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THE CANONICAL DISTRIBUTION OF COMMONNESS AND RARITY: PART II

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THE "DEPAUPERATE" FAUNAS AND FLORAS OF OCEANIC ISLANDS

Introduction

For a hundred years or more it has been a matter of comment that remote oceanic islands have limited, often very limited, faunas and floras. There is usually a tacit assumption that adequate faunas and floras never reached these islands, and no doubt there is often merit in the contention. Thus Australia may never have received placental land mammals other than bats, some rodents, the dingo and the Aboriginal. However, it apparently made up for this by developing *in situ* a rather rich fauna of marsupials and some monotremata. Much smaller isolated islands have evolved their own floras and faunas.

However, it is usually true that, area for area, an oceanic island will not have a fauna and flora as rich in species as a piece of a continent; and the present section suggests that this may arise from the fact that islands, if sufficiently remote, act as "isolates," while equal areas on the mainland act as "samples." And we have seen, assuming that individuals are as thick on the ground in the one case as in the other, the sample will have many more species than the isolate for this is the most characteristic feature of a "sample."

Indeed we can go further and show, since we have an approximate relation between the total number of individuals and the total number of species, that some islands that have been declared impoverished or depauperate really have the number of species that should be expected, so that the agreement is quantitative and not merely broadly qualitative.

The fauna and flora of Madagascar and the birds of the Comoros

There is one island, Madagascar, in the world which has apparently been isolated since Triassic times, which is essentially tropical and should

therefore be rich in species and individuals, and which is large and therefore probably suited for statistical examination. It should have developed a well-defined complete canonical ensemble by this time. Its latitude averages 19°S and its area is 2.29×10^5 square miles. According to the 1949 edition of the Encyclopedia Britannica its flora consists of 3178 species that are certain, its butterflies number about 800 species, and its birds 260. Rand (1936) gives 237 species of birds as his estimate.

We have seen in Part I that the 4 Comoro Islands average about 200 mi² in area and have a species-count of breeding birds of 33. Such a count is reached in the eastern deciduous forest of North America at an area of 60 or 80 acres, and in the mainland tropics of Panama at perhaps 8 or 10 acres. Thus it might appear that the Comoros are extraordinarily depauperate. This however is not the right way to look at it.

When the area is expressed in square miles rather than acres, but ρ remains as a density per acre, our formula connecting the expected number of species with area becomes approximately

$$N = 10 A^{0.27} (\rho/m)^{0.27}$$

and if we assume that $m = 1$ approximately, as it has often been found to be, and if $\rho =$ one pair per acre, this gives $N = 10 A^{0.27}$, which for Madagascar comes to 280 species.

This calculated figure represents almost perfect agreement with observation so far as birds are concerned. And even if ρ and m differ somewhat from our simple estimate, they occur to a low fractional exponent, so the estimate of N will not change greatly. We might venture to say therefore that Madagascar is not depauperate in the number of species of birds. A similar computation for the Comoros calls for a breeding bird count of 40 species per island, as against the observed average of 33. So if the avifauna is "depauperate," it is only slightly so.

The explanation is that on isolated islands we must have an approximation to internal equilibrium and presumably to a self-contained canonical distribution and, since an island can hold only a limited number of individuals, the number of species will be very small. But on the mainland a small area is not in internal equilibrium; it is in equilibrium with areas across its boundaries and is a sample of a vastly larger area. This is a matter that does not seem to have been considered previously in studies of Species-Area relationships.

Returning once more to Madagascar, we find that the situation with butterflies and plants is less easily tested but comes out reasonably. For butterflies, 800 species of them, if we assume that $m = 1$ but ρ has to be found, then using the same formula we get $\rho = 50$ per acre. This is perhaps reasonable. The computation is obscured by the uncertainty as to whether we count caterpillars as well as adults or whether we count the total number of adults produced in a generation and divide by the area of the island.

For plants, a similar computation gives $\rho = 9,000$ plants per acre or 2 plants per square yard. This again is well within the limits set by Williams, who indicates that we can expect less than one plant per square yard in forest, though a good many more in grassland. So far as the meagre evidence goes, it does not indicate that Madagascar is depauperate in birds, butterflies, or flowering plants. I may mention in passing that the Butterflies of Java by a similar computation, with 500 species or more on 48,000 square miles, come out at about 40 (individual) butterflies per acre, which is comparable with the figure for Madagascar.

The birds of Australia

This island continent of roughly 3×10^6 mi² is certainly peripheral and somewhat isolated so far as birds are concerned, though not so thoroughly isolated as it has been for mammals. In latitude it is partly temperate, partly tropical. Much of it is desert, and it seems unlikely that bird-density will be much more than one pair per acre, averaged over the whole continent. If the continent is acting substantially as an isolate, with a complete canonical distribution of abundance among its birds, then we should expect about 556 breeding species, and this is just about what we do find.

New Zealand and other remote islands

The area of New Zealand is about 103,000 mi². It has no snakes and virtually no native mammals. The implication is that if mammals are introduced, a substantial number of species can establish themselves, thrive, and co-exist, and this seems

to have been proved by experiment. I do not think the same experiment has been tried with snakes, but a guess can be made that it would support a few species, though it lies in rather high latitudes. When first discovered by the white man it was fairly well off for native birds and it was still better off before the Maoris went to work on the Moas. Theoretically it might hold about 250 species. If the native species were much fewer than this, a substantial number of introduced species could make good; and many have, though they may not represent an ecologically balanced fauna.

A number of other islands may be examined, with data provided by de Beaufort (1951) or Darlington (1957). For instance New Caledonia, with an area of 6500 mi² is credited by Darlington, quoting Mayr, as having 68 native species of land and fresh water birds. No doubt it has sea birds too. With one pair per acre, we should expect about 107 species, somewhat above the observed total of 68 for land and fresh-water species only.

Much smaller Lord Howe Island is credited by Darlington with 5 mi² and about 15 native species, some of which are now extinct. The computed expectation is about 16 species. Norfolk Island (Darlington, p. 526) is 13 mi² in area and has 14 or perhaps slightly more native species. The expectation is roughly 20.

All of these values are subject to the hypothesis that $m = 1$ and ρ (birds per acre) also is unity in our basic equation, and we know that there could be little stability if the rarest species were actually down to a single pair. Thus m is probably more than 1. If it is about 5 pairs and the other species are likewise adjusted, the computed value of N , the total number of species, would come out some 30% less. Generally speaking, for the examples thus tested, the agreement is good.

We may note that the conclusions we have tentatively advanced seem to be in direct opposition to those of Yule (1925), who, in a footnote says, "I see no practical limit to the number of species, but only to the total number of individuals." According to my view, the number of individuals sets a limit to the number of species and, in an "isolate," virtually specifies the number of species within rather narrow limits. It might be possible to check the interpretations of the present paper if a reasonably good estimate could be made, not only of the number of species of some taxonomic group, but also of the number of individuals of each species.

WHAT IS AN ISOLATE?

The question of what constitutes an "isolate" deserves consideration. We have seen that for

land animals (and perhaps plants) islands are examples of isolates, but they are not necessarily the only ones. Referring to Fig. 37, we have a set of curves plotting the course of isolates of different size and of different ρ/m values. We also have 2 curves showing the course of samples, and these curves cut through the others. They are flatter than the isolate curves at the left end but, as the size of the "quadrat" increases and we move toward the right, they reach a point where they lie among the isolate curves without crossing them. Here they are behaving for some distance as if they were isolate curves. This happens when, as in the case of the Nearctic birds, rather large areas are involved, comparable with the whole area of the eastern deciduous forest. It might appear that that forest is itself somewhat of an isolate so far as breeding birds are concerned, but this is a biological problem, and it probably does not depend on sharp ecotones at the forest edge. From our point of view in the present paper, a thing is an isolate that acts like one, that is, if we can increase and diminish its size considerably and find it to obey the law $N \propto A^{0.27}$ over this range. This probably happens at very different size ranges for different phyla.

It seems probable that the matter can be stated thus: with small quadrats our areas are "samples." The equilibrium of the sample is decided by external forces acting from beyond the perimeter. As the size of the quadrat increases the perimeter increases linearly with the diameter but the area increases as the square thereof. A point is therefore reached at which the external forces become insignificant compared with the internal forces. It is now the internal equilibrium that is important, and thus any area that is big enough (and its size depends upon the phylum we are considering) acts like an isolate whether it is visibly an isolate or not.

Since this is surmise, it should not be accepted uncritically till adequate evidence is forthcoming. This can probably be best provided by plant ecologists and perhaps more especially by studies of plants in the tropical rain forests. From what we know at present it will be no small undertaking to deal with plants running into several hundred species per quadrat; the quadrats may have to be very large.

A theoretical picture of isolates and samples

At the moment it seems unnecessary to consider the question of how isolated an isolate has to be. Obviously isolation can be imperfect and usually it is a matter of degree. Until more precise information becomes available we may get some

useful background by studying a theoretical situation.

Suppose that the earth has a diameter (d) of 8000 miles; its surface area is $\pi d^2 = 2 \times 10^8$ mi². Suppose that from the equator north and south to Latitude 30° it is a uniformly excellent habitat for birds and that beyond this belt it is so poor as to be negligible. (The supposition would be much more nearly true of many groups other than birds.) Then the area of the central belt is $\pi d^2/2 = 10^8$ mi². Suppose that the belt is land and the rest is ocean. If this were a single area of land averaging 1 pair of birds per acre and if $n = 1$ for the whole ensemble, the number of species we could expect would be

$$N = 10 A^{0.27} = 1450 \text{ approximately.}$$

Now suppose that we surrender half this area to the sea by making straits across it from north to south, each strait 50 miles wide and each strip of land 50 miles wide. Then we shall have 250 such strips and 250 such straits. Let us suppose that birds rarely cross those straits so that we have 250 ecological ensembles that evolve substantially separately, each on an area of $10^8/500 = 2 \times 10^5$ mi². Then the stable equilibrium for each island is $N_1 = 10(2 \times 10^5)^{0.27} = 270$ approximately, and on the whole 250 strips the number of species is $\Sigma N_1 = 250 \times 270 = 67,500$.

Note that this tremendous increase in total species, in the ratio of $67,500/1,450 = 47$ fold, is in spite of our having reduced the total land area of the world by a half and delivered $3/4$ of all the earth to the ocean. Note also that the area of each strip is comparable with the area of Madagascar, which has 2.29×10^5 mi² and that its avifauna, 270 species, is comparable with that of Madagascar which has about 260 species.

Each of our strips is about 4000 miles long from north to south. Let us cut 39 channels through them from east to west, each channel 50 miles wide, leaving islands now about 50×50 miles in size, 10,000 of them all told. Again let us suppose that birds rarely cross from one island to another so that speciation can occur and ultimately we have 10,000 separate and different, but complete, ensembles. Then each island should have $N_2 = 10(2500)^{0.27} = 82.5$ species and the whole 10,000 islands have $\Sigma N_2 = 825,000$ species of birds.

This again is a big increase in total species in the world in spite of our having once more reduced the land area by half, and delivered now $7/8$ of the earth's surface to the oceans. Note that each island, with 2500 mi² area, is comparable with Puerto Rico (3435 square miles), and its 83

species more or less comparable with Puerto Rico's 79.

Let us now go back to our original continuous belt of equatorial land. We separate out just one single island of 2500 mi² by a strait which birds have not crossed since the early Pliocene and keep the rest of the belt intact. The island has 82 species of birds, the continent 1450. We now drop a quadrat, as large as the island, upon the continent. This will be a "sample" of the continent, and it should have a truncated lognormal distribution, not a complete one. It will therefore be much richer in species than the island.

Let us suppose that as we shrink or swell the size of the quadrat, we find that it gives a value of z of 0.14. This is the average of the values for the Nearctic avifauna ($z = 0.12$) and for the Neotropical ($z = 0.16$) (Preston 1960). It corresponds, as we have seen, to a sample which extends about one standard deviation beyond the mode.

If we make the further assumption that this value of z holds good to a fair approximation for all sizes of quadrat from the original continental size downwards, then the number of species we can expect is given by

$$N_3/N = (A_3/A)^{0.14} = (2500/10^8)^{0.14}$$

which, since $N = 1450$, gives $N_3 = 329$ species. This is the count for the continental or mainland quadrat, compared with the 82 species we can expect on an island of the same size, and it comes about because the island must adjust its count of species downward till the individuals make a complete lognormal, while the quadrat is under no such restriction. If we were to take all the species of birds that occur on the mainland and plant them on the island, preventing any from crossing the channel under their own power, the results would be the same; on the island the 1450 species would dwindle to about 82. It seems to me possible that it is this situation that keeps oceanic islands seemingly "depauperate," rather than the infrequency of landfalls of additional species of birds.

We can carry the argument down to an island and quadrat of 90 acres. The island should have a population consisting of 6 species of birds and the quadrat might have as many as 78 species. (In the case of the island the number of species is too small to make up a good lognormal ensemble, so it is subject to great statistical uncertainty.) The quadrat also might be precarious; it has no surplus of species for good statistical estimation, but probably has enough. The actual number of breeding species on the quadrat depends on how many years we watch. Hicks (1935), studying

80 acres, averaged 63 species in a single year and accumulated 86 species in 10 years.

Computing the number of species of higher plants in the world from a knowledge of the number of species of birds

This may be regarded as a slightly far-fetched but amusing exercise. If there were no isolates or partial isolates of birds in the world the total number of species would not reach 2000, assuming that over the land surface of the globe the density of birds averages around one pair per acre. Actually there are about 9000, so that the world is the richer for the degree of compartmentalization that at present obtains. We might make the assumption that the means of dispersal are comparable for birds and plants and that the amount of compartmentalization is therefore somewhat similar. However, the number of plants to the acre is enormously greater than the number of birds. It is hard to define what constitutes an individual plant but suppose we assume that, taking into account forests, deserts, and grasslands, with their widely varying concentrations of plants per unit area, the average density comes out at one plant per square foot.

Assume furthermore that m has the same value for plants and birds, and that the total area available to both groups is similar. Then the ratio of species of plants to species of birds should be $(\text{one acre/ft}^2)^{0.27}$ or $(44000)^{0.27} = 18$, and so the total species of plants should be about 18×9000 or about 160,000. Dr. O. E. Jennings of Carnegie Museum says that in 1941 the known Angiosperms and Pteridophytes totaled about 200,000. The agreement is good, but is largely fortuitous, since the estimate that there might be one plant to a square foot is obviously rough in the extreme.

An equally rough calculation could be made on the total number of insects. At Rothamsted in England the soil insects alone, in fertile soil, were estimated at 8×10^6 to the acre, some 180 times the density we assumed for plants and about 1.5 per in.² In the tropical forest the insects are stacked on top of one another from below ground to the highest treetops and the biting and stinging kinds at least are very plentiful. It seems probable that over a large part of the land surface of the earth there are several insects per square inch, and if so the total number of species should be of the order of a million. Less than this number have been described but considerably more than a million are believed to exist.

Summary

It will be evident that from a mathematical

standpoint the difference between isolates and quadrats (or samples) is that the one has a species-area curve which (on a log-log basis) has an exponent around 0.27, while the curve for the other has an exponent that may be only half this. When the quadrat is enlarged till it becomes equal to the isolate or quasi-isolate, perhaps the continent of Australia or the eastern deciduous forest area of North America, the quadrat and isolate are indistinguishable and must have the same fauna. It is when we go to smaller areas that the great difference in faunal or floral richness manifests itself. It is simply a matter of whether we are descending a steep slope or a gentle one, on the lognormal curve.

From a biological, as opposed to a mathematical, viewpoint the matter seems equally simple. In a sample, such as the breeding birds of a hundred acres, we get many species represented by a single pair. Such species would be marked for extinction with one or two seasons' failure of their nests were it not for the fact that such local extirpation can be made good from outside the "quadrat," which is not the case with an isolate. Indeed, we can imagine that if some night, when breeding was in full swing on our quadrat, the rest of North America were to disappear beneath the sea, the 50 or 60 species of land birds on our hundred acres would in the course of a year or two be reduced to 5 or 6. Similar reductions would take place over the years in plants and insects.

THE BEHAVIOR OF GENERA AND FAMILIES

Introduction

Hitherto we have concentrated on species. This taxonomic unit is occasionally hard to define, but it is usually conceded to be less arbitrary than a genus or a family. Since broad questions of taxonomy are outside the scope of this paper, I think we must assume that a species is a natural unit and that we know pretty much what we mean when we talk of a species.

It follows, I think, that in the present paper we should work with species when we can, as being the most natural of units, but sometimes this policy cannot conveniently be followed. With pollen, for instance, fossil or recent, it is often much easier to classify to genus than to species, and much of the published information is in genus form. Again, in trying to use the fossil record of most animals, we find that most species have left no fossil record, but the record may be reasonably complete for families. Still again, if we wish to compare the present-day (or some earlier) fauna of one region with that of another, we may wish to compare them at some taxonomic level

other than that of species. For instance the bird faunas of western North America and of eastern North America may appear distinctly different at the species level but very similar at the family level. And once more, for some of the less well-known groups of animals we may not even know the geographic range for a large fraction of the species though we may have a good idea of the distribution of genera or families. For this reason, Wallace (1876) tended to concentrate on the higher categories, and more recent zoogeographers also have found it convenient to do likewise.

Before we can use the principles of this present paper in some applications, therefore, the question arises as to what happens if instead of assigning individuals to species we assign them directly to genera or families. Will the distribution be lognormal? Will it be not merely lognormal but canonical? If so, is the fact biologically significant or does it arise by accident? Does it come about because, if species have a well defined lognormal distribution, it is going to take a major effort to produce an arbitrary set of genera or families in which a substantial image of the species-distribution is not discernible?

Let us examine some instances where the number of individuals is large, and the number of species seemingly sufficient, and see what happens if we use genera and families instead of species. Then let us also invent absolutely artificial pseudo-genera and pseudo-families by combining the species by means of "random numbers" into completely meaningless groupings. The examples I propose to take are Merikallio's breeding birds of Finland and the 7-year total of Audubon Christmas bird counts of North America.

Orthodox Genera and Families

The birds of Finland

Merikallio's (1958) breeding population may be assigned to 206 species or to 119 genera or 41 families. He rounds off his estimates, as a rule, to no more than 2 significant figures; this seems a very proper procedure, and even so I suppose it is possible for the 2nd of these figures to be somewhat in error. Accordingly we have computed the distributions on the basis of the number of digits that appear in the count, for instance, from 10,000 to 99,999 there are 5 digits in the count, the logarithms lying between 4.0 and 4.99; then we have computed the means and standard deviations by an approximate method based on the number of digits rather than on the actual logarithms. In each case the distribution is roughly lognormal, though slightly skew because of the

TABLE XIV. The breeding birds of Finland assigned to species, genera and families*

Assigned to:	Q	Logarithmic Means	σ Orders of Magnitude	σ Octaves	a-Modulus of Precision	y_0 Modal Height
Species....	206	4.27	1.405	4.7	0.151	58.7
Genera....	119	4.50	1.501	5.0	0.142	31.7
Families...	41	5.00	1.500	5.0	0.142	10.9

*The Modulus of Precision assumes that the abscissa is measured in octaves; the modal height assumes that the abscissa is measured in orders of magnitude. The logarithmic mean is the average number of digits at the mean, not the logarithm of the average number of individuals in a species at the mode.

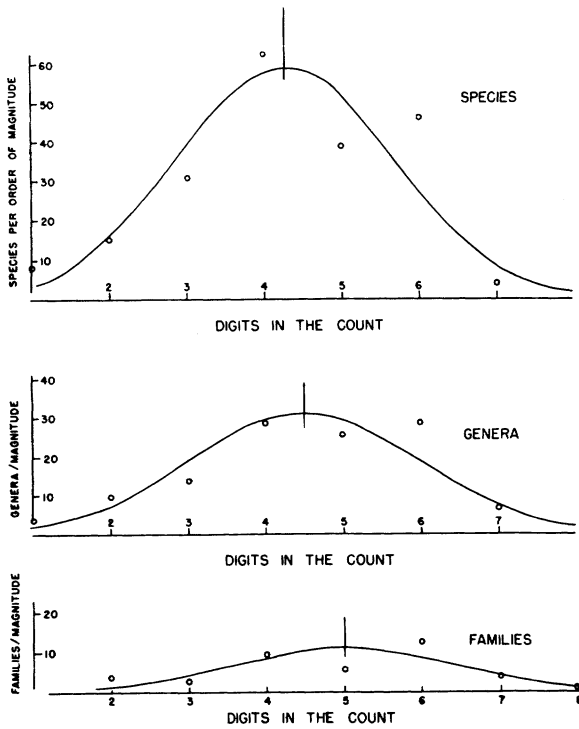


FIG. 32. Lognormal curves for species, genera, and families using Merikallio's Birds of Finland.

large number of species that have 6 digits in the count, *i.e.* that have between 100,000 and 999,999 individuals.

In Table XIV we give the essential data, and in Figure 32 we graph these. Note that the standard deviation remains approximately constant near 1.45 orders of magnitude or a little less than 5 octaves. This is a little higher than we expect on theoretical grounds, which would call for 4 octaves or slightly less for genera and families. The ratio of standard deviation to average is substantially constant at 30%. It seems therefore to be a logical expectation that if we used subspecies, on which we have no information, we should again come out with the same standard deviation. The other quantities listed in Table I are of less interest at the moment. The constant "a," the modulus of precision, is calculated as

$a = 1/\sigma \sqrt{2}$ where σ is in octaves, and the modal height y_0 is computed from $y_0 = Q/\sqrt{2\pi} \cdot \sigma$, where σ is in orders of magnitude, to fit the present comparison.¹

The Audubon Christmas bird counts of nearctic America

These counts involve more species, genera, and families than the birds of Finland, and to that extent may be an improvement. The counts are not strictly random but are probably satisfactory. After omitting 44 species that were not encountered at all in the first 4 years we have about 83 million individuals accumulated in 7 years (Preston 1958), assignable to 516 species or 280 genera or 67 families. In Table XV we give the distribution and in Figure 33 we graph it. It

TABLE XV. The Audubon Christmas bird counts assigned to species, genera, and families

Assigned to:	Q	Logarithmic Means	σ Orders of Magnitude	σ Octaves	a-Modulus of Precision	y_0 Modal Height
Species....	516	3.562	1.54	5.1	0.139	133.5
Genera....	280	3.921	1.54	5.1	0.139	71.7
Families...	67	4.91	1.39	4.6	0.154	19.2

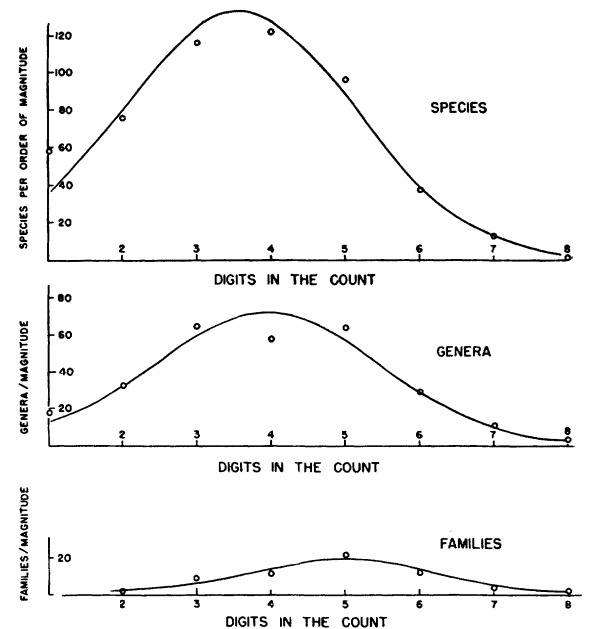


FIG. 33. Lognormal curves for species, genera, and families using the Audubon Christmas bird counts for North America.

¹ Here I have written Q rather than N , to distinguish the observed number of species from the number theoretically present, which would be a little higher, at least in the Audubon Christmas count that follows. A similar remark applies with slightly less force perhaps, to genera. In the case of families it is probable that $Q = N$ to all intents and purposes.

will be observed that the standard deviation has roughly the correct value, the theoretical value being 4.5 octaves, at the species level and declines slightly, as it should, as we go to families, which are fewer in number. It thus appears likely that the distribution is not only lognormal but canonical to a fairly good approximation whether we are dealing with species, genera, or families. The implication seems to be that the taxonomists have done a good job of producing a fairly natural phylogenetic classification.

Pseudo-genera and pseudo-families

There are necessarily fewer genera, and still fewer families, than species. It happens that in the Nearctic avifauna there are roughly half as many orthodox genera (280) as there are species, and about one-eighth as many families (67). We may for our purposes construct an artificial set of categories, declining in the ratio $\frac{1}{2}$ (for genera), $\frac{1}{4}$ (for subfamilies), and $\frac{1}{8}$ (for families). To accomplish this we deleted, by random methods, 4 species out of the (genuine) total of 516, leaving 512, and so produced 256 pseudo-genera, 128 pseudo-subfamilies, and 64 pseudo-families. Having obtained the number of individuals in these various pseudo-taxa, we can calculate the logarithmic standard deviation at each pseudo-taxonomic level, and compare it with what we expect from theory and also (except that this was not done for subfamilies) with what we obtain with orthodox, *taxa*.

In the first test we assigned 2 species to each genus, 4 to a subfamily, and 8 to a family. The new pseudo-taxa contained some strange combinations, such as loons mixed with passerines. In a 2nd test we distributed the species by still more random methods to 64 families in such a way that not only did the species have strange bedfellows, but varying numbers of species arrived in the same bed, in this case in the same family, for we tested only at this level. The results of the 2 random methods were not very different from one another, but were very different from the results obtained with the orthodox taxa. The criterion in each case is simply the value of σ that we obtain.

Note first that according to the canonical hypothesis the σ -value to be expected decreases with decreasing number of "species" or, in this case, taxa. So we must expect a lower value of σ for families than for species, which are 8 times as numerous. In Figure 34 we have drawn as a heavy line the theoretical expectation. In the original report on these Audubon Christmas counts (Preston 1958) we noted that the logarithmic

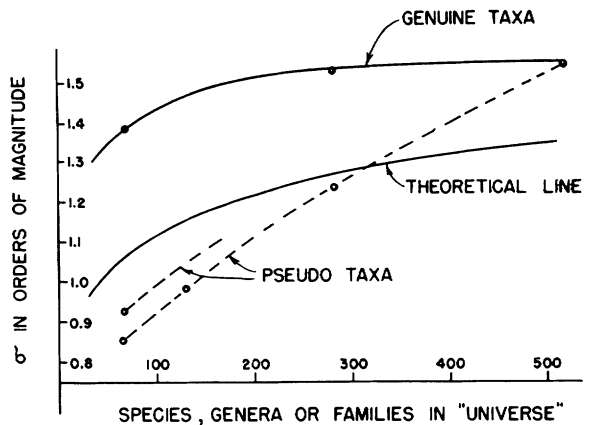


FIG. 34. Comparison of Logarithmic Standard Deviations for genuine taxa and pseudo-taxa, using Audubon Christmas bird counts. Also the theoretical relationship if the counts reflected nothing but actual commonness (and not conspicuousness or other matters).

standard deviation was somewhat higher than we had expected, and I tentatively ascribed it to some species being so much more conspicuous than others. With the more accurate methods of the present paper, we find that, while some dispersion still exists, it is not so much above expectation as was then thought. Whether this is due to conspicuousness as such, or to the fact that in mid-winter many species are "flocking," and therefore "positively contagious," or to both of these factors or to neither of them, I am not at present clear. I merely record the fact, and also the fact that this rather high value persists at the genus and family level. The upper unbroken line of Fig. 34 parallels the theoretical line fairly well, and I construe this as meaning that the taxonomists have probably produced a fairly "natural" taxonomy for North American birds.

When we come to the pseudo-taxa, a very different kind of curve results. This is shown by the broken lines of Fig. 34. The standard deviation falls off very rapidly, and quickly passes below even the theoretical line. This seems to mean that we are producing too uniform a series of families (for instance) which hold too nearly similar numbers of individuals. The distribution is becoming over-regularized. This happens for both our methods of sorting the species into false categories.

The data from which the figure is constructed are given in Table XVI. This examination suggests that genuine higher taxa may be treated very much as we have found practicable with species. Admittedly it proves nothing about the taxonomy of insects or molluscs, or even the taxonomy of birds other than nearctic ones. I

TABLE XVI. Comparison of pseudo-taxa with orthodox taxa and with theory = Audubon Christmas bird counts. σ -values (and N values in brackets) : σ is in orders of magnitude, not octaves

	Species	Genera	Subfamilies	Families
Genuine, or orthodox...	1.54 (516)	1.54 (280)	—	1.39 (67)
Pseudo-taxa with equal numbers of species per taxon.....	1.543(572)	1.242(256)	0.976(128)	0.854(64)
Pseudo-taxa with random numbers of species per taxon....	1.54	—	—	0.926(64)

think however that we may, with some caution, proceed on the assumption that any reasonably competent taxonomy is likely to be usable for the purposes of the present paper.

THE EQUILIBRIUM OF QUASI-ISOLATES AND THE SIMILARITIES OF THEIR FAUNAS AND FLORAS

Introduction

We might almost describe the early part of this section as dealing with interactions across a boundary. Some islands, or even continents, betray a large degree of isolation from one another but such isolation is rarely complete and has not been complete over the geological past. Otherwise some areas would be as barren as the moon.

Consider 2 hypothetical islands, A and B, of exactly equal size and very similar topography, climate, and tropical latitude. They may have a luxuriant vegetation and be the home of many land animals. Let them, however, be separated by a sufficient distance so that land plants and animals can rarely be exchanged between them and let them be sufficiently far from a mainland to prevent frequent landfalls from the continent.

It may appear that there is nothing to prevent the 2 islands having identical floras and faunas. This is theoretically conceivable, but statistically most unlikely. We can, for instance, imagine that the islands each have the same 50 species of land birds, and of each species each island has identical numbers of individuals. In practice, since the numbers of a species vary from season to season as the young hatch or the old die, and fluctuate from year to year, it is not likely that the count of individuals will at any instant be identical. And it is still less likely for plants or insects. But it might appear that we could reasonably expect identical species.

Now bring the islands closer together, till they touch, and we have in effect a single island, C. This has an area twice as large as either A and B, and its equilibrium number of species is therefore $2^{0.27} = 1.21$ times as many as A or B, but it

actually has only 50 species, the same as A or B. The combined island is depauperate to the extent of some 21% of its proper number of species.

It follows that even before we brought the islands into contact, if they were not eternal isolates but were in some degree of biological contact and therefore of interaction and of equilibrium, they should have 21% more species than either one taken separately. They must have had a number of species in common but each must have had some that the other did not. Thus equilibrium is not attained with identity of species. If too many species are identical the islands may be regarded as biologically separate but as being samples of one another or of some larger area. If too few species are identical, then there is insufficient interaction between the islands. They are isolates, and have been for some time. Their degree of isolation, or the length of its duration, can be ascertained in mathematical terms and stated quantitatively. It will be, in general, different at the species level from what it is at the genus or family level. It becomes particularly interesting to investigate the similarity of the major zoogeographical regions.

The resemblance equation

Let us remove the restriction that the islands must be of equal size. Let their areas be A_1 and A_2 , so that their combined area is $A_1 + A_2$. Then the number of species on the one should be, from Equation 18, $N_1 = K A_1^{0.27}$, on the second $N_2 = K A_2^{0.27}$, and on the combination it should be

$$N_{1+2} = K(A_1 + A_2)^{0.27} \tag{34}$$

and K ought to be the same constant in all cases. If N_{1+2} satisfies this condition we may say that the areas are in equilibrium across their boundary. If it does not satisfy the condition it will satisfy

$$N_{1+2} = K(A_1 + A_2)^z \tag{35}$$

where z , which is assumed to be the same for the 2 areas, and is the exponent of the Arrhenius equation is some value other than 0.27. The equation is better written in reverse:

We have $A_{1+2} = A_1 + A_2$
 so $(N_{1+2})^{\frac{1}{z}} = (N_1)^{\frac{1}{z}} + (N_2)^{\frac{1}{z}}$ (36)

and this is merely a statement that the areas are additive.

If the 2 areas are in fact very similar, Equation (36) may be regarded as a statement of equilibrium, but if they are not, the equation may be regarded as a statement of resemblance. It will be satisfied for some value of z between zero and unity, and the numerical value of z will specify quantitatively the degree of resemblance.

Since we have restricted " N " to species, and

there is no reason why the similarity or resemblance should not be examined at the genus or family level, I prefer to write F for N , where F is a mnemonic for Family or Fauna or Flora. Then dividing throughout by F_{1+2} , and writing n for $1/z$, we have

$$\left(\frac{F_1}{F_{1+2}}\right)^n + \left(\frac{F_2}{F_{1+2}}\right)^n = 1$$

or still better, $x^n + y^n = 1$ (37) which I call the Resemblance Equation. Here x is the fraction (of the joint wild life) that is found on the first island, y is the fraction found on the 2nd. Both x and y are positive and lie between 0 and +1.

A quantitative statement of the resemblance between 2 faunas or between 2 floras has been sought by zoologists, and a number of formulae have been proposed. Simpson proposed a formula, and Burt (1958) criticized it on the grounds that the outcome depends on whether you take the larger (more populous) area or the smaller one first, a point which Simpson (1960) conceded. This difficulty does not arise if we use Equation (37). The resemblance of 2 areas is given by the value of n (or its reciprocal z) that satisfies Equation (37), and it does not matter which area has the subscript 1 and which has the subscript 2. The equation is completely symmetrical and gives only one answer.

The value of z lies between 0 and 1. If it is very near to zero, the faunas (or floras) are identical. If it is unity, they have not a species (or family) in common. If it is 0.27, the 2 areas act as if they are isolates in complete equilibrium with one another. If the index is less than 0.27 the two areas are "samples" of some larger unit, perhaps of their joint area. If it is above 0.27, but below unity, there is some degree of interaction, but it is incomplete, and there is, and long has been, some degree of genuine isolation. Examples of all these situations are given below.

It should be noted that the expression is not empirical, but goes back to first principles. The only serious objection to it that I can see is that it is a transcendental equation, whose solution cannot, except in one or 2 special cases, be written down immediately on inspection. This practical difficulty we now proceed to deal with.

Solving the resemblance equation

If $F_1 = F_2$, so that $x = y$, the solution is simple:

$$2x^{1/z} = 1, \text{ and } z = -3.32 \log x \quad (38)$$

(Since x is less than unity, $\log x$ is negative, and z is positive.)

If x is nearly equal to y

$$z = -3.32 \log \left(\frac{x+y}{2}\right) \text{ approximately.}$$

A more accurate result is obtained by biasing $(x+y)/2$ in favor of the larger value.

Suppose x is the larger: then

$$z = -3.32 \log (0.6x + 0.4y) \quad (39)$$

gives a fairly close estimate, valid at least as far from equality as $x = 2y$.

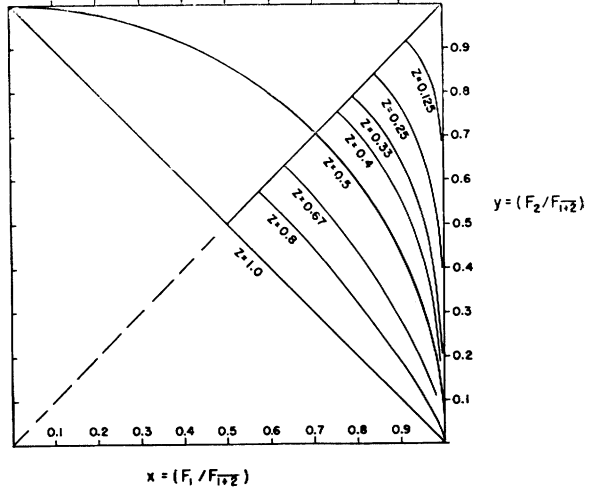


FIG. 35. Graphical depiction, and solution, of the Resemblance Equation. Here z is the index of the resemblance equation, the quantity which we wish to estimate. F_{1+2} is the total number of species in the 2 areas to be compared, F_1 , the number in the first area and F_2 the number in the other.

Graphical solution

Some examples of Equation 37 are graphed in Figure 35. We note that whatever the value of n or $1/z$ ($n > 1$), the equation is always satisfied at the points 0,1 and 1,0, so all the curves must pass through these 2 points. We note also that if $n = 1$, we have a straight (sloping) line passing through these 2 points.

Again, if $n = 2$, (or $z = 0.5$, we have a circle passing through these 2 points and with its center at the origin, ($x = y = 0$). Also since $dy/dx = -(x/y)^{n-1}$, then, provided only that $n \neq 1$, the tangent to the curve is always horizontal at 0,1, and always vertical at 1,0. Since the equation is not changed by interchanging x and y , the curves are symmetrical about the diagonal line $x = y$.

Finally, since x, y , and n are necessarily positive, the whole family of curves lies within the square 0,1; 1,1; 1,0; and 0,0. In fact, since z can range only from zero to unity, all curves lie in the upper right-hand half of this square, and if we choose to let x be the larger of the 2 values, our graph can be confined to a triangular area equal to $1/4$ of the square.

Example

Suppose $F_1 = 40, F_2 = 20, F_{1+2} = 44, C$ (number of taxa common to both areas) $= F_1 + F_2 - F_{1+2} = 16$. We have $x = 40/44 = 0.91$ $y = 20/44 = 0.455$ and plotting this point on the graph we see that it lies between $z = 0.4$ and $z = 0.5$, and closer to the latter, so that we estimate $z = 0.47$.

TABLE XVII. Solution of the resemblance equation (See text for explanation) *

x/y	0.52	0.54	0.56	0.58	0.60	0.62	0.64	0.66	0.68	0.70	0.72	0.74	0.76	0.78	0.80	0.82	0.84	0.86	0.88	0.90	0.92	0.94	0.96	0.98
0.02	1.00000																							1.00000
0.04	0.92216																							1.00000
0.06	0.85334																							1.00000
0.08	0.79525																							1.00000
0.10	0.74746																							1.00000
0.12	0.70866																							1.00000
0.14	0.67716																							1.00000
0.16	0.65181																							1.00000
0.18	0.63123																							1.00000
0.20	0.61481																							1.00000
0.22	0.60176																							1.00000
0.24	0.59145																							1.00000
0.26	0.58328																							1.00000
0.28	0.57681																							1.00000
0.30	0.57173																							1.00000
0.32	0.56781																							1.00000
0.34	0.56492																							1.00000
0.36	0.56295																							1.00000
0.38	0.56181																							1.00000
0.40	0.56145																							1.00000
0.42	0.56173																							1.00000
0.44	0.56259																							1.00000
0.46	0.56384																							1.00000
0.48	0.56547																							1.00000
0.50	0.56746																							1.00000
0.52	0.56977																							1.00000
0.54	0.57239																							1.00000
0.56	0.57525																							1.00000
0.58	0.57834																							1.00000
0.60	0.58157																							1.00000
0.62	0.58492																							1.00000
0.64	0.58834																							1.00000
0.66	0.59181																							1.00000
0.68	0.59539																							1.00000
0.70	0.59907																							1.00000
0.72	0.60286																							1.00000
0.74	0.60675																							1.00000
0.76	0.61073																							1.00000
0.78	0.61481																							1.00000
0.80	0.61899																							1.00000
0.82	0.62328																							1.00000
0.84	0.62767																							1.00000
0.86	0.63216																							1.00000
0.88	0.63675																							1.00000
0.90	0.64145																							1.00000
0.92	0.64623																							1.00000
0.94	0.65111																							1.00000
0.96	0.65609																							1.00000
0.98	0.66117																							1.00000

* The figures are the values of z that satisfy the equation $z^2 + y^2 = 1$.

By the analytical method we have

$$\begin{aligned}
 z &= -3.32 \log \\
 &(0.6 \times 0.91) + (0.4 \times 0.455) \\
 &= -3.32 \log (0.728) \\
 &= -3.32 (\bar{I}. 862) = -3.32 (-0.138) = 0.46
 \end{aligned}$$

in close agreement with the estimate from the graph.

Interpretation of z

z is a measure of the dissimilarity of 2 faunas or 2 floras. If *z* = 1, its limiting value at one of its range, the faunas are completely dissimilar; there are no taxa in common. If *z* approaches zero, at the other extreme, there is no dissimilarity; there are no taxa in the smaller group that are not present also in the larger one.

Solution from a table

I have not been able to find any tabulation of the function which we have called the Resemblance Equation, but through the courtesy of the Owens-Illinois Glass Company and Mr. T. C. Baker, head of the physics laboratory of that firm, and Mr. Charles Cook, chief of the computer section, I am able to include herewith as Table XVII, a table giving the values of *z* (*z* = 1/*n*) for values of *x* and *y* increasing by intervals of 0.02. The table was computed on an electronic computing machine. We assume that *x* is the larger value (larger than *y*) merely for the minimizing of the table entries; the opposite assumption would merely result in the same values appearing at another place in the table. This confines the table to one quarter of the complete square or matrix of 9 x 9 entries, just as we restricted the area of the graphs in Fig. 32 without loss of generality. The matrix can in effect be regarded as the counterpart of the graph, and could be superposed on it, so to speak, but, in accordance with universal practice, it is inverted; that is, whereas *x* in both graph and table increases from left to right, *y* increases upwards in the graph and downwards in the table.

Examples of resemblance and approach to equilibrium

Most often we are given *F*₁, *F*₂, and the number of species or families (*C*) common to the two. Then:

$$F_{1+2} = F_1 + F_2 - C \quad (40)$$

The birds of the 4 Comoro Islands at the species level. From Benson (1960)

The subscripts 1, 2, 3, and 4 in Table XVIII refer to Grand Comoro, Moheli, Anjouan, and Mayotte respectively.

These are the values of $\frac{F_1}{F_{1+2}}$ and of $\frac{F_2}{F_{1+2}}$,

and so on, which we have called *x*, and *y*, each combination of 2 islands producing 2 values, and the larger being treated as *x* and the smaller as *y*.

In this matrix we have listed above the sloping line the dissimilarity (*z*) of the various pairs, computed from the *x* and *y* values of the previous matrix, and more for psychological reasons than necessity have tabulated below the line the similarity, (1-*z*). The results are interesting. Most of the pairs of islands have values of *z* near 0.27 or 0.28, indicating that they are in nearly perfect equilib-

rium at the species level. The pair 1-4, Grand Comoro and Mayotte, is somewhat short of equilibrium, and one pair, Moheli and Mayotte, rather further out.

The map (see Benson) shows that #4, Mayotte, is somewhat more remote from the other 3 than these are from each other; that is, it is geographically more of an isolate, as the matrix says of its biological situation. Further the map shows that

TABLE XVIII. Data on birds of the Comoro Islands

<i>F</i> ₁ = 37	$\frac{C}{1+2} = 27$	Hence $\frac{F}{1+2} = 43$
<i>F</i> ₂ = 33	$\frac{C}{2+3} = 24$	$\frac{F}{2+3} = 41$
<i>F</i> ₃ = 32	$\frac{C}{3+4} = 23$	$\frac{F}{3+4} = 36$
<i>F</i> ₄ = 27	$\frac{C}{4+1} = 22$	$\frac{F}{4+1} = 42$
	$\frac{C}{1+3} = 26$	$\frac{F}{1+3} = 43$
	$\frac{C}{2+4} = 20$	$\frac{F}{2+4} = 40$

TABLE XIX. The data of Table XVIII reproduced in matrix form

No.	Island	F	1	2	3	4
1	Grand Comoro	37		43	43	42
2	Moheli	33			41	40
3	Anjouan	32				36
4	Mayotte	27				

TABLE XX. Second matrix, continuing the analysis of Comoro Island birds

No.	1	2	3	4	
		Values of <i>y</i>			
1		0.767	0.745	0.643	
2	0.862		0.782	0.675	
3	0.862	0.806		0.751	
4	0.882	0.825	0.890		
		Values of <i>x</i>			

TABLE XXI. Third matrix analyzing the Comoro Island birds

No.	Island	1	2	3	4
			Values of <i>z</i>		
1	Grand Comoro		0.28	0.29	0.36
2	Moheli	0.72		0.31	0.42
3	Anjouan	0.71	0.69		0.27
4	Mayotte	0.64	0.58	0.73	
			Values of (1- <i>z</i>)		

Mayotte is nearer geographically to #3 (Anjouan) than it is to #2 or #1, while the matrix also says that its resemblance to Anjouan is greater than to the others.

Thus "resemblance" seems to have something to do with geography, as might be expected; relative proximity, in the Comoro Islands, is an important factor in promoting "resemblance." Benson comments that while Moheli (#2) is much smaller than Mayotte, (#4), it has distinctly more species. This indicates the importance of working with "fictive areas" ($N^{1/2}$) rather than actual areas (A) in assessing resemblance.

The families of birds of the major Sclater-Wallace zoogeographical regions

Wetmore (1949) has given a list of the known families of birds and their geographical distribution. This includes fossil and extinct forms, and I have omitted these. It also gives the distribution in terms slightly different from those used by Sclater and by Wallace, but I think I have interpreted them correctly. I have, however, omitted some families that occur only in minor zoogeographical regions like Madagascar, New Zealand or its neighborhood, and Hawaii. This makes little difference in the end. The major regions are 6 in number, and, omitting the intermediate steps which were illustrated for the Comoro Islands, the final matrix comes out as follows:

TABLE XXII. Matrix of the families of birds in Sclater-Wallace regions

REGION		F						
No.	Name		1	2	3	4	5	6
			$z = \text{Dissimilarity}$					
1	Neotropical	95		0.38	0.58	0.58	0.56	0.60
2	Nearctic	67	0.62		0.29	0.48	0.47	0.56
3	Palearctic	67	0.42	0.71		0.29	0.32	0.34
4	Ethiopian	84	0.42	0.52	0.71		0.15	0.42
5	Oriental	74	0.44	0.53	0.68	0.85		0.27
6	Australasian	73	0.40	0.44	0.66	0.58	0.73	
			$(1-z) = \text{Similarity}$					

Again the results are interesting. Note first that consecutive numbers, 1-2, 2-3, etc. denote regions that have a land frontier in common, and that 3-5 (Palearctic-Oriental) also has a common frontier. Across these common frontiers the index z is most often not far from 0.27 or 0.28, implying virtually perfect equilibrium. There are 2 exceptions. The Neotropical-Nearctic figure is 0.38, implying, perhaps, that not enough time has elapsed since the common frontier was established in mid-Pliocene times to bring regions into complete equilibrium at the family level. Or it may imply that the taxonomists' views as to what

constitutes a valid family is somewhat different in Neotropical regions. The other exception is the Ethiopian-Oriental pair. Here the index is low, only 0.15, implying that these 2 regions are, so far as families of birds are concerned, not separate regions but 2 phases of a single one, the "old world tropics."

The families of mammals of the world

Simpson (1957) has given a very complete listing of mammal families, from which I have omitted extinct ones, and also whales and their allies as being pelagic and not easily assigned to a Wallace-Sclater region. I have omitted seals and their allies with perhaps less justification. On the other hand I have included Sirenia (dugongs and manatees) as being estuarine and riverine rather than pelagic, and I have included the bats, which have, however, quite exceptional powers of dispersal. This gives us 107 families. I have included New Zealand with Australia (it is virtually mammal-free anyway), Madagascar with Ethiopian Africa, and the West Indies with North America.

The final matrix comes out as follows:

TABLE XXIII. Matrix of the families of mammals in Sclater-Wallace regions

REGION		F						
No.	Name		1	2	3	4	5	6
			$z = \text{Dissimilarity}$					
1	Neotropical	43		0.46	0.71	0.80	0.74	0.87
2	Nearctic	31	0.54		0.50	0.74	0.69	0.86
3	Palearctic	27	0.29	0.50		0.55	0.65	0.84
4	Ethiopian	50	0.20	0.26	0.45		0.40	0.80
5	Oriental	43	0.26	0.31	0.35	0.60		0.75
6	Australasian	21	0.13	0.14	0.16	0.20	0.25	
			$(1-z) = \text{Similarity}$					

This matrix indicates that the Sclater-Wallace Regions are much better defined isolates for families of mammals than for families of birds, and nowhere has equilibrium been fully established across boundaries. As with the birds, the closest resemblance is between Ethiopian and Oriental regions, but for mammal families the regions are distinct and not part of a single region. This fact, seen from the viewpoint of the natural history of a century ago, is what established them as separate regions in the first instance; a heavy reliance was placed upon mammals and a somewhat secondary one on birds. Australia is very thoroughly isolated from all the rest of the world so far as mammals are concerned, but is in fairly good contact with the Palearctic and in equilibrium with the Oriental, where bird families are involved.

The Darlington chain

The order in which I have listed the major zoogeographical regions is that preferred, in effect, by Darlington (1957). Wallace had given a very similar diagram much earlier, but Darlington's has the advantage of laying special emphasis on the importance of the "Old World Tropics," i.e. the combination of the Oriental and Ethiopian regions. We might say that the land areas of the world consist of one large land mass and 2 smaller ones, South America and Australia, lying in opposite directions off its perimeter. The Neotropical is now, since mid-Pliocene times, connected by narrow bridges with the Nearctic. The sea

barrier remains between Australia and the rest to this day.

In Figure 36 we give a sort of polar diagram of the Darlington chain. The distances between any 2 regions are the reciprocals of (1-z) from Table XXIII, and it is interesting but perhaps accidental that it is possible to get all the reciprocals to agree on such a diagram. The statement made by the diagram is that a reasonably coherent plane diagram can be constructed showing graphically the relative similarity of all major regions to one another.

The flora of the Galapagos Islands (at the species level)

Kroeber (1916) has given information on the number of species on each of 18 islands, and has tabulated the values of C_{1+2} , etc., the species common to any 2 islands. From these we proceed as before to construct the 18 x 18 matrix giving the values of z and $(1-z)$, Table XXIV. At the lower right hand corner a few spaces are left blank. In view of the small number of plants on the last 3 or 4 islands, any attempt to fill in these blanks would be subject to great statistical uncertainty.

It is evident that none of the islands is even approximately in equilibrium with any other. It is a matter beyond the scope of this paper to decide whether this is due to speciation in situ or to the different islands having initially received different faunas. By analogy with the giant tor-

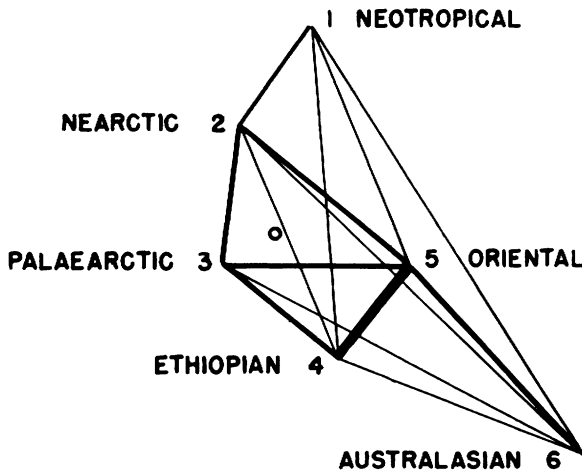


FIG. 36. The "Darlington Chain." Graphical depiction of the resemblances of the major Sclater-Wallace regions, as measured by families of extant mammals.

TABLE XXIV. Flora of Galapagos*

Island	Total species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
		Dissimilarity (z)																	
1 Albemarle	325		.55	.54	.44	.50	.50	.60	.52	.60	.73	.76	.73	.67	.70	.75	.83	.90	.96
2 Charles	319	.45		.51	.60	.57	.60	.62	.67	.57	.70	.73	.56	.70	.70	.75	.80	.90	.90
3 Chatham	306	.46	.49		.60	.55	.58	.62	.67	.60	.67	.69	.73	.73	.71	.70	.72	.82	.98
4 James	224	.56	.40	.40		.55	.58	.58	.69	.67	.71	.79	.74	.78	.70	.80	.82	.90	.94
5 Indefatigable	193	.50	.43	.45	.45		.58	.62	.69	.65	.60	.74	.70	.72	.62	.80	.73	.80	.94
6 Abingdon	119	.50	.40	.42	.42	.42		.61	.71	.69	.73	.79	.73	.70	.69	.67	.73	.83	.98
7 Duncan	103	.40	.38	.38	.42	.38	.39		.77	.58	.73	.73	.71	.88	.69	.81	.90	.90	.95
8 Marborough	80	.48	.33	.33	.31	.31	.29	.23		.73	.82	.75	.83	.75	.80	.83	.85	.90	.93
9 Hood	79	.40	.43	.40	.33	.35	.31	.42	.27		.67	.60	.45	.73	.76	.72	.73	.90	.90
10 Seymour	52	.27	.30	.33	.29	.40	.27	.27	.18	.33		.69	.69	.85	.77	.80	.80	.85	.90
11 Barrington	48	.24	.27	.31	.21	.26	.21	.27	.25	.40	.31		.59	.82	.73	.77	.78	.93	.93
12 Gardner	48	.27	.44	.27	.26	.30	.27	.29	.17	.55	.31	.41		.75	.77	.73	.80	.87	.75
13 Bindloe	47	.33	.30	.27	.22	.28	.30	.12	.25	.27	.15	.18	.25		.84	.73	.87	.83	.90
14 Jervis	42	.30	.30	.29	.30	.38	.31	.31	.20	.24	.23	.27	.23	.16		.80	.92	.98	x
15 Tower	22	.25	.25	.30	.20	.20	.33	.19	.17	.18	.20	.23	.27	.27	.20		x	x	x
16 Brattle	16	.17	.20	.28	.18	.27	.27	.10	.15	.17	.20	.12	.20	.13	.08	x		x	x
17 Wenman	14	.10	.10	.18	.10	.20	.17	.10	.10	.10	.15	.07	.13	.17	.02	x	x		x
18 Culpepper	7	.04	.10	.02	.06	.06	.06	.05	.07	.10	.08	.07	.05	.10	x	x	x	x	
		Similarity or Resemblance (1-z)																	

*The values of z are interpolated from graphs and subject to the uncertainties of approximate interpolation, as well as to the statistical fluctuations to be expected in nature. Further, the values near the diagonal are more accurate than those far from it, and those in the lower right hand corner are very uncertain even though near the diagonal.

toises or Darwin's finches, we might suspect it is the former.

Summary of these four examples

It appears probable that the resemblance or similarity of 2 faunas or floras can be assessed usefully by the method outlined, and it seems to work at either species or family level, and will no doubt do so at other levels. By comparing the index " z " for 2 areas at the level of subspecies, species, genera, and families, something might be learned of the geological history of the areas, or, given the geologic history, perhaps something could be learned of the overall rate of evolution, or of the comparative rates of evolution of different groups.

By way of illustration imagine the following experiment: Take one of the Comoro Islands and exterminate all the birds upon it. Then introduce a thousand new species, each represented by several pairs. In a short time most of these species will have disappeared, and after a modest time 30 or 40 species will remain. Some of these will be represented by many hundreds of pairs and some will be very rare. This is the equilibrium situation for an isolate. But we have seen that the Comoro Islands are not complete isolates, but quasi-isolates, in pretty good equilibrium with one another. This means that over a sufficient length of time birds from the other Comoros or from Madagascar or Africa will make landfalls on our island and will establish themselves. This will cause still more of our original thousand species to become extirpated, and finally we shall have perhaps half a dozen species surviving on our island. On the other hand a few of our thousand may make landfalls on the other Comoros and establish themselves there at the expense of some of the presently native species. Presumably the establishment of equilibrium among all the Comoros may be a much longer process than establishment of internal equilibrium on a single island, but the evidence is that such an equilibrium will ultimately be achieved.

It will be obvious that the "Resemblance Equation" is not restricted to comparing the faunas, or floras, of two regions; it can equally well be used to compare the floras (say) of the same region at different times, for instance it could be used to measure the rate of "succession" in a recently deglaciated area, or of the changes taking place from year to year, as a Carolina Piedmont cultivated field, when abandoned, reverts to more natural vegetation cover (see Oosting 1942). Or it could be used, on a greater scale, to measure the differences between the faunas of

the western United States in the Oligocene, Miocene, and Pliocene. Undoubtedly quite different results will be obtained according as we use, in the one case, herbs and long-lived forest trees, and in the other mammals or mollusca. The problem accordingly becomes one of detail for biological specialists, and not one permitting a general overall answer.

Kroeber's paper is much concerned with the contribution that one island can make to the flora of another. He emphasizes that this contribution may be decided principally by how many forms the donor island has to offer and, of course, this is so. He is inclined to minimize other factors such as distance of separation, wind and ocean currents though he does not dismiss them entirely. It seemed to me that we might obtain some light on the effect of separation, now that we have a definition of similarity ($1-z$) that seems to meet the requirements, by using the vast amount of data that Kroeber has provided.

Because our definition of similarity ($1-z$) calls for 100% similarity to represent identity, the curve should pass through the point 0, 1, and it should be asymptotic to the axis $x = 0$, which represents total dissimilarity, which may be assumed, mathematically speaking, to be achieved at infinite separation. We have, unfortunately, in the Galapagos Islands no instances of floral resemblances or similarities reaching as much as 60%, and thus it is difficult to estimate the position of the upper end of the curve except by pure theory.

The simplest assumption we could make is that the curve fulfilling the requirements of the last paragraph would be a declining exponential. As a matter of fact, in so far as such scatterplots can be "graduated" at all, a declining exponential with the equation

$$(1-z) = e^{-0.75d}$$

fits fairly well, though not too well at the extreme right or asymptotic end where, however, we must expect our experimental results to be subject to considerable uncertainty since the only really remote islands are 2 very small ones with very few species of plants (see Figure 37).

It is clear that the distance of separation is more or less inversely correlated with resemblance of floras, as must be expected, but we can agree with Kroeber's thesis that distance, if important at all (and Kroeber seems a little doubtful on the point), is not the only important matter. Kroeber's criteria of similarity, such as the number of species in common, or the percentage of species in common, are less satisfactory, it appears to me, than the index z of our transcendental equation, and

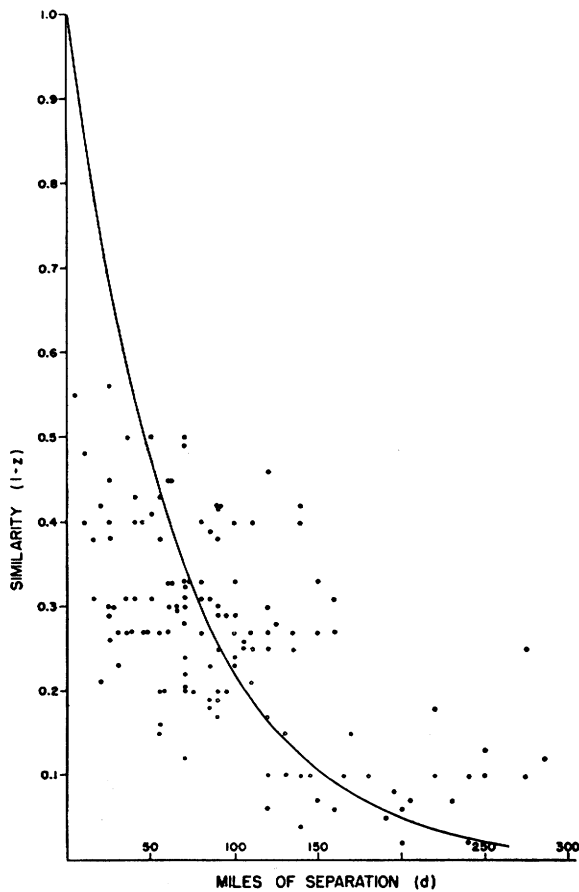


FIG. 37. Plants of the Galapagos Islands. The effect of separation (inter-island distances) upon floral similarity.

this brief note may be regarded as an attempt to see how the new criterion can be applied to Kroeber's problems.

In appraising the graduating curve, especially at the tail end to the right, it should be noted that experimental errors or errors of calculations cannot depress the points much below the graduating curve; they have to stay above the line $(1-z) = 0$. But there is room for much greater departures above the graduating curve. Thus we must expect the true position of the graduating curve to lie much lower than the "center of gravity" of the observed points.

Further, in interpreting the scatter of Fig. 37, it should be remembered that the Galapagos Islands are not all tiny compared with the distances between them, so it may be difficult to judge with any accuracy what should be taken as the distance that must be travelled by a migrating plant. Moreover in some cases there are "stepping stones" on the way and in others there are not. Evidently a number of factors are involved, of which the nominal water gap is only one. Clearly the relation is curvilinear with respect to this, and

if one were to wish to use an analysis of variance it looks as though the variable might better be the reciprocal of distance ($1/d$) rather than d itself. However, it does not appear to me likely to prove useful to over-analyze this situation.

EXTIRPATION AND EXTINCTION

Introduction

Since the earth has a limited carrying capacity for individuals, whether plants or animals, and since the number of species seems to be related somewhat strictly to the number of individuals, the number of species on the earth might be assumed always to have been much what it is now, and the same might be true, perhaps with less precision, of other taxonomic levels. This assumes, however, that the carrying capacity of the earth has been constant throughout time. If desert conditions were as widespread in Triassic times as some geologists think, the carrying capacity may then have been rather low. If epicontinental seas have at times been very much more widespread than at others, this would have had an adverse effect on a land flora and fauna, but an encouraging one on the marine fauna. The effects of an ice-age are obscure. By withdrawing land through covering it with ice, it should adversely affect the land populations, but by withdrawing water from the sea it extended the land areas of the Sunda Shelf, and other present-day shallow seas, and this might permit the expansion of the land fauna. However, the duration of the Pleistocene may have been too short to permit much speciation. On the other hand the contraction of the seas may have caused a reduction in the marine fauna. As against this it may be observed that the percentage contraction of the oceanic areas was quite small.

A further complication exists in the fact that stability or equilibrium is not instantly, or even very promptly, attained. Species may indeed be exterminated rapidly, but they can be created only slowly. If, therefore, geographic and climatic changes are slow, the evolutionary tempo can follow then. But a succession of rapid changes might result in a great impoverishment of species, even though within a million years, or much less, the climate and distribution of land and water might be back to normal, and even though at no time did the world lack a congenial climate over at least part of its area.

Species disappear obviously and catastrophically, like the Passenger Pigeon or Great Auk. New ones are produced more slowly through subspeciation. Since this takes longer, many more species must be in the subspeciating condition than are being exterminated. If it takes 5 million years

to produce a species and we lose a species every 50 years or so, then to keep up our present 8,000-10,000 species of birds we need 100,000 species in the making. Indeed, since some of these subspecies will not reach full species rank, we need more than ten subspecies developing, on the average, from each existing species. If this is not the case, the world count of species of birds is going to decline drastically in a million years or so.

Consideration of the Quaternary record led Wallace (1876) to remark that "It is clear that we are now in an altogether exceptional period of the earth's history. We live in a zoologically impoverished world, from which all the hugest, and fiercest, and strangest forms have recently disappeared." He ascribes the holocaust to the great ice age. Similar thinking led Theodore Roosevelt (1910) to describe the East African railway as a "Railroad through the Pleistocene," comparing Africa of 50 years ago to Europe in the Pleistocene. Martin (1958) however considers that the great extermination came not with the ice but after it, and is largely the work of man. But whatever the cause, the problem of maintaining even a semblance of a steady number of species, genera, and families, over the ages calls for some quantitative consideration.

Fluctuating areas and the extermination of species

As we expand an area we have reason to expect more species, since the number of species appears to be related to the number of individuals. The rate at which the species-count increases depends on whether the areas are "isolates" or "samples." For the moment let us treat the case of isolates.

Suppose that we have a large island, isolated from the rest of the world, and populated with a canonical ensemble of birds, moths, or other organisms. Let some strange accident divide the island into identical halves with an impassable strait between them. Half the birds are on one island and half on the other. According to our hypothesis, a few species, 3 or 4, become extinct. These may be birds that demand a lot of territory, or for some reason are adversely affected by proximity of the sea. The theory does not explain extinction, it merely predicts that a few species will die out. Let us suppose that they are the same species on both islands.

According to current ideas, after a million years or so, each island will have evolved a closely allied, but nonetheless specifically distinct, avifauna.

Now a new accident, let us suppose, eliminates the strait and brings the islands into full contact once more. We now have too many species for

the area or for the total number of individuals, and many species must perish. The first accident reduced the species count from 100% (say) to 80%; the processes of evolution then enlarged the 80% to 160%. The 2nd geostrophism now eliminates 60% of the 160%, and we are back where we started.

The mammals of North and South America

The above situation is not entirely hypothetical. We have at least one instance where it can be put to some sort of a test, provided we can use families instead of species. Until the Pliocene, South America was an island continent much as Australia still is. Then the narrow isthmus of Tehuantepec came into existence and a corridor connected North and South America. This brought the mammal populations of the 2 continents into contact and conflict. We do not know how many species of mammals were exterminated as a consequence of this joining, but we do know the number of families, probably quite accurately.

Simpson (1940) states that before the mid-Pliocene, North America had 27 families of mammals and South America 29, excluding bats and marine mammals, with only one or two families in common. (Thus the total number of families would be about 55.) After the continents were joined intermixing took place, and today, after considerable extermination, there are 27 families in common. In North America there are 38 families and in South America 34. Thus North America has 11 that are not found in South America, and South America has 7 not found in the North; the total number of families is therefore now 45.

The areas of the continents are comparable and, judging by the early Pliocene situation, the appropriate number of families of land mammals in each of them should be about 28. When the 2 areas are fused into one, the total number of families in equilibrium should be about.

$$28 \times 2^{0.28} = 34 \quad (41)$$

This is 21 families less than could be accommodated in the early Pliocene on 2 separate continents. It is 11 less than the 2 conjoined continents presently possess. Thus we are halfway to equilibrium, after perhaps some 5×10^6 years. The process of admixture is continuing and at least 2 more families are on the point of crossing into the new territory. Presumably, along with admixture will go more extermination, and in another 5×10^6 years we may reduce the outstanding discrepancy by half, once more. In that length of time, of course, the narrow corridor may have been broadened, thus increasing the rate

of admixture, either by natural agencies or by man's activities. From the point of view of checking on the present theory, it is a pity the corridor was not a wide one over the last few million years. So far as it goes, however, the evidence is favorable. From the point of view of an interesting zoological world, it is a pity the connection ever formed. Indeed, it is a pity there are not more island continents, and less interaction among the Sclater-Wallace Regions than there is.

Expansion and contraction of biomes

At present the surface of the world consists of about 3 parts water and one part land. Let us suppose the proportions to be rather rapidly reversed. The biological consequences might be complicated but, superficially, marine animals have to decrease in numbers of individuals, while terrestrial ones should increase. However, we have seen that there ought to be an organic connection between the number of individuals and the number of species so some marine species should become extinct and some new terrestrial ones should be developed. Let us consider first the marine ones.

The naive assumption would be that all species may survive, but their numbers of individuals must be decreased by two-thirds. This cannot be done if the rarest species consist only of a single pair. It cannot be done successfully if the number is higher than one pair, but as low as the genetic pool can safely go. Thus there will be a reduction in the total number of species. But this mild comment does not prepare us for the holocaust predicted by equation (15). This says that if the new number of species is N' , and the old one was N , then

$$N'/N = (A'/A)^{0.262} = (1/3)^{0.262} = 0.75 \quad (42)$$

That is, 25% of all marine species will become extinct. And this comes about merely by shrinking the area of the oceans, and without taking into account any "side effects," such as the great increase in the depth of the ocean abysses to hold the water, with consequent reduction of littoral zones, or vast increase of benthic turbidity currents or of run-off from the land.

Next consider what happens to the terrestrial species. Once more, if we can believe our equations, we can write

$$N'/N = (3)^{0.262} = 1.33 \quad (43)$$

which states that equilibrium is not reached till 33% additional species come into being. There is, however, no source of these additional species except in the existing ones, under the circumstances we have postulated, and therefore there will be an impulse toward extensive subspeciation.

Not all of these subspecies will make the grade to full species level, so the number of subspecies developed will presumably be much more than 33% of " N ".

We have considered an extreme case but a less drastic change must produce substantial effects. The Pleistocene glaciation will immediately come to mind, with huge areas of land first withdrawn from the habitat of life and then restored to it, and vast volumes of the ocean water first locked up in ice and then restored to the oceans. And once more we do not consider side effects, such as the increase in ocean salinity when millions of cubic miles of pure water are withdrawn; or the desiccation of the Sahara in post-Pleistocene times.

We may note in passing that since the exponent 0.262 in equation (15) is less than unity, the total number of species in the world would be a maximum if the areas of sea and land were equal or, more generally, it will be a maximum when the areas are so adjusted that they carry equal numbers of individuals.

Present rate of evolution

If the expansion and contraction of biomes provides a driving force for evolution, we may be in a period of unusually rapid evolution. Mountain building has recently been active, and has produced (in North America for instance) rain-shadow deserts and prairies where forests existed earlier. Comparable changes have gone on elsewhere. The withdrawal of the oceans from much of the continental shelves in glacial, and its return in interglacial, periods should have had a similar effect. The recent apparently abrupt rise in oceanic surface temperatures, 11,000 years ago must have expanded greatly the biome of warm-water plankton and greatly reduced that of cold water forms. Since there has not been time to evolve new species, but plenty of time to exterminate old ones, during the rapid cycling of temperatures of the Pleistocene and Recent, we probably live in a zoologically impoverished world, even more generally impoverished than Wallace (1876) envisaged. The relatively recent joining of North and South America, the latter having been till the mid-Pliocene an island continent like Australia, has produced a mixing of faunas and a wholesale extinction of forms, from Kerr's (1950) oversize rattlesnake to marsupial sabre-tooths, (See Rensch 1959) and not merely of placental mammal families.

It seems a reasonable inference that since so much extinction has recently taken place, the stage has been set for replacement through sub-

speciation and speciation at a rapid tempo. While therefore it is regrettable that our fauna is so impoverished, and while it is exasperating that a theory of the steady state of ecological ensembles is difficult to test in a world undergoing such rapid changes, we may hope that a study of the changes in progress will ultimately prove an unusually interesting one, and we may even be glad to live in a world of rapid transition.

The dangers of specialization

In an era of comparative stability there will be a tendency for specialization to go to maximum lengths. Specialization, in the ecological sense, means the development and use of every conceivable technique for exploiting the environment, and a concentration by each species on such techniques as are not equally developed in other species. This results in a maximum number of species for a given number of individuals and a given density of individuals and it produces an overall minimum of "competition" and competitive pressure on the total fauna and flora. The state is, in fact, a biological analog of the physicists' conception of a state of maximum entropy. So far as the present paper is concerned it drives the value of "m" down to the lowest possible level.

A contraction of the biome causes the extirpation or extinction of a number of species, because there is not enough habitat to supply a living for all and, further, there is a limit below which m cannot be forced. The question arises, which species will be extirpated? It would appear likely to be those which have highly specialized techniques, for there will not be enough material for them to exploit. Those species on the other hand that can exploit several "niches," that is, have several techniques, and hence are "more generalized," will be the survivors. On this argument, a fluctuating environment favors generalized species; a static one encourages the formation of specialists.

The limitations of wildlife preserves

If what we have said is correct, it is not possible to preserve in a State or National Park, a complete replica on a small scale of the fauna and flora of a much larger area. If the major part of the State, for instance, is given over to a complete disclimax, whether urbanization or mining or agriculture, the preserved area becomes an isolate or an approximation thereto, and the number of species that can be accommodated must apparently fall to some much lower level. A park can no doubt be "managed," in some cases, so as to preserve certain particularly attractive species, but the total number of species must in the long run fall to a rather low level. The only remedy is to

prevent the area from becoming an "isolate" by keeping open a continuous corridor with other preserved areas. Even then there will be a nationwide impoverishment due to mere reduction of area as natural conditions are replaced by unnatural ones. In the words of Dr. E. S. Thomas, "The long-range outlook for wildlife is dark."

INTERPENETRATION OF POPULATIONS, AND THE PROBLEM OF "m"

In the previous sections we have spoken of equilibrium as if a boundary or frontier were a line of contact or a defended military border. Actually contact is established by interpenetration of faunas and floras: the mixed populations must attempt to exist over an area, and must co-exist in space and time if they are to establish an equilibrium. Otherwise we have merely isolation.

The combining of populations

Let us suppose that we have 2 fairly large areas, similar as to size and climate, which have been isolates but are suddenly confronted with the removal of a barrier and are now potentially in contact. Suppose there have been equal numbers of individuals (I) in each, and equal numbers (N) of species, each area having achieved a high degree of internal equilibrium. They now have to achieve a joint equilibrium.

If each population could be represented by a distribution

$$y = y_0 e^{-(aR)^2} \quad \text{as in equation (1)}$$

the joint distribution is initially

$$y = y_1 + y_2 = (2y_0) e^{-(aR)^2} \quad (44)$$

This distribution is lognormal, but not canonical. There is required a fixed relationship between a (or σ) on the one hand and the height at the mode on the other. To get a canonical distribution with 2N species requires that the height at the mode be decreased to about (1.8y₀) and that σ be increased slightly. Then, so far as a purely mathematical argument is concerned, we have met the requirements. It amounts to saying that we must establish a greater range of commonness or rarity in our combined population than we had originally.

But now what happens to the individuals? If we have a fixed relationship between I/m (i.e. ρ A/m) and N, in accordance with equation (18), viz

$$N = K (I/m)^{0.27}$$

and if we try to double N we ought to increase I by some 10 or 12 fold, if m is to remain constant. But in our case we try to double N and to double I, and this can only be done by a drastic change in m, the minimum number of individuals

required to keep a species in existence. This, as we have seen earlier, amounts to shifting the species curve to right or left along the axis of R . Is this displacement stable?

We seem to find in practice a tendency for m to approximate to unity where species are concerned, in the few cases we have been able to examine by observation. It is not clear, as a matter of mathematics, why m may not have any value whatever, though obviously a value far below unity would cause the rarest species to be represented by a small fraction of an individual, and in practice this would mean that our distribution is at least slightly truncated, even for the complete universe. Perhaps we should say that it is not clear why m may not have any value greater than one, and that normally m should be greater than one. If the mathematics does not give an answer biological considerations may.

Differentiation of species

If the value of m increases far above unity in a given province or area then there must be fewer species than if $m = 1$. For the carrying power of the land is fixed so far as individuals are concerned, and the effect of increasing m is to displace the curve to the right, calling for more individuals per species. In fact if $m = 2$, the number of species is cut by almost 20%, and if $m = 12$, the number of species is approximately halved. Into such a universe it is conceivable that additional species could be introduced without exterminating any of the existing ones, provided the new ones were properly chosen.

Each species has its repertoire of techniques by which it exploits its environment, and this repertoire is known as its "niche." There has been some considerable discussion in recent years of the thesis that 2 species cannot co-exist if they "occupy the same niche," *i.e.*, if they have identical techniques or behavior. There is thus a perpetual pressure to develop modified techniques or additional techniques so that the environment can be exploited in more ways. Such developments constitute, ecologically speaking, new species. This specialization must in the long run be pushed to its limit, and that limit will be reached when the number of species is the maximum consistent with the total number of individuals. In turn, this presumably means when N reaches the value that makes $m = 1$.

Co-existence of populations

In practice we have found values of m that are less than unity. It was slightly less than this for the bird population of Finland. It is probable that for the Neotropical Region the m -value for

the avifauna is about $\frac{1}{12}$. What meaning can we attach to this?

If we combined in our calculations 2 equal areas that are actually isolated, such as the United States and Australia, each having, let us say, in round figures, 600 species of birds, and perhaps about equal numbers of individuals (a surmise, since we have no adequate data), and did not know that they should be treated as isolates, we should get a value of m of about $\frac{1}{12}$, since $(\frac{1}{2})^{3.7} = \frac{1}{12}$, or $(\frac{1}{12})^{0.27} = \frac{1}{2}$.

This suggests that perhaps the Neotropical Avifauna consists ecologically of 2 avifaunas of about equal size, completely isolated from one another. More likely it consists of several avifaunas between which, at the species level, there is very imperfect interaction, and a considerable measure of isolation. Since, in view of the high density of individuals, the number of families in South America is not disproportionate compared with other regions, while the number of species seems about twice what it should be, we are tempted to surmise that while families were established in a single ecological system, there has been a rapid proliferation of species in more recent times. This is conceivable; the rise of the Andes, separating eastern and western forms, and the filling in of the Amazonian basin may have produced some such result. There is some geological evidence that comparatively recently a large part of the basins of the Amazon, Orinoco, and perhaps Paraguay, were under the sea, and that South America may have been for a time an archipelago rather than a continent. This could have produced 2 or more collections of endemics as isolates, whose isolation has since broken down. A detailed examination of the geographical distribution of species and genera within South America might throw some light on the subject.

In shifting the Species-curve along the R axis and in combining or separating sub-universes or canonical ensembles, stability seems to center around $m = 1$, yet there are instances from $m = 10$ or more to $m = 0.1$ or less. In the latter case we probably have imperfect interaction or more than one ensemble; in the former we may have depauperate situations where more species can be accepted. However, this probably does not explain the matter fully. The problem of determining what group is a legitimate one for the sort of calculations we have made is difficult, and why taxonomic groups instead of ecological assemblages apparently work so well is something of a mystery.

The world has recently been through a period of intense mountain-building, followed by a

period of extensive glaciation. The withdrawal of water from the oceans has cleaned the continental shelves of much of the mud that presumably is normally there and the seas are perhaps cleaner than usual. From a zoological point of view however there have been created, in recent times, either by disastrous action or by the lowering of sea level, many opportunities for faunas and floras to come into contact, and this, as we have seen, may have reduced greatly the variety of plant and animal forms. Over large areas, in addition, life was recently almost extinguished by the continental glaciers. At the present time vast areas are being repopulated; faunas are adjusting themselves to newly-created mountain ranges and to growing areas of desert. We are not dealing with a well-stabilized situation of long standing. This may account for some of our difficulties in fitting existing situations into a theory which concerns itself only with final equilibrium.

CAUSES OF THE CANONICAL DISTRIBUTION

The observation that commonness and rarity are often distributed approximately lognormally must be treated as being at present merely an observation. The hypothesis that all possible lognormals are not equally likely, but that the distributions tend to cluster close to that particular lognormal I have ventured to call Canonical, is also without obvious theoretical basis. It would be a great help if we could discover a sound theoretical reason for expecting the results of the present paper. In the absence of such a reason the possibility remains that we may have dealt only with a substantial group of observations that accidentally fitted our surmises and that we may later find others that depart widely from them.

For many years I have been impressed by a parallel that seems to exist between the distribution of wealth among the individuals of a human community and the distribution of numbers of plant or animal individuals among the species of an ecological community or of a given area at a given time. The distribution of wealth was treated by Pareto in a massive treatise many years ago; a very brief account will be found in Preston (1950). Pareto found that in all communities, ancient or modern, civilized or primitive, wealthy or poor, whatever wealth there is tends to distribute itself according to a law which, plotted on a log-log basis is always a straight line, and, what is more important for our present purposes, the slope of the line, or the exponent of the equation, is always approximately the same. This may be the equivalent of our finding that our lognormals are canonical, though I am not sure that Pareto or his

successors have yet given a good reason for it.

It may be added that the Pareto law does not apply to the very poor, and, when these and the very rich are taken into account, the curve begins to approximate to a lognormal. This again suggests to me that the analogy with our species-curves may not be fanciful. But some of my friends, including one of my most helpful critics, say that the argument "leaves them cold." Perhaps it would be truer to say that they have no confidence in my argument that if talent, skill, or "fitness" is distributed normally, then wealth or numbers of individuals will be distributed lognormally.

I myself distrust the argument because even if it were possible in this fashion to account for a lognormal distribution, we still should not have accounted, so far as I can see, for the constancy of the exponent in Pareto's distributions, or for the lognormals being "canonical" in our ecological work, and that is the whole subject matter of the present paper. Accordingly I merely mention the matter here, wishing to stress that the results of this paper, even if confirmed by further work, will always be unsatisfactory till we have a sound theoretical basis for them.

CONCLUSION

There are 2 difficulties into which we run in trying to appraise the correctness of the views expressed in this paper or in trying to formulate a better hypothesis. The first is common to most research work; the numerical data do not exist. The "taxonomy is in bad shape"; the geographical range of many species or genera is not adequately known; for many groups, such as most orders of insects, a large number of species probably exist but have never been described; for very few groups is the density (individuals per acre) known; for very few cases has the distribution of individuals among the various species been ascertained over any but small areas or small samples; and so on. These are human shortcomings and could be overcome if the matter appeared sufficiently important.

The other difficulty is seemingly more serious and less easily rectified. Our theory deals only with stable conditions, not with transitory ones, and the world is in a very transitory stage at present. Primarily, this is due to the recent ice age, which has caused great fluctuations in the area of habitable land and in the temperatures of the oceans over the last million years or so. And since it seemingly takes over a million years to create a species, we must regard most of the world as being in a stage short of true "climax." It

will take several million years, in the absence of further ice invasions, and in the absence of the activities of men, to achieve a semblance of climax in the geological sense.

The distortion of the picture is of course worst in the glaciated areas or areas near to them, and these are precisely the areas in which the greatest amount of ecological work has been done. When climax is attained, it should much more resemble the tropical forest than the present temperate forest. But even if we could transfer most of our ecologists to the tropics, a consummation devoutly to be wished, they would still be dealing with a seriously disturbed ecological situation. For, though the temperature of the tropics has probably been disturbed much less than the temperature of the Holarctic, the lowering of sea level during the Pleistocene must have created geographical changes far too rapid for evolutionary change to follow. Thus those islands of the East Indies that perch on the Sunda Shelf have undergone immense changes of area, have been connected and disconnected, and this is true also of New Guinea and Australia, Ceylon and India, and the drowned eastern coasts of South America. When the sea level dropped several hundred feet the coral islands of the Pacific must have undergone great changes. The Amazon Basin would not have experienced tidal bores for many hundreds of miles inland, nor perhaps would the lowlands have flooded with the annual rains to anything like the extent they do at present; the valleys would then have been trenched deeper and the river courses would have been much more sharply defined. Further, the Andes have been rising during the last million years, the Amazon drainage may have been reversed, the Congo drainage has apparently been radically altered, and so perhaps nowhere on earth, not even in the seemingly little-disturbed tropics, have conditions been quiescent enough for long enough to allow the plant and animal world to achieve ecological stability. Nonetheless we are inclined to suspect that work in the East Indies, the Congo, and the Amazon-Orinoco regions might be much more helpful in clarifying the long-range ecological problem than any amount of work in the depauperate Holarctic.

Summary

1. When individuals and species are tallied for some group until a fairly large number of species has been accumulated, it sometimes (perhaps regularly) happens that we can assign the individuals to species according to a finite distribution which approximates a lognormal distribution.

2. The "individuals curve" seems quite often to

terminate at its crest. When this is so the equation of the curve has no disposable constants, and, given the total number of species in the population or "universe" (not the number in a "sample"), the distribution can be written down at once with all its numerical constants. Such a distribution I call "canonical."

3. There is also a fixed relation between the number of individuals and the number of species in the "universe" (again, not in the sample), and this leads to a theoretical equation for the Species-Area curve. This equation is complicated, but to a first approximation is of the Arrhenius type with a specific exponent: viz., $N = KA^z$, where $z = 0.27$ approximately.

4. Using a series of examples of "isolates," viz., islands in various parts of the world, and various groups, we find agreement between theory and observation.

5. When "nested quadrats" or any form of "sample areas" is used, the distribution of commonness is a truncated lognormal, having, however, the same modal height and logarithmic dispersion as the "universe" from which it is drawn. Such sample areas, if small, have the property of being much richer in species, for a given number of individuals, than isolates of the same size, provided the individuals are not "contagiously distributed." The value of z can now vary over a wide range. For large samples and sometimes for smallish ones, a value of z around 0.12 to 0.17 appears to be frequent. It corresponds, apparently, to a random collection that includes 70 to 80% of the species present in its "universe," and to a universe that itself tends to expand as the sample is expanded.

6. The difference between the z values for isolates and for samples may explain the so-called "depauperate" faunas (and floras) of oceanic islands. Many of these islands are not depauperate in any absolute sense. They have the correct number of species for their area, provided that each area is an isolate, but they have far fewer than do equal areas on a mainland, because a mainland area is merely a "sample" and hence is greatly enriched in the Species/Individuals ratio.

7. Not only species, but also genera and families tend to be distributed lognormally and, moreover, with about the same logarithmic dispersion as species.

8. When isolation is, and has for geological ages been, complete, the exponent z in the expression

$$F_{1+2} = (F_1^{1/z} + F_2^{1/z})^z$$

tends towards unity. But if the isolation is such that an island (say) must form a canonical distri-

bution of individuals on its own soil, and yet the isolation is sufficiently imperfect that the island is in equilibrium with other nearby islands, then z approximates to 0.27. This last value holds for the (families of) birds of the major Sclater-Wallace Zoogeographical regions, including the Australasian region. The value for mammal families is higher, around 0.4, indicating that mammals are more easily isolated than birds, and reaches a value around 0.9 for the Australian mammal fauna.

9. The extirpation and extinction of species can be understood as a purely mathematical matter, as a property of the fluctuating size of habitable areas. Subspeciation and speciation can similarly be understood, since there is a definite relation between number of species and number of individuals, or between species and area.

10. The mechanism, or possibly the biology, by which the adjustment of total species to total area is brought about is considered briefly in terms of the interpenetration of species and the adjustment of "niches."

11. A suspicion exists that a lognormal, canonical, distribution of individuals among species may in some fashion be analogous to Pareto's law of the natural distribution of wealth among the individuals of a human community. This argument will not appeal to everyone, and is at present somewhat nebulous.

As we emphasized at the outset, this paper is not so much an attempt to account for the facts of nature as an attempt to trace the consequences of a hypothesis. These consequences we can then compare with the facts of nature, and in many cases we seem to find good, and often interesting, agreement. Thus the original hypothesis may have some practical utility. It seems to me practically certain that there is a better way of formulating the hypothesis in purely algebraic language, and this might lead to other interesting conclusions and perhaps to a coherent theory embracing many ecological phenomena.

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A POPULATION CENSUS OF SEVENTEEN-YEAR PERIODICAL
CICADAS (HOMOPTERA: CICADIDAE: *MAGICICADA*)

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INTRODUCTION

Periodical cicadas live underground as nymphs for exceedingly long periods—exactly 17 years in northern United States. They all emerge from the ground together in enormous numbers every 17th year: in 1939, 1956, 1973, in the Chicago area where our study was made. Several observers have given numerical data, but in very few cases was anything even approaching an adequate census technic used. The earlier enumerations, which consisted of counting or estimating the number of emergence holes of the nymphs under a single tree, or of counting the number of emergence holes in a unit area (apparently selected for maximum density) were summarized by Marlatt (1907). These figures cannot be relied on, but it is inter-

esting that they fall within the range of estimates made by later and more careful workers. Andrews (1921), after gathering by hand the cicadas from "about one acre of ground" and guessing at the numbers eaten by a flock of ducks allowed to forage in the area, estimated the population density at "upward toward one hundred thousand per acre" (Baltimore, Brood X, 1919). Cory and Knight (1937) estimated the population at about 1,394,000 per acre, based on the minimum count of 32 nymphs per square foot, in two heavily infested mountainside orchards at Hancock, Maryland (Brood X, 1936). Very similar densities, also in orchards, were obtained by Graham and Cochran (1954) for the next emergence (1953) of Brood X in western Maryland in "several acres