The 'Age and Area' Hypothesis and the Problem of Endemism.

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IN a series of recent papers Dr. Willis[1, 2, 3] has brought forward an hypothesis as to plant distribution which is called by him that of 'age and area' and which is based chiefly on his studies of the distribution and affinities of the floras of Ceylon and New Zealand. This hypothesis may be summarized briefly as follows: The area occupied by a given species in a given region in which there occur no well-marked barriers depends in the main upon the age of that species in that region—the older the species, the wider its range. This necessarily involves also the hypothesis that the 'dying out' of a species happens very rarely indeed, and then, it is believed, only by 'accident' or as the result of a geological convulsion or other important environmental change.

The importance of this interesting hypothesis, in support of which Dr. Willis has brought forward an abundance of evidence, would obviously be very great if it should be proved correct. It would upset the traditional belief in Natural Selection as the most important factor in determining distribution. It would make it possible to tell at a glance the relative antiquity of the various elements in any flora and thus to reconstruct with ease the phytogeographical history of a region. It would enable us to identify the most widespread species in a given genus or the most widespread genus in a given family as the most ancient type in that particular genus or family, and thus to clear up at once many vexatious problems of phylogeny. Perhaps no other single hypothesis bears directly upon such a multitude of problems, and its verification is consequently a matter well worthy of our attention. The purpose of the present paper is to bring forward certain facts which

[1] Willis, J. C.: The Endemic Flora of Ceylon, with reference to Geographical Distribution and Evolution in general. Phil. Trans., B, vol. ccvi, 1915, p. 307.

[2] Ibid.: The Evolution of Species in Ceylon, with reference to the Dying Out of Species. Ann. of Bot., vol. xxx, 1916, p. 1.

[3] Ibid.: The Distribution of Species in New Zealand. Ann. of Bot., xxx, 1916, p. 437.

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emphasize the complexity of the whole problem and which throw doubt on the universal applicability of some of Dr. Willis's conclusions.

In the first place there seem to be many factors other than age which are important in determining the extent of territory over which a species is dispersed. No region of any considerable area can be said to be without 'well-marked barriers' of many sorts, such as differences in temperature, moisture, and soil composition, and the presence of competing or parasitic types, all of which are recognized as powerful factors in limiting the area occupied by a species. Ecologists find that even plants growing side by side are frequently living under very different conditions, and that a region which is superficially uniform may actually present considerable environmental complexity and may possess many barriers to certain plant types. A species limited on all sides by effective barriers will not be able to extend its limits, no matter how long it may exist; and with types which have thus reached the boundary of their possible ranges, area of dispersal will obviously afford no clue as to antiquity. 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.

Very many species, however, have apparently not yet attained by any means the extreme possible limits of their ranges, and are still expanding. It is among such types that the relation between age and area may be looked for; but even here, there are such decided differences between plants in the rapidity with which they are able to extend their boundaries that no hard and fast rule can safely be laid down. 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.

Another factor of decided importance in determining the area occupied, and one which is perhaps worthy of special emphasis because it has usually been overlooked, is the growth habit of a species. A. de Candolle noticed many years ago that trees have narrow ranges and herbs wide ones. His list of 117 species which are found over at least half of the land area of the globe includes nothing but herbaceous types. This is probably due in part to the fact that most herbs are able to produce seed in a very short time and in very great abundance, and in part to the fact that their short vegetative period enables them to take advantage of temporarily favourable conditions and to thrive in many places where they would not be able to maintain a permanent existence above ground. It is of interest to note the distribution of the three important growth forms—trees, shrubs, and herbs—represented in Trimen's 'Flora of Ceylon', the data from which furnished the basis for the hypothesis under discussion. Willis divides the species of the island into three groups on the basis of the extent of their range: (1) those which are endemic or limited to Ceylon; (2) those which are of somewhat wider

range but are confined to Ceylon and adjacent Peninsular India; and (3) those which occupy a still wider area. The following table shows the composition, as to growth habit, of these three classes :[1]

TABLE I.

	Trees %.	*Shrubs %.*	*Herbs %.*
Endemic	45	33	22
Ceylon-P. I.	25	35	40
Wide	20	26	54

It is evident that among the endemics, trees possess more than twice as many species as herbs; in the Ceylon-Peninsular Indian class only five-eighths as many, and among the 'Wides' less than two-fifths as many. Shrubs, it will be noticed, are in every case intermediate between trees and herbs.

Still more convincing is a study of the relative areas occupied by members of the three growth forms in Ceylon itself. Trimen divides the species into six classes of progressively greater rarity, using 'Common' in the sense of widespread and 'Rare' in the sense of restricted in range. These classes he designates as Very Common, Common, Rather Common, Rather Rare, Rare, and Very Rare. The percentage of trees, shrubs, and herbs in each class is shown in Table II.[1] (Herbs comprise 37 per cent. of the dicotyledonous flora as a whole.)

TABLE II.

	Trees %.	*Shrubs %.*	*Herbs %.*
Very Common	11	29	60
Common	28	28	44
Rather Common	29	27	44
Rather Rare	35	30	35
Rare	31	33	36
Very Rare	30	33	37

Here again it is evident that herbs preponderate among the 'Common' species but form a much smaller portion of the 'Rare' ones, whereas with trees just the reverse is the case. Figures like the ones cited in these two tables could be multiplied almost indefinitely for other floras. Habit of growth is clearly an important factor in determining the area occupied by a species.

A recognition of the fact that there are many effective influences other than age which decide what a plant's range shall be is not the only difficulty which the 'age and area' hypothesis must meet, for a strict application of it leads to conclusions which are not easy to defend. In the floras of Ceylon and New Zealand, for example, the endemic species have, in the great majority of cases, a much narrower range than do the non-endemic species; and this fact necessarily causes Dr. Willis to conclude that the endemic

[1] Dicotyledons alone considered.

element in a flora is its youngest element, consisting of species which have recently been developed, each in a definite locality, and which have as yet not had time to extend their ranges widely. The non-endemic types he looks upon as the oldest element, the first invaders of a region from abroad which have had time to become widely distributed and common.

This idea that endemics are always young species is open to two objections. First, it disregards the evidence that many endemics are not of local origin but are 'relicts', ancient types which were formerly widespread but which now survive only in isolated corners of the world. We are familiar with many species the range of which is widely discontinuous; for example, that interesting group which is to-day confined to Eastern Asia and to a small area in the south-eastern United States, or that group of antarctic species many of which are also found near the Arctic Circle but nowhere between. In such cases we are driven to the conclusion that these plants were once much more widely distributed, and that if extinction should progress a little farther they would survive in only one of their two present homes. They would then constitute a part of its 'endemic' flora, but would obviously not be of recent and local origin there. Many of the species and genera in Ceylon have to-day a discontinuous distribution similar to that which we have mentioned. They find their co-types or their nearest relatives in the Himalayas, perhaps, in the Malay Peninsula, in East Africa, or in Australia. Many New Zealand species, in the same way, are identical with or closely resemble others found in Patagonia, South Africa, Hawaii, or other distant places, and nowhere else. Such types certainly have the appearance of being remnants of species and genera once much more widely spread, in which a little more 'dying out' would result in the production of forms definitely endemic in one of their present areas. The conclusion is hard to escape that certain of the Ceylon and New Zealand endemics have had such a history. To imagine the monotypic endemic genera, at least (of which there are many), as having arisen by a single leap is to tax heavily the imagination of even an ultra-mutationist.

Another objection to the conclusion that endemics are always of recent development is the fact that in the floras under discussion, and other ancient ones, the endemics include a very much higher percentage of trees and shrubs than do the non-endemics. In a former paper by the writer and Professor Bailey[1] it was shown that in Ceylon the non-endemic species (according to Willis the ancient stock of the island from which the endemics have developed) included only 55 per cent. of trees and shrubs; whereas of the endemic species, 77 per cent. belonged to these woody growth forms. In New Zealand, in the same way, only 19 per cent. of the non-endemic species are woody, but 49 per cent. of the endemics. This rarity of trees

[1] Sinnott, E. W., and Bailey, I. W.: The Origin and Dispersal of Herbaceous Angiosperms. Ann. of Bot., vol. xxviii, 1914, p. 547.

and shrubs in the non-endemic element and their much greater frequency in the endemic element was invariably found in the ancient floras examined and is briefly set forth in Table III.[1]

TABLE III.

	Non-endemic Species.		*Endemic Species.*	
	Woody %.	*Herbaceous %.*	*Woody %.*	*Herbaceous %.*
Australia	38	62	73	27
New Zealand	19	81	49	51
Hawaii	24	76	85	15
Fiji	74	26	98	2
Galapagos	20	80	59	41
Juan Fernandez	6	94	82	18
St. Helena	27	73	77	23
Socotra	15	85	76	24
Mauritius	41	59	87	13
Ceylon	55	45	77	23

In all of these regions the non-endemic element, presumably the original stock, contains a comparatively small proportion of woody forms; but the presumably recent endemic element contains a percentage which averages well over twice as high. This necessarily implies that the production of new species since the colonization of the island has been very much more rapid among trees and shrubs than among herbs. The writer has recently brought forward evidence [2] that just the opposite is apparently the case, and that herbs, from the brevity of their life cycles and their consequent ability to accumulate heritable changes more quickly, are producing new species much faster than are woody plants, where the generation or period from seed to seed is very much longer.

Another objection to the 'age and area' hypothesis is that it necessarily implies a greater antiquity for the herbaceous than for the woody vegetation of the earth. The fact above mentioned, that in all 'ancient' floras the non-endemic element is preponderantly herbaceous, must mean that the original plant population of those regions was composed overwhelmingly of herbaceous species. The general rule which we have cited, that herbaceous species have a much greater average range than woody ones, also implies the greater antiquity of the herbaceous type, if we follow Willis. The consensus of opinion among botanists and geologists, however, is diametrically opposed to this view on account of the abundant evidence that the primitive Angiosperms were woody plants, and that the bulk of our modern herbaceous vegetation is of comparatively recent origin.

In connexion with the hypothesis that 'dying out' of species rarely takes place, we have already spoken of evidence that many plants seem on the high road to extinction. Whether in every case, as Dr. Willis believes, this is due to 'accident' or not, it seems to have been a very common

[1] Dicotyledons alone considered.

[2] Sinnott, E. W.: Comparative Rapidity of Evolution in Various Plant Types. American Naturalist, vol. l, 1916, p. 466.

occurrence, for the very many species, genera, and families among the Angiosperms which are isolated in distribution and in relationships can only be explained (unless we are extreme mutationists) by assuming an enormous amount of extinction to have occurred in the past.

But extinction in this sense seems not to be the only way in which species die out. Dr. Willis believes that the present endemic floras of Ceylon and New Zealand have been developed from species of early arrival in those regions from India and Australia, species which now form the non-endemic and most common element in their respective floras. In the case of Ceylon, however, there are no less than sixty-three genera among the Dicotyledons alone, or 8 per cent. of the whole, which, though not endemic in Ceylon, are represented *only* by *endemic* species. *Dipterocarpus*, *Shorea*, *Hopea*, *Xylopia*, *Euonymus*, *Gymnostachyum*, *Actinodaphne*, *Lasianthus*, *Mangifera*, *Semecarpus*, and others are examples. In New Zealand ninety non-endemic genera of Dicotyledons, or 43 per cent. of the whole, are similarly represented only by endemic species, and among these genera are some of the most important in the islands. In these cases, where is the parent species or group of species in each genus which has supposedly given rise to all these endemic forms and which should now be Very Common? If it has not 'died out', what has become of it? The fact that the proportion of such genera (not endemic but containing only endemic species) is lowest in those regions where the arrival of new species has apparently been of frequent occurrence, and highest in regions which are most isolated, suggests that these parent species tend eventually to disappear altogether. As to what happens to them we cannot be sure. Some may simply be exterminated outright and some, by continual crossing with new forms, may ultimately lose their specific identity. We are tempted to believe that the longer a successfully invading species remains in an isolated area like Ceylon or New Zealand (after its first rapid spread) the less common it tends to become until it is actually 'swamped' out of existence—quite the reverse of the 'age and area' idea.

Certain minor objections may be urged against Willis's conclusions, such as, first, that the great majority of endemic types in Ceylon are on the southern end of the island instead of the northern, the point nearest the bridge to India, where they should be according to analogy from his arguments as to New Zealand; and, secondly, that the flora of New Zealand was in all probability derived not only across a northern bridge from Australia but also, in large part, across a southern bridge from Antarctica at the time of the northward migration of the 'antarctic' flora. This fact should result, according to the hypothesis in question, in the concentration of a much larger number of species at the southern end of the South Island.

There is doubtless much truth in Willis's main contention that, other things being equal, the longer a species lives, the wider the range it will cover.

The chief argument on which the hypothesis is based is the fact, which in the face of the data presented cannot well be doubted, that endemic types have comparatively narrow ranges and non-endemic types comparatively wide ones. To a certain extent, particularly in genera which are rich in endemic species and which seem to be developing new forms rapidly, such as *Impatiens*, *Eugenia*, and *Strobilanthes* in the Ceylon flora, this restricted dispersal among the endemics is doubtless due in part to their youth. In many cases it may also be due to the fact that a given species is a tree and therefore slow to spread. The belief is hard to escape, however, that 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. In previous publications the writer has stated his conviction that in ancient insular floras and those of the great land masses of the Southern Hemisphere the endemic element is in general more ancient than the non-endemic, and he sees no reason to modify this belief; for endemics are either 'relicts' and thus very ancient, or else they represent types which have been in the region long enough so that their original characters have been lost. The hypothesis which perhaps seems to fit best all the facts at hand 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.

The whole problem of endemism is exceedingly complex. We must recognize that there exist two widely different types of endemic forms—'relicts' and 'indigenes'; we must recognize that species differ in their adaptability and competing power and in the rapidity with which they may extend their ranges, and that these factors are very important in determining whether a plant shall be local or widespread; we must recognize that certain types are phylogenetically younger than others and that their distribution is accordingly affected; and we must recognize that plant types differ widely in the rapidity with which they produce new species, and hence in the rapidity with which an endemic element will arise among them. The purpose of the present paper is to point out certain of these complexities and to show that no single hypothesis like that of 'age and area', however valuable it may be in explaining certain facts, can be used as a key to the whole problem.

Summary.

1. Dr. Willis's 'age and area' hypothesis assumes that the area occupied by a species depends primarily upon its age (the older the species, the wider its range); and that 'dying out' of species occurs very rarely.

2. The following objections may be raised against this hypothesis:

(*a*) Many effective factors other than age determine the area occupied by a species, notably physical and climatic barriers, the adaptability of species under different environments, the rapidity with which they may become dispersed, and the growth form to which they belong.

(*b*) An analysis of various floras shows that the hypothesis necessarily implies that trees and shrubs are producing new species very much faster than are herbs, a conclusion against which there is much evidence.

(*c*) The fact that herbaceous species have a much wider average range than woody ones necessarily implies that the herbaceous element in the vegetation of the world is more ancient than the woody element, a conclusion against which there is also much evidence.

(*d*) 'Dying out' of species is apparently taking place in many cases, both by actual extermination, which causes the last survivors to appear as 'relict' endemics; and by the 'swamping' of isolated members of old species by crossing with newly developed forms.

3. The various factors which determine the occurrence of endemism are discussed, and the complexity of the whole problem emphasized.