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Jaccard's Generic Coefficient and Coefficient of Floral Community, in relation to the Logarithmic Series and the Index of Diversity

BY

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IN a series of papers published between 1902 and 1941 Paul Jaccard, largely as a result of the study of the flora of Alpine Valleys in Switzerland, developed two concepts in connexion with the structure of plant communities, which he called 'the Generic Coefficient' and the 'Coefficient of Floral Community'.

The 'generic coefficient' was defined as the number of genera required to yield one hundred species at the same average number of species per genus as in the sample available.

Thus, if there are S species and G genera in the particular portion of the association or community under study,

$$\text{the generic coefficient} = 100 \frac{G}{S}.$$

In other words, it is 100 times the reciprocal of the average number of species per genus (which latter value he calls the 'generic quotient'). He uses it as a measure of the generic diversification of the species contained in the association. For example, if two areas each contained 50 species, the first representing 30 genera, and the second 40 genera, his coefficients would be 60 and 80; the higher the coefficient the greater the generic diversity.

Jaccard's 'coefficient of floral community', on the other hand, was intended as a measure of relationship between two different samples, such as two quadrats of similar area; in fact he defines his quadrats to be of one square metre. He defines it as

$$100 \times \frac{\text{The number of species common to the two quadrats.}}{\text{The total number of species on the two quadrats.}}$$

For example, if two quadrats, each of one square metre, had 31 species in all, of which 23 were common to both, the coefficient would be $100 \times 23/31 = 74.2$ per cent. The higher the value of the coefficient the closer the similarity between the two samples.

If there are several quadrats Jaccard calculated all the possible combinations in pairs and gave an average coefficient for the series.

Jaccard's 'coefficient of floral community' is dependent on the relation between numbers of individuals and numbers of species in the communities

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to be compared. His 'generic coefficient', on the other hand, is dependent on the number of species and the number of genera in one particular community; but it can also be used to compare conditions in different communities.

Maillefer in 1929 criticized Jaccard's generic coefficient and said that it depended on the size of the sample or the area under consideration.

Jaccard in 1941 replied to some of Maillefer's criticisms and suggested that the size of the sample alone was insufficient to account for the differences and resemblances found in the generic coefficients of different plant communities, and restated his claim that the coefficient indicated real ecological properties of the floras.

In recent years it has been found that in both animal and plant population the frequency distribution of genera with different numbers of species is in a mathematical form which can be closely represented by the logarithmic series (see Williams, 1944 and 1947a). It has been also found that in animal populations, and probably in plant populations, the number of species with different numbers of individuals is represented by the logarithmic series (see Fisher, Corbett, and Williams, 1943; Williams, 1944 and 1947b).

The logarithmic series can be written in two ways:

$$\begin{aligned} \text{either} \quad & n_1; \frac{n_1}{2}x; \frac{n_1}{3}x^2; \frac{n_1}{4}x^3; \dots, \\ \text{or} \quad & \alpha x; \alpha \frac{x^2}{2}; \alpha \frac{x^3}{3}; \alpha \frac{x^4}{4}; \dots. \end{aligned}$$

In each case the first term, n or αx , is the number of groups with one unit (i.e. species with one individual, or genera with one species), the second term is the number of groups with two units, and so on. In the series x is a constant (for the sample) less than unity; and α is a constant for all samples of whatever size from the same association, and we have called it the 'Index of Diversity'.

The logarithmic series is convergent and gives a finite sum for both groups and units. If we know the total number of groups and of units in any one sample we can calculate not only n , x , and α , and hence the whole series, but also the number of groups for any larger or smaller sample selected at random from the same population.

For example, in a random sample of an insect population, made by means of a trap, there were 15,600 insects representing 240 species. It follows from this (for methods of calculation see Williams, 1947b) that n_1 is approximately 40 (i.e. 40 species are each represented by a single individual), $x = 0.99743$, and α is also approximately 40.

The conception of this 'Index of Diversity' has proved to be of very considerable ecological interest. It is a property of the population sampled, and not of the sample, and it is a measure of the extent to which the units are associated into groups, or the groups divided into units. It is high when there

is great diversity, e.g. a large number of species for the numbers of individuals. Considerable discussion on it will be found in Fisher, Corbett, and Williams (1943) and in Williams (1944 and 1947a).

One of the properties of a population in which the units and groups are arranged in a logarithmic series is that, except for very small samples, the number of groups represented in a sample is proportional to the logarithm of a number of units. If, for example, a sample from a particular population consists of 1,000 individuals with 100 species, then each time the number of individuals is doubled, approximately 19 species will be added. Thus 2,000 individuals will give 119 species, 4,000 individuals 138 species, 8,000 individuals 157 species, and so on.

When an attempt is made to transfer these theories of population structure on the individual-species level from animals to plants, we find two important differences, one making things easier and the other more difficult. In animal populations, and particularly in flying animals such as insects, it is often difficult to know whether a particular individual found in a sample really belongs to the community being studied or is merely a casual visitor, here to-day and gone to-morrow. In plants this difficulty does not occur; each plant has a definite location from which it does not move.

On the other hand, it is with animals very easy to say that a sample contains a particular and definite number of individuals—each individual is a clear-cut entity. But in plants this is not so; it is very difficult in many cases to say where an 'individual' begins and ends, particularly when you get vegetative reproduction by stolons, tillers, &c.

It is, however, possible to a certain extent to evade this difficulty by making the assumption that, in a series of random samples of different sizes from a single plant association, the number of 'individuals', or perhaps better 'plant units', is proportional to the area of the sample. We can then avoid this problem of the actual number of units by comparing two or more samples.

Where a study is made of the number of species of plants represented in areas of different sizes in the same association (Williams, 1944) it is found that, within close limits, the number of species present is proportional to the logarithm of the area of the sample. It will be seen, therefore, that there is evidence of the existence in plant populations of exactly the same type of individual-species structure as has been found in animals—a structure which can be closely represented by the logarithmic series.

This leaves us in a position to discuss the two coefficients suggested by Jaccard on the assumption that the logarithmic series can be used to represent the structure of the individual-species and the species-genera relations in plant communities, and also that the conception of the 'Index of Diversity' as a measure of richness is applicable to plant populations.

Jaccard's 'Generic Coefficient'

The relation between the frequency of genera with different number of species has already been shown to be closely represented by a logarithmic

series both in animals and plants. For plants evidence is brought forward in Williams, 1944, pp. 23–32, for the flowering plants of the world, and for British flowering plants in both Bentham and Hooker's and Babington's classifications; also in Williams (1947a) for the genera and species in comparatively small plant communities.

On the assumption that this interpretation is sound it can be shown that the average number of species (S) per genus (G) in a sample from a population based on a logarithmic series with Index of Generic Diversity α is given by¹

$$S/G = \frac{e^{G/\alpha} - 1}{G/\alpha}.$$

$$\text{Therefore Jaccard's coefficient} = 100 \times \frac{G/\alpha}{e^{G/\alpha} - 1}.$$

In other words, his coefficient is dependent on the ratio between the number of genera represented in the sample and the richness of the population sampled. If α remains constant, i.e. if a series of samples of different sizes are taken from the same community, the coefficient varies with the size of G , that is, with the size of the sample.

If, on the other hand, samples with the same number of genera are taken from two communities with different value of α , then the coefficient will vary with α .

For example, if a sample containing sufficient species to represent 20 genera is extracted from a population with an Index of Generic Diversity of 10, the average number of species per genus will be

$$\frac{e^2 - 1}{2} = \frac{6.4}{2} = 3.2$$

and Jaccard's coefficient would be 31.

If a sample sufficiently large to contain 40 genera was selected from the same association, the average number of species per genus would be

$$\frac{e^4 - 1}{4} = 13.5$$

and Jaccard's coefficient would be 7.7.

Jaccard's coefficient is therefore a double function depending on the generic richness of the population and also on the size of the sample taken. It is therefore not so good a measure of the ecological structure of the population as the Index of Diversity alone.

Jaccard's 'Coefficient of Floral Community'

It can be shown that the number of species (S) represented by a number of individuals (N) taken by a random sample from a population arranged in a logarithmic series with the Index of Specific Diversity α is given by

$$S = \alpha \log_e \left(1 + \frac{N}{\alpha} \right).$$

¹ e is the base of the Naperian logarithms = 2.71828.

The number of species in a sample twice the size, or in two samples of the same size, is therefore

$$\alpha \log_e \left(1 + \frac{2N}{\alpha} \right).$$

If N is large compared with α , as it should be for a good representative sample, it is possible to neglect the 1 in comparison with N/α , and from this it can be shown (see Williams, 1947b, p. 269) that the increase in number of species by doubling a sample is equal to $\alpha \log_e 2 = 0.69\alpha$.

Thus, if two quadrats of the same size (say one square metre as defined by Jaccard) are taken from a population, which is arranged in a logarithmic series, and if each contains S species, then the two together will contain $S + \alpha \log_e 2$ species. It follows that each quadrat must contain on an average $\alpha \log_e 2$ species not found in the other quadrat, and therefore the number common to the two quadrats must be

$$S - \alpha \log_e 2.$$

It is interesting to note that this is actually the number of species found on half a quadrat.

Thus, Jaccard's Coefficient of Floral Community

$$= 100 \frac{S - \alpha \log_e 2}{S + \alpha \log_e 2} \quad \text{or} \quad 100 \times \frac{S - 0.69\alpha}{S + 0.69\alpha}.$$

It is thus dependent upon S , the number of species in one quadrat, which is in turn dependent on the size of the quadrat, or the number of plant units it contains; and also on α , the Index of Specific Diversity of the population.

If within the same population the sample size is increased, Jaccard's coefficient rises; if the same-sized samples are taken from a richer flora, the coefficient falls.

The following is a numerical example:

In a population with an Index of Specific Diversity of 10
if 1 square metre contains 46 species

then 2 square metres will contain 52 species approximately

$$\begin{array}{ccccccccc} 10 & " & " & " & 69 & " & " \\ 20 & " & " & " & 76 & " & " \end{array}$$

Thus for two areas of 1 square metre Jaccard's coefficient

$$= \frac{(2 \times 46) - 52}{52} \times 100 + 77 \text{ per cent.}$$

but for two areas of 10 square metres the coefficient would be

$$\frac{(2 \times 69) - 76}{76} \times 100 = 82 \text{ per cent.}$$

Even with Jaccard's restriction of quadrat area to 1 square metre this difficulty is not eliminated, as it is the number of plant units in the quadrat which must be kept constant, and the number of plant units in quadrats of the same area is not the same in different associations.

Jaccard's coefficient can also be written as

$$100 \times \frac{\log_e(1 + \frac{1}{2}(N/\alpha))}{\log_e(1 + 2(N/\alpha))}$$

when N is the number of 'plant units' per quadrat.

It is thus apparent that all pairs of quadrats with the same N/α ratio will give the same coefficient.

In any community which has an individual-species structure in the form of a logarithmic series Jaccard's 'Coefficient of Floral Community' is thus also a measure of two factors: one, N is a property of the size of the sample; the other, α , or the Index of Diversity, is a property of the population sampled. The coefficient contains no information that is not more clearly stated by the Index of Specific Diversity alone.

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