ON THE RELATION BETWEEN SPECIES AND AREA[1]

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In a recent article Arrhenius has attempted to reduce to a mathematical formula the general relation between the number of species and the size of the area.[2] This contribution was preceded by two others in which the same subject was discussed, neither of which I have been able to consult. Although the problem attracted the interest of some of the early phytogeographers, Arrhenius is, so far as I know, the first to develop an equation for the expression of his results. Since this equation appears to be wholly erroneous, a brief discussion of the question may not be out of place.

Arrhenius's work was done in the vicinity of Stockholm, where he made careful counts of the number of species in thirteen different and distinct associations. In every case he chose as a basis for his work, and as the unit area in his calculations, a quadrat of one square decimeter. For each association he examined a number of quadrats: 100 each in twelve associations and 300 in the other. For the former cases his quadrats were then combined by doubling into areas of 2, 4, 8, 16, 32, 64, and 100 square decimeters, and in the latter into areas of 1, 2 . . . 256, and 300 square decimeters. He does not say whether the quadrats as counted were contiguous or scattered. In every case he finds, as is already well known, that the larger areas contain the larger number of species, and this number is checked against the formula

$$\frac{\text{Area 1}}{\text{Area 2}} = \left(\frac{\text{Species 1}}{\text{Species 2}}\right)^n,$$

in which n is stated to be a constant for each association. If this formula is correct, the number of species must increase continually as the area increases, and this conclusion is emphasized by him. The exponential ratio n varies in the associations examined from 2.0 to 12.5, the higher ratios giving the lower rates of increase in species.

Let us first demonstrate the fallacy of Arrhenius's equation. He does not state the total size reached by any of the associations examined by him, but it is fair to presume that some of the woodland associations should certainly extend over an area of at least a square kilometer, which is equal to 100,000,000 square decimeters. In his "herb-*Pinus* wood," an average decimeter

[1] After this article was in type, a reprint was received of Du Reitz's contribution on the same subject, in Botaniska Notiser 1922: 17–36.

[2] Arrhenius, Olof, "Species and Area," Journ. Ecol. **9**: 95–99. 1921.

quadrat contains 4.8 species; a square meter contains an average of 33 species in fact and 41 in theory; the exponential ratio is 2. Substituting these values in his equation for a square kilometer, we have the equation

$$\frac{100}{100{,}000{,}000} = \left(\frac{33}{x}\right)^2.$$

Solving for x we find that a square kilometer should contain the alarming total of 33,000 species. By the same formula, a single hectare of *Empetrum* moor should contain 319 species, while a square kilometer of "*Vaccinium vitis-Pinus* wood" should contain only between 9 and 10 species. In the first case the result is impossible; in the latter two it is incredible.

In my work on the structure of the plant association, statistics on the flora of the aspen association of northern Michigan have been secured, covering 240 quadrats of 1 square meter each.[2] This area contains a total of 27 species of vascular plants; a single quadrat averages 4.375, and the exponential ratio is therefore 3.01. The whole association, as developed in the immediate vicinity in one unbroken tract, covers not less than 25 square kilometers, and the total number of species according to Arrhenius' equation should be about 1,255. As a matter of fact, it is less than 100, and the total flora of the region, covering more than ten times this area and including numerous associations, is not known to equal the calculated flora of the one association.

A careful study of the distribution of species in any association brings to light certain interesting conditions affecting the general relation of species and area. Chief among these is the imperfection of associational uniformity. In every association certain species with high frequency index are uniformly distributed over the area. Species of low frequency may be uniformly distributed, but if they are of recent introduction into the area, or have poor means of dispersal, or are poorly adapted to the environment, they are often strongly localized. *If* the association were uniform, and *if* a quadrat were chosen of a size sufficient to provide the necessary space for the species, a single quadrat would contain the whole flora, and larger areas would, of course, show no increase in number of species. Such conditions of uniformity are never realized in nature, and a quadrat of such size is seldom chosen as a basis of investigation. Certainly it was not chosen by Arrhenius, who took a square decimeter as his unit.

If a smaller quadrat is chosen as the unit, each increase in size, by doubling the quadrats, will add some species until the area becomes large enough to include them all, and after that no increase will occur. The greater the uniformity of the association, the sooner will this limit be reached.

If each new set of quadrats examined is immediately contiguous to those of the preceding set, the resulting increase in species is different from that

[2] Gleason, H. A., "Some Applications of the Quadrat Method," Bull. Torrey Bot. Club **47**: 21–34, 1920.

obtained when the quadrats are all scattered throughout the whole area under investigation. This is due to the localization of many species, which may be completely absent from some sections of the area. In contiguous quadrats they may not appear at all, while in scattered quadrats there is a fair probability of some of them appearing early and of most of them appearing in any series of some size. The result in the former case is a relatively slow but long-continued increase in the flora as more quadrats are counted, while in the latter case there is a rapid initial rise followed by an early decline in the rate of increase. But in both cases the rate of increase shows a steady decline.

Arrhenius's error lies primarily in choosing quadrats of only a single square decimeter. Continuing them even to the number of 300 is not sufficient to reach a conspicuous reduction in the rate of increase of the species included; the exponential ratio remains practically the same, and he concluded that it would be maintained indefinitely. It is strange, however, that he has no inkling of what would happen on larger areas, since in 8 of the 13 associations examined his actual results for the maximum number of quadrats examined fell short of the expectation, and this shortage was the more evident the greater the number of species examined.

TABLE I. *Increase in number of species with increasing area, on contiguous quadrats as compared with scattered quadrats*

Area in square meters	Contiguous quadrats		Scattered quadrats	
	Species	Exponential ratio	Species	Exponential ratio
1	4.375		4.375	
2	5.817	2.43	6.667	1.64
3	6.900	2.37	8.750	1.49
4	7.600	2.98	10.367	1.70
5	8.208	2.90	11.292	2.61
6	8.950	2.16	12.650	1.61
8	9.667	3.73	13.800	3.30
10	10.333	3.35	14.875	2.98
12	11.250	2.14	16.250	2.06
15	12.250	2.62	16.938	5.36
16	12.000	Negative	16.667	Negative
20	12.917	3.04	17.667	3.83
24	13.500	4.12	19.400	1.81
30	15.125	1.96	20.000	7.34
40	16.167	4.34	20.333	17.36
60	19.750	2.14	22.750	6.42
80	20.000	23.13	22.667	Negative
120	23.50	2.51	25.000	2.77
240	27	4.99	27	8.99

The 240 quadrats of the Michigan aspen association have been given careful study in an attempt to discover whether or not the increase in species follows any regularity. In doing this they have been grouped into complexes of various sizes, and these complexes have been formed of both contiguous and scattered quadrats. Thus the group of ten contiguous quadrats has been formed of unit quadrats 1–10, 11–20, etc., while the group of ten scattered quadrats has been formed of units 1, 11, 21, . . . 231; 2, 12, 22, . . . 232, etc. The result is shown in Table 1.

In the contiguous quadrats it is seen that doubling the size causes a relatively slow increase in the flora, but this rate of increase is maintained fairly well throughout the series. In the scattered quadrats the rate of increase is at first more rapid, but is later retarded, until the two series are again equal when the whole area is regarded as a single quadrat. This is better illustrated by comparing the increase from 1 to 15 quadrats with that from 15 to 240 (Table 2).

TABLE 2. *Increase in number of species with increasing area*

Area in square meters	Contiguous quadrats		Scattered quadrats	
	Species	Exponential ratio	Species	Exponential ratio
1	4.375		4.375	
15	12.250	2.61	16.938	2.00
240	27	3.51	27	5.94

If these figures for scattered quadrats are plotted, using the areas as the abscissae and the number of species as ordinates, a somewhat irregular curve is obtained. When smoothed out free hand, it is seen to resemble the quadrant of an ellipse. If the ordinates of the smoothed curve are measured and the exponential ratios again calculated, a steady and gradual rise is discov-

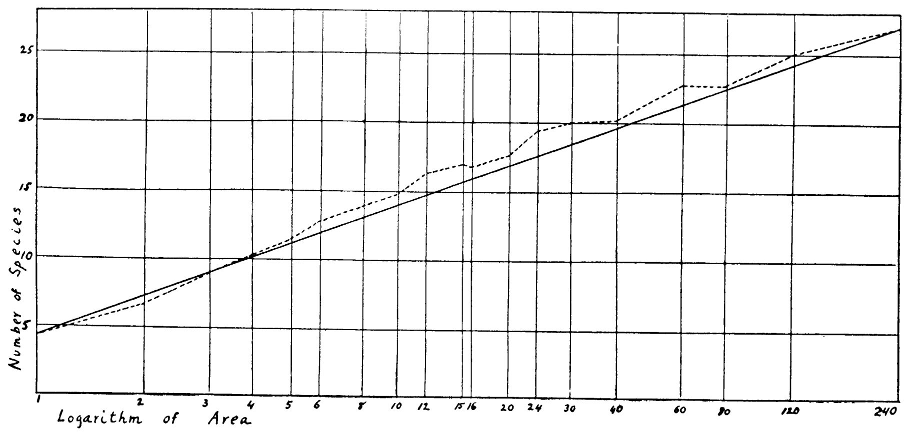

FIG. 1. Relation of species to area in the aspen association of northern Michigan. The horizontals indicate the area in square meters spaced according to the logarithm of the area. The verticals indicate the number of species. The dotted line indicates the number of species observed; the solid line indicates the number of species expected according to the logarithmic exponential equation.

ered, indicating a progressive decrease in the rate of increase in the flora. The exponential ratio is therefore not a constant, as considered by Arrhenius. Over small areas, such as Arrhenius used, it may appear constant, but its variable character is revealed at once when larger areas of vegetation are examined.

Now, let another curve be plotted, as shown in figure 1, using as the abscissae not the areas proper, but the logarithm of the area, and using the number of species as the ordinates as before. The curve now approximates a straight line, and on this line the theoretical number of species per area may be read off directly. The greatest deviation between actual and theoretical numbers of species is found to exist at 24 quadrats, about 1.7 species or about 9 percent, whereas Arrhenius's formula produced much larger errors. In fact, the average deviation is only 0.87 species. A new exponential ratio may again be calculated in the original way and found to be 1.57. Applying this ratio to the whole area, estimated at 25,000,000 square meters, the total flora is calculated at 56 species. Since the counted quadrats were located only in the treeless portions of the association, and since several additional species are confined to the aspen thickets, this theoretical result corresponds closely with the known total of approximately 80 species. Similarly, new exponential ratios may be calculated for Arrhenius's plots. For the herb-*Pinus* wood the ratio is 1.22, for the *Empetrum* moor 1.13, and these figures indicate a total flora for one square kilometer of the former of 81 species, and for a hectare of the latter as 21 species. These figures are certainly much closer to the truth than those obtained by his original equation. The same results may also be obtained graphically.

It remains to be seen whether all plant associations exhibit a similar logarithmic relation of species to area. A large bulk of data collected for this and related statistical purposes by the writer was unfortunately lost, but the whole relation can be easily tested by any one so disposed.