Zeitschrift: Boissiera : mémoires de botanique systématique

Band: 7 (1943)

Artikel: Adaptation

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DOI: https://doi.org/10.5169/seals-895643

Adaptation

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(Manuscrit reçu le 14 novembre 1942)

Few subjects have been so much discussed as adaptation in the last seventy years, for it is the basis of Darwin's great theory of evolution. Though a very old conception, evolution had never been accepted as a working theory because no satisfactory mechanism that could operate it had been brought forward. The want was met by Darwin, with the simple mechanism now always known by his name of natural selection. It was familiar to everyone in daily life under the name of competition, or, as Darwin called it, the struggle for existence. By this the best individuals were picked out for survival and reproduction. This use of a familiar mechanism gave the theory a great appeal, and it rapidly captured public favour—so much so that to it, rather than to the great theory of evolution, was given the name of Darwinism. Evolution itself soon proved its great value, and it now stands in an unassailable position as a bedrock of biological science, needing no help from natural selection.

The general idea underlying the whole position was the notion that natural selection picked out *adaptational* improvements. As structural difference was the only thing to show that evolution had gone on at all, it was taken for granted that this also represented adaptational difference. Things that gave any advantage in the constant and remorseless competition—as, for example, a longer root that might absorb more food—were the things to be selected, and if the advantage were further improved in succeeding generations, it might ultimately become of specific importance.

The first rude shock to natural selection was FLEEMING JENKIN'S criticism in 1867, showing clearly that though any individual might carry a valuable improvement, it would certainly be lost by crossing with others that did not show it. An assumption had to be made that the same improvement was shown in all the plants upon a considerable area. We have never had any evidence that such is the case, so that natural selection has never really stood upon a sound and unassailable basis. In recent years, the work of selection in evolution has been made still more difficult by the general substitution of the small mutations of DE VRIES for the older idea of gradual change, for how could selection determine that these small mutations, which practically never have any adaptational value, should occur at all?

The writer has devoted many years to showing the unsound and illogical position of natural selection as a theory, which thus weakens also that part of the theory of evolution that depends upon it. This he has done mainly in two books, *Age and Area* [1], and *The Course of Evolution* [2]. Both treat the subject together with geographical distribution, for it has always been admitted that no theory of evolution can stand unless it can explain the latter, and this is just what natural selection, though it was at first promising, has failed to do. Distribution still has to explain a vast mixture of plants of every possible family, genus, and species, and of every possible size and dispersal, intermingled in every possible way. Few principles have been disen-

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[1] WILLIS, J. C. *Age and Area.* Cambridge (1922).

[2] IDEM *The Course of Evolution.* Cambridge (1940).

tangled from the confusion to help in its explanation, and still fewer show any relation to the theory of natural selection, which is an essentially individual phenomenon, bringing forward some individuals and killing out others, regardless of the particular species to which they may belong. The only branch of distribution really to progress in recent times is ecology, which deals with the distribution into local societies or associations, inhabiting regions of very similar conditions, of those plants available in the flora of a given country. How the country got its flora matters nothing to the ecologist, who is concerned with the adaptation of the plants to their local surroundings. In dealing with such a society, one of the first things to strike one is, that though adaptation is supposed to be structural, there are no structural features common to a society that can be pointed out as having something to do with its mode of life, unless that happen to be in one of the two extremes of water-plants or xerophytes; and even then they are rarely specific.

In *Age and Area* the writer showed that so long as one keeps to closely allied forms, the area occupied by a group of say ten is to the area occupied by another group in the proportion of their age—the older the species or genus, the larger the area (law of age and area). He also showed that the more species a genus had (again keeping to groups of allies) the greater the area (space) occupied (law of size and space). From these two laws there follows the complementary one of age and size, that the larger genera in a group of allies are the older.

None of these three laws is in any way concerned with any supposed action of natural selection; they are arithmetical or mechanical laws, yet they easily explain a great proportion of the facts of distribution. They were mainly worked out upon floras that contained many endemics, like CEYLON and NEW ZEALAND. Endemics were supposed, upon the Darwinian theory, to be old species, defeated in the struggle for existence, and now dying out, but it was shown in *Age and Area* that they were in general new species and genera, the youngest in their circles of affinity, which had not yet had time enough to spread very widely. There are many endemics in south EUROPE, which have been shown to belong mainly to the larger genera there ([1 and 2]), which by the law of size and age are the oldest there. They have thus had time to produce endemics in the south, and to get to north EUROPE soon enough to become the largest genera there also, and some of them even to produce endemics in the north, especially in the ALPS.

Reasoning from these three laws as a basis, and with a great deal of further evidence, the author then went on to show, in *Evolution*, that evolution itself was largely, if not entirely, independent of natural selection, and that it proceeded in the *reverse* direction to that demanded by the theory of natural selection, a family, genus, species, or variety being produced at a single mutation. One such mutation might, for example, produce a new form which would represent a new family, consisting of one new genus with one new species—all of course the same individual. This by further mutations when it had established itself would produce new genera in the family, each at first of one species only, and by still «smaller» mutations would produce new species in the genera, probably according to their age. The result would be the growth of a family by compound interest, one genus becoming two, the two four, and so on, again an arithmetical law. We shall see below that this is very much what actually happens.

But if the whole *structural* difference between species or genus A (the parent) and B (the offspring) is thus produced

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[1] WILLIS, J. C. *Some further studies in Endemism* in *Proc. Linn. Soc.* CXLVIII, 86 (1936).

[2] IDEM *Some Conceptions about geographical distribution* etc., *l.c.*, CL, 162 (1938).

at a single step by a sudden mutation, one can no longer regard its production as being by the selection of adaptational improvement, for this difference (if it *be* an improvement, as to which there is very rarely any evidence) appears at once. We have no evidence that selection has anything to do with the change, and it is better at present to leave it out of consideration. On the other hand, the usually intense and ruthless competition, into which the newly born species is at once thrown, will ensure that unless it is fully adapted to the local conditions *from its birth*, it will be unable to survive. One will expect that most often, perhaps, the new species will survive, as it will probably inherit most of the adaptation of its parent, with slight changes that have come about by reason of the slight structural changes that have occurred in forming the new species. These changes, we suggest, give it an adaptation that is not stretched in a one-sided way like that of the parent, born as it was with an adaptation to somewhat different conditions. The new adaptation of the new species will *centre* upon the conditions that prevailed at the time and place of its birth. In the vast majority of cases there is no evidence whatever that the structural peculiarities of a species have anything to do with local adaptation [1]. In the extreme cases of water-plants and xerophytes, some few of the structural features show characters that may be looked upon as more or less adaptional. But so long as one tries to explain distribution upon a basis of structural adaptation, one finds so few facts to go upon that one is never out of great difficulty. No picture of distribution other than local can be painted upon an adaptational background.

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[1] WILLIS, J. C. *On the Lack of Adaptation in the Tristichaceae and Podostemaceae* in *Proc. Roy. Soc.* B, LXXXVII, 532 (1914). It is shown there, that the most variously constructed Podostemaceae live side by side in the most uniform conditions possible, yet showing the widest possible structural differences.

In a paper published in CEYLON in 1907, we suggested that « it is possible, if not probable, that a group of allied species represents so many more or less stable positions of equilibrium in cell division » and in a paper as yet unpublished[1] we have suggested, as a working hypothesis to explain this sudden production of new forms, that trâvel into different conditions seems to put some kind of strain upon the nucleus of the cell, to which it reacts by some re-adjustment like that which occurs when one slightly turns a kaleidoscope. This produces a new species at one step by alteration of the structure, but this alteration seems to have no necessary reference to any adaptation to the environmental conditions. The adaption is functional, and unless fairly perfect, the new species cannot survive.

This is obviously a complete change from the former outlook upon biological problems. The new theory, that evolution goes in the direction family—genus—species, though it dates back at least to GEOFFROY ST-HILAIRE, and is thus older than Darwinism, is supported by a great mass of evidence, much of which is worked out in *Evolution* in the form of 34 crucial testcases between the two theories. Many more could be added, and all give good, some almost overwhelming, evidence in favour of Divergent Mutation, as I have called the theory on account of the usually well marked divergence of the earlier mutations. If accepted, it brings a new outlook upon problems of distribution,hitherto a rather hopeless confusion, which is summed up by an opponent in the phrase « for some reason the plant has advantages which enable it to spread ». This is all that the theory of the selection of adaptational advantages has been able to do towards explaining distribution.

If, however, as the new theory enables us to do, we drop adaptation, especially structural, as the determinant of

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[1] WILLIS, J. C. *Evolution in Plants by kaleidoscopic Mutation* in *Proc. Roy. Soc.* B (Nov. 1942).

distribution, and realise that this is mainly a mechanical phenomenon, we can get a clearer view of what is going on. There is no need to suppose any adaptation other than that which must be possessed at birth by any species that survives at all. Together with this it must evidently have some further adaptability to enable it to resist even the changes of conditions that may occur, and that within a short time, at its place of birth. With the aid of this adaptation and this adaptability it can probably and usually establish itself, and can spread from its birthplace into places round about, and gradually to places further away. How far it has spread up to the present time will depend simply upon how fast it can move, how much time has been available since its birth, and to what extent the many barriers to spread, physical, climatic, and ecological, have interfered. Some types of genera may spread at rates quite different from others; *e.g.* a *Senecio* may differ much from a *Sequoia*, but little from a *Taraxacum*.

When genera come into conditions that are really very different from those in which they began, for example when genera of the temperate regions come into the tropics, they seem to show what may be a tendency to slow down in their vital phenomena. In general one will expect the oldest genus of a family to keep in front of later ones, for however close to the then limit of the parent the offspring may begin, it will need time to establish itself, during which the parent will be able to progress further. But offspring, once established in the conditions of their birth, may be able to travel in them more rapidly than the parent, which was born under, and medially adapted to, different conditions. There is no evidence that any genus *cannot* go anywhere, given time enough, as the presence in the tropics of so many of the larger (older) genera of temperate regions shows. But that they are not quite at home there is perhaps shown by their small numbers of species, they being again represented by many when they reach the cooler regions of the south. Thus *Ranunculus* has 70 species in SPAIN, 2 in CEYLON, and 41 in NEW ZEALAND.

If distribution is thus so mechanical a process, it fits in better with the ordinary theory of distribution of populations when applied to what one may perhaps call injections of new population at casually situated spots, corresponding to the appearance of new species in our case. Ecology shows that at a certain time and place only those plants can live which have a very considerable degree of adaptation to the conditions then and there existing, the plants that show this adaptation forming there a society or association. But conditions are not permanent even at one place, the mere growth of the plants altering the soil, for example. As conditions change, some plants will disappear, but will usually get their chance elsewhere, while other different species will appear. On the whole, upon large areas and in the long run, *i.e.* in the conditions with which plant geography, as distinguished from ecology, has to deal, dispersal will probably go on at a fairly uniform rate, though some types will perhaps move faster than others. The case is parallel to that of the human society in any one place, where for example the old type of horse-shoeing blacksmith tends to disappear if he cannot adapt himself to the new conditions, and the motor mechanic comes in.

Dispersal being so mechanical, many features should show simple arithmetical relationships. Many of these have already been brought up in [1 and 2], and there are others. YULE [3] has shown that if the law of compound interest be followed, the average proportion of monotype genera in a

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[1] WILLIS, J. C. *Age and Area*. Cambridge (1922).

[2] IDEM *The Course of Evolution*. Cambridge (1940).

[3] YULE, G. U. *A Mathematical Theory of Evolution, based on the conclusions of Dr. J. C. Willis* in *Phil. Trans. Roy. Soc.* B, CCXIII, 21 (1924).

large family should be about 38%. In 31 such families, 8 have 37 or 38%, and 18 in all are between 41 and 35%, a close agreement with theory, with the vicissitudes that plants have to undergo.

We have shown in *Age and Area* how the families, when arranged with their numbers of genera containing one, two, or more species plotted from a base line, form curves of the type which I have termed « hollow »—such curves as are made by a strongly bent bow. Much the largest numbers of genera have only one species, and there is a sharp drop to the twos, and again to the threes. *Compositae*, for example, show 446/1, 140/2, 97/3, 43/4, and so on. The corner is turned between three and five species, and there is a long and gradual tapering out to the largest genus (here *Senecio* with 2000 spp.). In *Age and Area*, 187, I have given these curves for all the largest families, and so accurately is the general arithmetical rule followed that no curve overlaps any other, even approximately, when they are placed parallel to one another. When plotted by logarithms, these curves become straight lines, all with a good general tendency to parallelism, which shows that « inasmuch as all families, both of plants and animals, show the same type of curve, whether graphic or logarithmic, it would appear that in general the manner in which evolution has unfolded itself has been relatively little affected by the various vital and other factors, these only causing deviations this way and that from the dominant plan »[1].

Since the publication of *Age and Area* we have been working out the divisions of all families (sub-families, tribes, etc.), and find that the same rules hold in the great majority, to such an extent in fact that when, as in *Apocynaceae*, they are not adhered to, it is evident that the family, as at present

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[1] YULE and WILLIS *Some statistics of Evolution and Geographical Distribution in Plants and Animals, and their Significance* in *Nature* CIX, 177 (Feb. 9, 1922).

accepted, is unnatural. As a simple, but good illustration, let us take two of the sub-families of *Acanthaceae*, IVA *(Contortae)* and IVB *(Imbricatae)*, and divide each by continents, when we find that the genera confined to each continent run as follows :

				gen.	spp
AMERICA	IVA	12, 10, 4, 2, 2, 2, 15/1 (15 of one sp.).	Total	21	47
	IVB	80, 45, 30, 25, 20, 12, 10, 10, 8, 8, 7, 6, 6, 6, 5, 4, 4, 4, 4, 4, 4, 6/3, 8/2, 32/1		68	373
AFRICA	IVA	35, 15, 15, 12, 8, 7, 7, 6, 6, 5, 5, 5, 4, 2/3, 8/2, 16/1		39	168
	IVB	50, 30, 25, 10, 10, 8, 7, 6, 4/5, 2/4, 4/3, 9/2, 24/1		51	228
ASIA	IVA	25, 25, 15, 8, 5, 5, 4, 2, 7/1		15	96
	IVB	30, 20, 20, 15, 15, 7, 6, 6, 5, 5, 5, 3, 7/2, 6/1		25	157

Total IVA 75 gen., 311 spp. IVB 144 gen., 758 spp.

It is clear from such figures, interpreting them by the light of the four arithmetical laws that we have given above, that important conclusions can be drawn about several things connected with distribution. For example, as to relative age, B is evidently older than A, especially in AMERICA. We have now several hundreds of such curves, for the « continental » ones, like those above, can be split into smaller and smaller hollow curves, for islands, and for portions of the mainland, leading to various inferences as to distribution, a subject which will, it is hoped, form a book to be published by the writer after the war.

It is clear that as under the theory of Divergent Mutation the oldest (world) genus of a family usually occupies (age and area) the largest area of any genus in that family, and as it starts at the very centre of all, it should be the most usual genus to occur in any country in which the family is found. This proves to be the case. In Switzerland for example, 68% of the families of flowering plants contain the oldest (largest) world genus. The second, but not the first, is found in 7%, the third similarly in 5%, the fourth in 1%. In Britain the first genus is found in 71%, in the Balkans in 81%, in Ceylon in 70%, and so on. The further away one goes from the original home of the family, the greater the chance for later genera to have passed the first upon the way (cf. above, p. 127), and in the southern hemisphere the proportion of the latter may fall to 50% or even considerably below that.

We shall expect many of the oldest (largest) genera in the world, as being upon the whole the most widely distributed, to be those most often found in any country, as we have just seen, but as we go down the list to smaller genera we shall expect a smaller and smaller proportion of them to appear in the flora of any given country. Thus if we take four large families from the Ceylon flora, we find

Proportion in Ceylon of genera with	Over 100 spp	51-100	26-50	11-25	6-10	1-5 in the world
Leguminosae	47.8%	21.4%	*27.5%*	18.0%	9.5%	3.1%
Rubiaceae	66.6%	53.3%	23.3%	19.1%	5.6%	3.7%
Orchidaceae	44.4%	37.5%	32.4%	17.5%	6.6%	2.5%
Gramineae	60.0%	*88.8%*	30.0%	23.5%	20.3%	8.4%
Average	51.6%	41.1%	28.4%	19.0%	10.2%	4.3%

The two figures in italics are irregular.

To attempt to make adaptation explain figures like these is evidently absurd.

Endemic or localised genera, which in the large majority of cases contain only one species, more rarely two or more, are supposed by the Darwinian theory to be relics of older vegetation. If so, it is a very remarkable thing that the monotypic genera, which are mostly so restricted in distribution that one would count them as endemic, should fit so well into the arithmetical arrangement given in the last paragraph. One cannot imagine genera becoming relics in arithmetical order, and in steadily decreasing numbers. Nor can one imagine «relics», though in fact it is the case, more numerous in proportion in larger families (which of course have proportionately more potential parents of monotypes) and genera. I have given abundant evidence in *Age and Area* to show that in the vast majority of cases endemics are not relics, but young beginners as genera.

It is clear that with our supposition that families, genera, and species are born each at a single stroke, and that they cannot survive in the hurly-burly of natural selection unless they possess, when born, the needful local adaptation with some further adaptability, we need make no further call upon adaptation to explain distribution in the broad sense. All ecological and local distribution will depend upon the adaptation that each plant has to the local conditions, and upon how far its adaptability will allow it to suit itself to them still more closely. But it was *born with* the adaptation to its birth-place, and did not acquire it gradually. With the adaptability that it must possess in order to survive, it can then become adapted to other conditions that do not differ too much or too rapidly from the first. There exists, all over the world, a vast variety of conditions, to which some species are born upon the spot, while others, born in conditions not too different, will gradually move into them by virtue of their adaptability, thus gradually forming societies suited to each of the many types of conditions that occur.

Exactly similar conditions may exist in places separated from one another by impassable barriers, or by mere distance, so that a plant will not be able to reach all positions where it might succeed, but only such as are attainable in the time allowed. But both adaptation and adaptability are functional, not structural, and are fixed at birth, while distribution is largely mechanical.