibility, for the same phenomenon is shown by other continents and islands, and Natural Selection could not produce such a regular and mechanical result, nor would relics be likely to exist in a steadily diminishing proportion, with the greatest number at the point of death.

But other problems arise out of these facts, which are perhaps even more difficult for the natural selectionist. How explain, for example, the fact that the actual numbers and proportions (from my Dictionary, 4th ed., as usual) of the genera confined to the three most isolated continents are :

	<i>Africa.</i>		<i>North America.</i>		<i>South America.</i>	
<i>Total of genera</i>	1,740		1,308		1,739	
With 1 species	835	48 %	612	47 %	887	51 %
2 "	254	14	224	17	263	15
3 "	136	7	111	8	125	7
5 "	97	5	58	4	87	5
10 "	56	3	42	3	59	3

The percentages are counted downwards; 48 % of the African genera are monotypes, 51 % of the South American.

Not only do the proportions decrease regularly, but they are closely the same for all three. Neither of these facts can be explained by Natural Selection, though they are quite simple to Age and Area, if we imagine genera to be 'casually' formed at different spots.

Or, to take another case, why, on the theory of Natural Selection, should Australia, which is a large island, have only 241 out of its 565 endemic genera monotypic, or 42 per cent.,¹ while Java has 57 out of 59, or 96 per cent.? The smaller islands than Australia, taken as a whole, have 1,037 out of 1,582 endemic genera monotypic, or 65 per cent. The explanation of relicdom is somewhat hardly pressed to explain such cases as this, or the still more difficult case that while Java has 96 per cent. of its endemic genera monotypic, Socotra has 89 per cent., Japan 80 per cent., Ceylon 76 per cent., Madagascar and New Zealand 70 per cent., New Caledonia 57 per cent., and the Hawaiian Islands merely 31 per cent. (cf. figures on

¹ i. e. less than Africa, North America, or South America.

p. 175 of my book). Why should there be so many more relics, both in number and in proportion, upon the islands that are nearest to the mainland and least isolated? The greater proportion of larger endemic genera upon the more outlying islands shows clearly that these genera were formed at an earlier date (on the whole), and thus, having had longer time in which to expand, have grown larger.

Why has tropical America, a comparatively continuous area, 13 per cent. of its endemic genera monotypic, while the much broken Old World tropics have only 6 per cent., and tropical Asia 36 per cent.? The general distribution of genera by sizes in different areas, more fully described in my book, offers very serious problems to the supporter of relicdom for most endemics.

PREDICTION APPLIED TO THE FLORA OF THE BRITISH ISLANDS.

The predictions hitherto applied with such success have been mostly in reference to the flora of New Zealand and its surrounding islands, and as the criticism has been made that though prediction may succeed in such regions that have been comparatively little interfered with by man, it would be valueless in such regions as the British Islands, an attempt at prediction is here made for the latter. The attempt is to forecast the flora of the county of Dublin (a region of which we possess a good and recent flora (1)) from what is known of the distribution of the plants of the adjacent island of Great Britain. For the latter there is no more recent general authority, so far as I know, than Watson's '*Topographical Botany*', 2nd ed., 1883, and I have kept rigidly to this. I have not the time available to consult all the innumerable papers in which more recent work is enshrined, nor is it necessary for such work as the present, for, as will be seen below, the prediction is perhaps more successful than were any of those which I made in regard to the flora of New Zealand.

It is generally admitted that Britain and Ireland were at one time united to one another and to the Continent, and received their floras thence. The nearest point to the Continent, and that a point not uncentral (in all probability) as regards the land union, is the South Foreland in Kent. For the purpose of prediction let us assume that this was the centre of the main continental (northward-moving) invasion, and draw circles round it as a centre. If we take a circle that includes the county of Dublin, it will be seen that it also includes the counties of Wicklow and Wexford, and then crosses Scotland by the south of Ayrshire, through Lanark, Peebles, and Edinburgh, reaching the North Sea near Dunbar in Haddington.

The prediction now is obvious. One will expect to find the flora of the south-east corner of Ireland made up, so far as this invasion is concerned, of those plants which reach Kent, and also reach Ayrshire or Haddington.

But there are many plants in the British Islands that seem to have

entered from the north-east. Let us, for the sake of prediction, suppose that this invasion centred at Duncansby Head, and draw a circle round that

FIG. 5. Map of the British Isles to show ranges of plants reaching co. Dublin.

to include Dublin county. This circle crosses England and Wales from Merioneth to the Wash, and one will expect the Dublin flora to contain those species that reach to this circle in Britain. There may have been other invasions, and the directions may not have been exactly as here

imagined (for example, there might have been invasion from the direction of St. Alban's Head, as shown in the third circle), so that this is really only a rough approximation. But on this basis let us see to what extent the flora of Dublin is predicted. The flora is helped out in a few instances by that of Wicklow and Wexford, especially in regard to mountain species.

Taking from Watson those plants that fulfil one or other of the two conditions laid down above as needful, one obtains a total of 739 species. Many of these are now regarded as aliens or introductions of some kind, and it would lead too far to go into the question in detail. Of these 739 our region includes 564 regarded as fully native, or 72 per cent. A further 47 (6 per cent.) are marked by Colgan as colonists, but all of them except *Anthemis arvensis* are marked in the 'Cybele Hibernica' as native in Ireland. Still another 49 occur in Dublin, marked by Colgan as Casuals, Denizens, or Aliens, and the Cybele marks 27 of these as native in Ireland. We thus find in all, $564 + 46 + 27 = 637$ out of 739, or over 86 per cent., predicted. Of the remaining 102, the Cybele gives 45 as native in parts of Ireland, so that only a few plants remain that are not found. Of the species found in Dublin, and *not* predicted, 40 in all, 12 are marked by Colgan as Aliens, Casuals, or Colonists. Considering the effects of man's occupation for so many centuries, this result must be looked upon as very successful prediction.

One may even apply prediction nearer home. A circle with centre at the South Foreland, and including Dorset, also includes much of Derbyshire, and one will therefore expect a great similarity between the floras of these two counties. Taking the floras of Mansell-Pleydell and of Painter, and comparing, one finds the species the same for page after page, the two counties having no less than 1,305 in common, i.e. 88 per cent. of the flora of Dorset, and 95 per cent. of that of Derby. Of the remainder of the Dorset flora, 84 are seacoast species, which one will not expect to find in Derby, and in Derby 23 are Highland types that cannot occur in Dorset. If we omit these from the respective floras, the 1,305 species in common represent 93.2 per cent. of the flora of Dorset and 97.2 of that of Derby. A more detailed study of invasions, and of local distribution in England, would probably make the approximation even closer; this is merely given as a rough illustration, and was chosen simply because I happened to have at hand the flora of Derbyshire.

A CORRECTION OF PREVIOUS WORK UPON THE FLORA OF CEYLON.

Mr. J. S. Gamble, C.I.E., F.R.S., informed me in conversation that in the course of his work upon the flora of Madras, a number of species had been discovered there which in my Catalogue of Ceylon Plants are recorded as endemic to Ceylon. It at once struck me that upon the theory of Age

and Area these would probably prove to be mainly among those recorded as possessing an unusually low degree of rarity (for endemics), and I asked for a list, which Mr. Gamble has kindly furnished. The species so far recorded are:

<i>Dillenia retusa</i>	<i>Microtropis Wallichiana</i>	<i>Osbeckia rubicunda</i>
<i>Uvaria macropoda</i>	<i>Vitis glyptocarpa</i>	<i>Casearia coriacea</i>
<i>Xylopia parvifolia</i>	<i>Sapindus erectus</i>	<i>Heracleum zeylanicum</i>
<i>Alphonsea sclerocarpa</i>	<i>Crotalaria Walkeri</i>	<i>Hedyotis Lessertiana</i>
<i>Garcinia echinocarpa</i>	<i>Eugenia Fergusoni</i>	<i>Urophyllum zeylanicum</i>
<i>Calophyllum trapezifolium</i>	<i>Eugenia olivifolia</i>	<i>Ixora Thwaitesii</i>
<i>Erythroxylon obtusifolium</i>	<i>Osbeckia buxifolia</i>	<i>Emilia zeylanica</i>
<i>Olex zeylanica</i>		

If one note, from Trimen's 'Flora', the recorded rarity of each of these in Ceylon, one finds that of the 22, there are VC 1, C 4, RC 11 (i. e. 16 below average rarity), RR 3, R 2, VR 1 (i. e. 6 above average rarity). The 22 species show an average rarity of $(22/70) 3.18$, much below the average for Ceylon endemics of 4.34. Their removal alters this to $(787/3,448) 4.38$. As only one place of decimals was employed in my calculations, it will be seen that the figures remain unaltered—a fact which may help to impress upon some objectors how little difference in the statistics is made by the alteration of a few individual figures. Incidentally, by removing 11 from the old list of 139 RC, and only 3 from the 136 RR, the change removes the only break in the regularity of my figures which has so far shown itself when dealing with considerable numbers.

SUMMARY.

This paper is chiefly concerned with a reply to the criticisms upon Age and Area that were made at the Hull meeting of the British Association, and special attention is once more directed to the most fruitful sources of difficulty, for little new criticism was brought up. People insist upon applying Age and Area to individual cases, or to unrelated forms, and in both instances, as has frequently been pointed out, this will only lead to error and difficulty. The law is only applicable to groups of at least ten allied forms. The other great difficulty is the view that endemic forms are chiefly relics, yet, though the latter are common enough, it is not properly realized that they are quite lost in the crowd when large numbers are considered.

Several original pieces of work are then inserted to illustrate what has been said. A definite reply is made to the criticism of Mr. Tate Regan, who was the leader of the opposition at Hull, and who made several animadversions upon Age and Area that do not seem to me to be justified. Incidentally a brief analysis of Guppy's work upon distribution of family

names is made, and it is shown that they have followed rules similar to Age and Area and Size and Space.

Some statistics are given of various British floras published from 1782 to 1908, and it is shown that the curves for sizes of genera for ten floras of this period agree very closely indeed with one another.

The next section is concerned with the distribution of genera by sizes in definite areas. Among other things it is shown that the nearer to the mainland an island is, the larger is the proportion of monotypes (usually supposed relics) among its endemic genera—a very difficult phenomenon for the advocate of relicdom to explain.

Further illustration of the ease and success of prediction is then given by predicting more than 86 per cent. of the flora of Dublin from what is known of the distribution of plants in Great Britain; and a further prediction that the floras of Dorset and Derby (apart from coast plants in the one, and highland in the other) will be much the same is borne out to the extent of 93 per cent. in Dorset and 97 per cent. in Derby.

Finally, a correction is added to previous work upon the flora of Ceylon. Twenty-two species, formerly supposed endemics, have been found in Madras, and prove to be, as would be expected by Age and Area, on the whole decidedly on the 'Common' rather than the 'Rare' side in their Ceylon distribution.

LITERATURE CITED.

1. COLGAN, N. : Flora of County Dublin, 1904.
2. GUPPY, H. B. : Homes of Family Names in Great Britain, 1890.
3. MATTHEWS, J. R. : The Distribution of Plants in Perthshire in relation to Age and Area. *Ann. Bot.*, xxxvi, p. 321, 1922.
4. REGAN, C. TATE : The Freshwater Fishes of the British Islands, 1911.
5. WILLIS, J. C. : Studies of . . . Podostemaceae. *Ann. R.B.G. Perad.*, i, p. 267, 1902.
6. ——— : The Lack of Adaptation in the Podostemaceae. *Proc. Roy. Soc., B.* lxxxvii, p. 532, 1914.
7. ——— : Some Evidence against . . . Natural Selection. *Ann. R.B.G. Perad.*, iv, p. 1, 1907, and Further Evidence, p. 17.
8. ——— : Sources . . . of New Zealand Flora. *Ann. Bot.*, xxxii, 1918.
9. ——— : Floras of Outlying Islands. *Ibid.*, xxxiii, p. 479, 1919.
10. ——— : Endemic Genera of Plants. *Ibid.*, xxxv, p. 493, 1921.
11. ——— : Age and Area, a Study in Geographical Distribution and Origin of Species. Cambridge, 1922.
12. ——— : Is the Theory of Natural Selection adequate? *Nineteenth Century and After*, Oct. 1922, p. 615.
13. ——— and YULE, G. U. : Some Statistics of Evolution and Geographical Distribution in Plants and Animals, and their Significance. *Nature*, 109, p. 177, 1922.

Willis, J. C. 1923. "Age and area: a reply to criticism, with further evidence." *Annals of botany* 37, 193–215.

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