SPECIES AND AREA

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Both for the plant-geographer and the ecologist it is of great importance to know if an area or a district is rich or poor from the point of view of vegetation. Often the lists of plants from different districts are quite incomparable owing to the different sizes of the areas investigated. The problem of comparing lists of flora from several districts of different size therefore is of great interest and many attempts have been made to solve the question. Most writers, however, have obtained no results except to confirm the well-known and obvious fact, that the larger the area taken the greater the number of species. In two recent papers (**1**, **2**) I have tried to solve the question and have ventured to propose an empirical formula. The material sampled showed that this formula is correct for areas of such different sizes as square decimetres, square metres and hectares.

As it is of great interest to know if the formula only holds for complexes of associations, floral districts, etc., or if it is also valid for pure communities, the summer of 1920 was used for collecting material from several (altogether 13) associations of different types all lying in the islands of Stockholm as described in *Öcologische Studien*[1]. The results are tabulated in the following table.

In the left-hand column the area is given in square decimetres, the next column gives the mean values for the different areas as observed in the field, while the third column gives the values obtained by the formula. The last column gives the deviations between the calculated and observed values estimated as percentages of the former. It is easily seen that the values calculated and observed agree very well. Generally there is an increase in the deviation corresponding to increasing area. This depends on the fact that the values of the smaller areas are the average of a greater number of observations than those of the larger.

As it is shown that the formula holds for all the values obtained from these communities and as these examples are picked out quite by chance it can be stated as a general rule that it holds for every association and as a consequence of this also for complexes of associations, formations, large areas, districts, etc.

[1] In *Öcologische Studien*, p. 15, there is a misprint, the equation is written in this way:

$$y^{\log 9} = a\left(\frac{x}{b}\right)^{\log 0}. \text{ For this read } y^{\log 9} = a^{\log 9}\left(\frac{x}{b}\right)^{\log 0}$$

Later (2) I simplified the formula to $\frac{y}{y_1} = \left(\frac{x}{x_1}\right)^n$ where x is the number of species growing on the area y, and x_1 that on y_1; n is a constant.

Table showing the differences between the observed and calculated numbers of species on areas of different sizes in 14 different communities.

obs. = observed number of species on each area. calc. = calculated ditto.
diff. = difference expressed as percentage of calc.

Weed-association

area in dm²	obs.	calc.	diff.
1	1·4	1·4	0
2	2·0	1·9	5
4	2·6	2·6	0
8	3·7	3·5	6
16	5·2	4·8	8
32	6·8	6·6	3
64	8·8	9·0	2
128	10·3	10·2	1
256	14·5	16·9	14
300	16	18·2	12

Calluna-Pinus wood

area	obs.	calc.	diff.
1	0·9	0·9	0
2	1·2	1·1	9
4	1·5	1·4	7
8	2·0	1·8	11
16	2·2	2·2	0
32	2·3	2·8	17
64	2·5	3·5	28
100	3·0	4·0	25

Aira-Pinus wood

area	obs.	calc.	diff.
1	1·2	1·2	0
2	1·4	1·4	0
4	1·8	1·9	5
8	2·4	2·4	0
16	3·3	3·2	3
32	4·6	4·0	15
64	5·5	5·2	6
100	7	6·1	15

Herb-Pinus wood

area	obs.	calc.	diff.
1	4·8	4·8	0
2	7·0	6·7	4
4	9·8	9·4	4
8	14·3	13·1	9
16	18·9	18·5	2
32	23·0	25·8	11
64	27·0	33·0	18
100	33	41	19

Vaccinum vitis-Pinus wood

area	obs.	calc.	diff.
1	1·4	1·8	22
2	1·9	1·9	0
4	2·0	2·0	0
8	2·1	2·1	0
16	2·2	2·2	0
32	2·3	2·3	0
64	2·5	2·5	0
100	3	2·6	15

Arctostaphylos-Pinus wood

area	obs.	calc.	diff.
1	1·4	1·4	0
2	1·6	1·6	0
4	1·8	1·8	0
8	2·1	2·0	5
16	2·2	2·3	4
32	2·3	2·5	8
64	2·5	2·8	10
100	3	3	0

Myrtillus-Picea wood

area	obs.	calc.	diff.
1	1·9	1·9	0
2	2·6	2·5	4
4	3·5	3·2	9
8	4·5	4·1	9
16	5·1	5·2	2
32	6·0	6·7	11
64	6·5	8·7	25
100	7	9·9	30

Herb-Picea wood

area	obs.	calc.	diff.
1	2·5	2·5	0
2	3·6	3·5	3
4	5·4	5·0	8
8	7·6	7·1	7
16	10·2	9·9	2
32	12·7	14·0	9
64	16·5	19·9	17
100	18	24·8	23

Empetrum-moor

area	obs.	calc.	diff.
1	1·3	1·3	0
2	1·5	1·6	6
4	2·0	2·2	10
8	2·8	2·9	3
16	4·0	3·9	3
32	5·6	5·2	4
64	6·5	6·8	4
100	8·0	8·0	0

Herb-hill I

area	obs.	calc.	diff.
1	3·3	3·4	3
2	4·4	4·2	5
4	5·3	5·2	2
8	6·7	6·4	5
16	7·5	7·7	3
32	9·0	9·6	6
64	11·0	10·7	3
100	12	13·5	11

Herb-hill II

area	obs.	calc.	diff.
1	6·8	6·8	0
2	9·1	8·8	4
4	11·6	11·4	2
8	14·8	14·8	0
16	17·2	19·1	10
32	22·3	25·0	11
64	27	31·0	13
100	30	38	21

Shore-association I

area	obs.	calc.	diff.
1	2·2	2·2	0
2	2·8	2·8	0
4	3·6	3·6	0
8	4·8	4·7	2
16	6·2	6·0	3
32	8·3	7·7	8
64	9·5	9·8	3
100	12	11·6	3

Shore-association II

area	obs.	calc.	diff.
1	0·9	1·0	10
2	1·4	1·4	0
4	2·1	2·0	5
8	2·8	2·7	4
16	3·2	3·6	11
32	4·3	4·9	12
64	4·5	6·9	32
100	6	8·5	29

If the floral territories also were uniformly distributed over the earth's surface it would be possible to calculate the number of species growing on the earth by the aid of the formula, but as they are not no formula can be found which will make such a calculation possible.

Name of association	Constant (n)
Calluna-Pinus wood ...	2·9
Aira-Pinus wood	2·8
Arctostaphylos-Pinus wood	6·2
Vaccinium-Pinus wood ...	12·5
Herb-Pinus wood ...	2·0
Myrtillus-Picea wood ...	2·7
Herb-Picea wood	2·0
Empetrum-moor	2·5
Herb-hill	3·3
,, ...	2·6
Shore-association ...	2·8
,, ,, ...	2·1
Weed ,, ...	2·2

In the formula there is a constant n. As it is of great interest to see if this constant varies from association to association the values of n for the associations examined are collected in above table, and the values are seen to vary from 2 to 12·5. In a recent paper (**2**) I thought I had found that the constant n does not vary. But there I was working almost entirely with complexes of associations and the n found was an average of values of n for the pure associations, so that the truth was obscured. This approximate formula is only an empirical one which is justified as long as it can be shown to be valid and it is therefore of great importance to ascertain this.

With this formula one is calculating the average number of species growing on the area. But why should there be a certain number of species on a specific area, in other words, what is the probability of finding a given number of species on the area chosen? There is a certain probability of finding each particular species on an area (lying in a certain association) and the sum of these probabilities is the probable number of species on the area.

If we know the absolute degree of frequency of a species (that is the number of individuals belonging to one species growing on a large area Y) we can calculate the probable occurrence on every area (y) which is smaller than Y.

If the probable occurrence of a given species on the area y is called a, and the probability of not finding it is $\left(1-\frac{y}{Y}\right)^{n_1}$, then $a_1 = 1-\left(1-\frac{y}{Y}\right)^{n_1}$. In the case of another species with a frequency n_2, $a_2 = 1-\left(1-\frac{y}{Y}\right)^{n_2}$, etc. The probable number of species (A) on the area y is

$$A = a_1 + a_2 + a_3 + \ldots = 1-\left(1-\frac{y}{Y}\right)^{n_1} + 1-\left(1-\frac{y}{Y}\right)^{n_2} + 1-\left(1-\frac{y}{Y}\right)^{n_3} + \ldots.$$

If one calculates the sum of species according to this formula the results obtained can be compared with the number of species found by the field survey. The results are given in the last table.

The agreement between the values calculated and observed is very good. The deviations between the values obtained by the approximate formula and the probability calculation are also not very great, but they do vary a good deal, and this must depend on the approximate formula holding in some cases and not in others. If the formula holds the number of species (A) must increase in a geometrical series.

Area in sq. dm.	Calluna-Pinus wood		Aira-Pinus wood		Vaccinium vitis-Pinus wood		Arctostaphylos-Pinus wood		Herb-Pinus wood		Myrtillus-Picea wood	
	O.	P.	O.	P.	O.	P.	O.	P.	O.	P.	O.	P.
1	0·9	0·9	1·2	1·3	1·4	1·8	1·4	1·5	4·8	5·5	1·9	2·3
2	1·2	1·2	1·4	1·6	1·9	1·9	1·6	1·8	7·0	8·2	2·6	3·0
4	1·5	1·5	1·8	2·1	2·0	1·9	1·8	1·9	9·8	11·8	3·5	3·6
8	2·0	1·9	2·4	2·9	2·1	2·0	2·1	2·1	14·3	15·7	4·5	4·2
16	2·2	2·1	3·3	4·1	2·2	2·1	2·2	2·2	18·9	19·2	5·1	5·1
32	2·3	2·3	4·6	5·5	2·3	2·3	2·3	2·3	23·0	22·8	6·0	5·9
64	2·5	2·6	5·5	6·5	2·5	2·6	2·5	2·6	27·0	25·7	6·5	6·6
100	3·0	3 0	7·0	7·0	3·0	3·0	3·0	3·0	33·0	33·0	7·0	7·0

Area in sq. dm.	Herb-Picea wood		Empetrum-moor		Herb-hill I		Shore-association I		Shore-association II		Weed-association	
	O.	P.	O.	P.	O.	P.	O.	P.	O.	P.	O.	P.
1	2·5	2·5	1·3	1·2	3·3	3·6	2·2	2·2	0·9	0·9	1·4	1·4
2	3·6	3·7	1·5	1·6	4·4	4·5	2·8	2·8	1·4	1·4	2·0	1·9
4	5·4	5·6	2·0	2·2	5·3	5·5	3·6	3·6	2·1	2·1	2·6	2·7
8	7·6	8·0	2·8	3·2	6·7	6·6	4·8	4·8	2·8	2·7	3·7	4·0
16	10·2	10·5	4·0	4·6	7·5	8·1	6·2	6·7	3·2	3·7	5·2	5·9
32	12·7	13·4	5·6	5·8	9	9·8	8·3	7·1	4·3	4·0	6·8	8·0
64	16·5	16·5	6·5	7·1	11·0	11·7	9·5	8·8	4·5	4·0	8·8	9·6
100	18·0	18·0	8·0	8·0	12·0	12·0	12·0	12·0	6·0	6·0	—	—

O. = observed number of species. P. = probable number of species.

As the relation y/Y varies from 0 to 1, the equation approximates to a geometrical series, as n_1, n_2, n_3, etc. approximate to 1. Expressed in words, the equation satisfies best the condition of a geometrical series when the species growing on the area have a low degree of frequency. It is seen from all the cases here cited that the distribution of species in plant associations follows the laws of probability.

This is of very great importance for the science of the organisation of plant associations, or synecology.

Several authors have worked on this subject in order to find the laws regulating plant associations, especially from the purely botanical standpoint. In a recent paper (**3**) this question is again taken up and analysed, and the authors give results which if true would make an epoch in the science.

For instance, they believe they have found that the association is a unit as well defined and limited as the species. The characteristics of the association are the *constants*, that is, species which will always be found in the association when a part of it larger than a certain area, the minimum area, is examined.

The authors try to find something more exact than the old words "leading species," etc. That there should be a certain skeleton of constants in every association is a very fascinating idea, which on the first view is supported by material taken from different associations.

But according to the probability calculation on page 97 we find that when there are on an average two individuals of a species on a plot the probability of finding it on every plot is 0·99, that is nearly 1. When the plant is found on every one of the small areas it is a constant according to the "Gesetze." But then every species belonging to the association can become a constant; it is only necessary to take the plots so large that the average number of individuals belonging to one species is about 2. Thus, one can say that the idea of a "constant" is too pretentious and rather a misleading substitute for the old terms. How the result is obtained is quite easily seen. The material used is collected from associations with one or two leading species and some rather rare ones. According to the laws of probability there must very soon, by increasing the area taken, be some species which become pseudo-constants and when very large areas are taken the other rarer species will also become "constants."

The number of species increases continuously as the area increases. A consequence of this will also be that there are very seldom any limits between different associations but the passage of one to another is quite continuous. The passage-belt between the associations may be very narrow but always exists.

The results may be concluded in the following summary. An approximate formula given in a former paper has been shown to hold within wide limits. Using this formula one is enabled to find a standard for the relative richness or poorness of a floral district.

The species in an association are distributed according to the laws of probability. The number of species increases continuously as the area increases, and the plant associations pass into each other quite continuously.

For valuable help in the field-work I must thank my wife. To Mr J. Östlind I am very much indebted for his kind help with the mathematical formulae.

LITERATURE CITED.

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