Measuring of the Dispersion of Individuals and Analysis of the Distributional Patterns

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Introduction

For the past forty years, the ecologists have paid much attention to the problem of spatial distribution of individuals in a population. The usual method for the investigation of this problem has been the one using the quadrat as the sampling device, and it may yet be an important technique for the present and future studies of plant and animal distributions, though a method that utilizes distant measurement has recently been advanced by several workers (Cottam and Curtis, 1949; Morisita, 1954, 1957; Clark and Evans, 1954; Hopkins, 1954; Cottam, Curtis and Catana Jr., 1957; etc.).

Based on the quadrat technique many indices which express the degree of aggregation or departure from randomness of distribution of individuals have been proposed (Blackman, 1942; McGinnies, 1934; Whitford, 1949; Fracker and Brischle, 1944; etc.). However, as have been noticed by several investigators the values of these indices usually change with the increase or decrease of the quadrat size taken as the sampling unit (Curtis and McIntosh, 1950; Evans, 1952; Greig-Smith, 1952; etc.).

Such an influence of quadrat size upon the index values seems to depend on the following two effects: (1) the effect caused by the change of the average number of individuals per quadrat, (2) the effect of combining or splitting the clumps due to the increase or decrease of the quadrat size (Morisita, 1950). The former corresponds to the influence of the mean population density per unit area and the latter reflects the structure of spatial distribution of individuals. As the main purpose of using the index of dispersion would be the exact quantitative expression of the distributional pattern of population, the ideal index should be what is independent of the

* Contributions from the Department of Biology, Faculty of Science, Kyushu University, No. 80.

influence of the mean density. However, none of the indices hitherto proposed has succeeded in separating these two effects. Consequently, the comparison of the distributional patterns of two or more populations with each other by these indices may sometimes be meaningless, since it may happen that the discrepancies of the index values are caused by the difference of the average densities, not by the difference of distributional patterns among these populations.

On the other hand, many trials for fitting various mathematical models of contagious distributions to the actual ones have also been put forward (Beall, 1940; Barnes and Stanbury, 1951; Thomas, 1949; Archibald, 1948; etc.), and it has been considered that, if a theoretical distribution would well fit to an actual one, the parameter values of the distribution function applied might be utilized for the understanding of distributional structure of the population. However, it is often found that, though the data obtained by the use of the quadrats of certain size fits well to a mathematical type, the use of quadrats of different size gives fit rather to another type (e.g. Numata, 1950; Numata and Suzuki, 1951), and when the local distribution of physical conditions on the examined area is very irregular, even a case may occur that the actual distribution does not follow any mathematical types which can be easily treated. Moreover, as pointed out by Iwata (1954) and Pielou (1957), a fittness of observed data to a theoretical distribution does not always mean that the actual spatial distribution of individuals is formed just as the parameter values of the theoretical one represent. The same has suggested by Thomson (1952), too, who has noticed that the Neyman's parameter values indicate the regularity of the spatial distribution of a plant species in spite of actual existence of distinct major clumps of the species in the examined area.

Concerning the distributional patterns of individuals, there is still an important problem which has been unnoticed by most of the ecologists but a few, that is, the problem of intra-clump distribution (Numata, 1954; Cottam et al., 1957; Morisita, 1957; Aberdeen, 1958). As an individual of plants or animals will require a space for getting nutritive materials or for other objects, a tendency of individuals to keep some distance from each other is supposed to be seen at least in some cases though they aggregate in clumps viewing on a smaller scale. Then, the degree of uniformity of distribution in a clump may possibly be a measure of competitive relationship among individuals, although the difficulties of determining the degree have compelled to tend to avert the eyes of investigators from this problem.

A problem that also has not yet been fully answered is the finding of clump size by the quadrat method. Some efforts have been made on this point (Numata, 1954; Cottam et al., 1957), but it seems that the rigid assumptions, on which the mathematical treatments have been based, make the application of the methods hitherto proposed to the complicated distributions of individuals in natural population difficult.

Therefore, finding out of such index that is neither affected by the mean density per quadrat nor standing on the assumption of any definite type of contagious distribution, and, if possible, is applicable also to the intra-clump distribution as well as to the determining of clump size will be most desirable. The object of the present paper is at first, to propose such a new index, and secondly, to describe methods for the analysis of the distributional patterns of populations through the use of this index. Several examples of the application of the methods to the artificial and natural populations shall also be given.

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New index of dispersion, I_δ

Dealing with the non-randomly distributed populations, the present author has put forward a theoretical consideration, that is to say, even if the individuals are distributed non-randomly over an area, the area may be divided into small subareas of various sizes on each of which the individuals occurred therein are distributed randomly or uniformly (Morisita, 1957)*. When the distribution of individuals on each subarea is at random, the spatial distribution of individuals within each of the quadrats taken as the sampling units, excepting the ones taken from the boundaries between subareas, will also be at random, though the numbers of individuals in the quadrats will significantly differ from each other. The larger the ratios of the sizes of the subareas to the quadrat size become, the more the chance that a quadrat taken at random is sampled from inside of any one of the subareas will be given. Then, if the subareas are very large as compared with the quadrat size, the probability that the spatial distribution of individuals in a quadrat is at random will be approximately unity.

* This consideration may be applied not only to the areas of discrete aggregations of individuals but also to the transitional parts of progressive increase or decrease of densities, because, if a small area is taken from a transitional part, the distribution of individuals on it may be considered as random or uniform at least approximately.

Now, let q quadrats be taken at random from the whole area, and n_i ($i=1, 2, 3, \ldots, q$) individuals be found in each of the quadrats, then putting

$$N=\sum_{i=1}^{q} n_i \tag{1}$$

and

$$\delta=\frac{\sum_{i=1}^{q} n_i(n_i-1)}{N(N-1)}, \tag{2}$$

δ will correspond to the unbiased estimate of Simpson's measure of diversity, λ, defined as $\sum \pi^2$ where π is the proportions of individuals in the various groups into which the individuals of infinite population are divided ($\sum \pi=1$) (Simpson, 1949), because the proportion of population density per unit area on each subarea surrounding each quadrat may correspond to the proportion of individuals in each group in Simpson's measure. Accordingly, δ will take a fixed value on an average independently of the size of N, as Simpson's measure does, so far as the number of quadrats and the proportions of population densities of the subareas from which the quadrats are taken are unchanged.

Then, by putting

$$I_\delta = q\delta, \tag{3}$$

the I_δ will be a measure of dispersion of individuals in a population which takes the value of unity at least approximately, if the individuals are distributed at random over the area and the number of individuals is very large, because δ equals $1/q$ when the distribution of individuals contained in the quadrats follows a Poisson series (Simpson, 1949). When the individuals are distributed uniformly over the area, I_δ will take the value smaller than unity, and if the distribution of individuals is contagious, the I_δ value will be larger than unity. When the individuals are found in none but one of the quadrats, δ equals unity and accordingly I_δ equals q.

The next problem is whether or not the I_δ value for a population is affected by the change of size and number of quadrats.

Let the number of subareas be t, and the number of quadrats taken from each of the subareas be r_m ($m=1, 2, 3, \ldots, t$), then we have

$$q=\sum_{m=1}^{t} r_m,$$

and

$$T=\sum_{m=1}^{t} N_m,$$

where N_m is the total number of individuals occurred in r_m quadrats and T is the total number of individuals in the total quadrats q. Let the number of individuals in each of r_m quadrats be n_{mi}, then, on the assumption of random distribution of individuals of a large number on each subarea, the size of which is very large as compared with the quadrat size, $n_{m1}, n_{m2}, n_{m3}, \ldots, n_{mr_m}$ are expected to follow a Poisson series at least approximately.

Then the mean value of $\dfrac{\sum_{i=1}^{r_m} n_{mi}(n_{mi}-1)}{N_m(N_m-1)}$ for any assigned value of N_m larger than 1 will be

$$E_{N_m}\left(\frac{\sum_{i=1}^{r_m} n_{mi}(n_{mi}-1)}{N_m(N_m-1)}\right) \doteqdot \frac{1}{r_m}. \tag{3}$$

Hence,

$$E(\delta) = E\left(\frac{\sum_{i=1}^{r_1} n_{1i}(n_{1i}-1) + \sum_{i=1}^{r_2} n_{2i}(n_{2i}-1) + \ldots + \sum_{i=1}^{r_t} n_{ti}(n_{ti}-1)}{T(T-1)}\right)$$

$$= E\left(\frac{N_1(N_1-1)}{T(T-1)} E_{N_1}\left(\frac{\sum_{i=1}^{r_1} n_{1i}(n_{1i}-1)}{N_1(N_1-1)}\right)\right) + E\left(\frac{N_2(N_2-1)}{T(T-1)} E_{N_2}\left(\frac{\sum_{i=1}^{r_2} n_{2i}(n_{2i}-1)}{N_2(N_2-1)}\right)\right) + \ldots$$

$$\ldots + E\left(\frac{N_t(N_t-1)}{T(T-1)} E_{N_t}\left(\frac{\sum_{i=1}^{r_t} n_{ti}(n_{ti}-1)}{N_t(N_t-1)}\right)\right)$$

$$\doteqdot \frac{1}{r_1} E\left(\frac{N_1(N_1-1)}{T(T-1)}\right) + \frac{1}{r_2} E\left(\frac{N_2(N_2-1)}{T(T-1)}\right) + \ldots + \frac{1}{r_t} E\left(\frac{N_t(N_t-1)}{T(T-1)}\right). \tag{4}$$

Now, let each of r_m quadrats be divided into k small quadrats of equal size, and the number of individuals occurred in each small quadrat be n_{mij}, then we will get on the assumption mentioned above

$$E_{N_m}\left(\frac{\sum_{i=1}^{r_m}\sum_{j=1}^{k} n_{mij}(n_{mij}-1)}{N_m(N_m-1)}\right) \doteqdot \frac{1}{k\,r_m}. \tag{5}$$

Therefore, letting the δ values of large and small quadrats be δ_1 and δ_2 respectively, we have

$$E(\delta_1) \doteqdot k \cdot E\left(\frac{\sum_{i=1}^{r_1}\sum_{j=1}^{k} n_{1ij}(n_{1ij}-1)}{T(T-1)}\right) + k \cdot E\left(\frac{\sum_{i=1}^{r_2}\sum_{j=1}^{k} n_{2ij}(n_{2ij}-1)}{T(T-1)}\right) + \ldots$$

$$+ k \cdot E\left(\frac{\sum_{i=1}^{r_t}\sum_{j=1}^{k} n_{tij}(n_{tij}-1)}{T(T-1)}\right) = E(k\delta_2). \tag{6}$$

Then it follows that

$$E(kq\,\delta_2) \doteqdot E(q\delta_1). \tag{7}$$

Since kq is the number of small quadrats, it is known that the I_δ defined as the product of the number of quadrats and the δ value of the sample is influenced neither by dividing of large quadrats into small ones nor by uniting small quadrats in large ones. If only one of k small quadrats is taken as sampling unit from each of the large quadrats, the I_δ value obtained from these small quadrats of total q will also be $q\delta$, since the value of δ will not be changed by the change of the mean number of individuals per quadrat. Then, a fixed value of I_δ will be obtained for a population in spite of the change of the size and number of quadrats used in sampling, if the intra-subarea (or intra-clump) distributions of individuals are at random and the sizes of subareas (or the clump sizes) are large as compared with the quadrat size. Therefore, it may be said that I_δ can be used as an appropriate index to express the degree of contagiousness of individuals in a population.

However, it should be noticed that the following two conditions are premised for the use of I_δ as a reliable index of dispersion: one is that the numbers of quadrats taken from the subareas should be proportional to the sizes of the subareas, and the other, at least one or more quadrats should be sampled from each subarea. Random sampling of the quadrats from the whole area may satisfy the first demand at least on an average, but the systematic or regular sampling seems to give better results since the sampling errors may be smaller in the latter method than in the former (Numata and Nobuhara, 1952; Morisita, 1957). To satisfy the second demand, a large number of quadrats, as many as possible, will be desirable, as the exact number of subareas will be unknown in usual. However, even a comparative small number of quadrats may sometimes be sufficient to give an I_δ value without much error, because the subareas of equal density can be considered as parts of one subarea, though they are located separately in actual, and hence, the number of subareas with different densities to be sampled may be much reduced.

Test of randomness

If $n_1, n_2, n_3, \ldots, n_q$ in the formula (2) follow a Poisson series,

$$\frac{\sum_{i=1}^{q} n^2_i - N^2/q}{N/q}$$

will have a χ^2-distribution with $(q-1)$ degrees of freedom approximately (Kitagawa and Masuyama, 1952).

From

$$I_\delta = q\frac{\sum_{i=1}^{q} n_i(n_i-1)}{N(N-1)} \qquad (8)$$

we have

$$\sum_{i=1}^{q} n_i^2 = \frac{I_\delta}{q} N(N-1)+N. \qquad (9)$$

Then, putting

$$F_0 = \frac{(I_\delta/q)\,N(N-1)+N-N^2/q}{(q-1)\,N/q} = \frac{I_\delta\,(N-1)+q-N}{q-1}\,, \qquad (10)$$

the significance of the departure from randomness of the distribution may be tested by the comparison of F_0 with the value of $F_{\infty}^{q-1}(\alpha)$.

An example of computation

A frequency distribution of individuals of *Ameria maritima* studied by Archibald (1948) and the procedure of computation of the I_δ value are given in Table 1.

Table 1. The frequency distribution of individuals of *Ameria maritima* (Archibald, 1948) and the computation of the I_δ value.

Number of individuals (n)	Observed number of quadrats (f)	fn	n^2	fn^2
0	57	0	0	0
1	6	6	1	6
2	12	24	4	48
3	5	15	9	45
4	5	20	16	80
5	5	25	25	125
6	7	42	36	252
7	1	7	49	49
8	0	0	64	0
9	1	9	81	81
10	1	10	100	100
11 and over	0	0		0
Total	100 ($=q$)	158 ($=N$)		786 ($=\sum n^2$)

$N(N-1) = 24806$ $\quad\quad$ $\Sigma\, n\,(n-1) = \Sigma\, n^2 - N = 786-158 = 628$

$\delta = \dfrac{\Sigma\, n\,(n-1)}{N\,(N-1)} = 0.025316$ $\quad\quad$ $I_\delta = q\delta = 100\times 0.025316 = 2.5316$

$F_0 = \dfrac{I_\delta\,(N-1)+q-N}{q-1} = 3.429$ $\quad\quad$ $F_{\infty}^{99}\,(0.01) = 1.36$

The I_δ value of the distribution of this species is about 2.53, and it is known that the distribution clearly departs from random expectation as the value of F_0 is larger than the value of F at the 1 per cent level of significance.

Analysis of distributional patterns by I_δ

As mentioned before, if the individuals are distributed at random over an area, the value of I_δ will be unity, and when the individuals are distributed contagiously

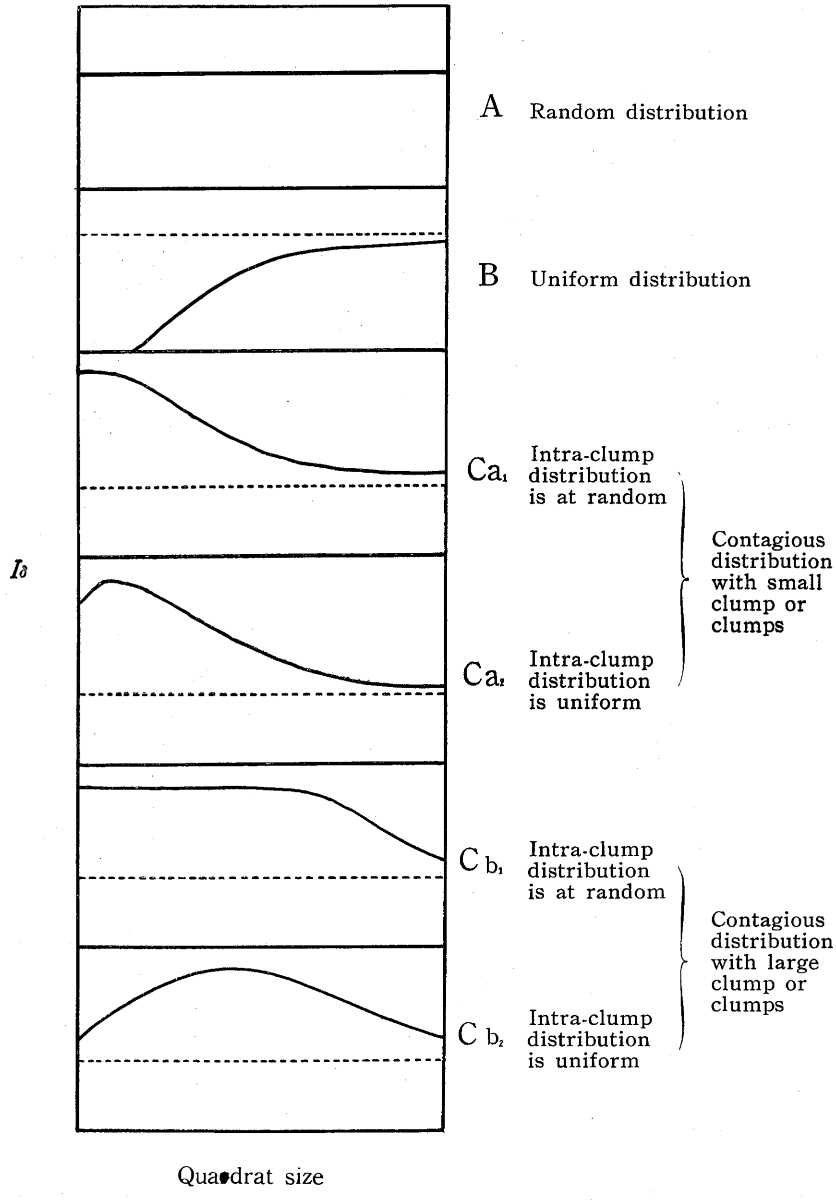


Fig. 1. Schematic representations of I_δ-quadrat size relations for various distributional patterns of populations. The broken lines indicate the value of unity.

or uniformly, the I_δ value will be larger or smaller than unity respectively.

Now, consider that the individuals make clumps with smaller sizes comparing with the quadrat size, then the spatial distribution of individuals in each of quadrats, containing a clump or clumps, will not be at random but contagious. Let each quadrat be divided into small quadrats of equal size, then the I_δ value obtained from the small quadrats will be larger than the value from the large ones in this case, since the variance of $n_{i1}, n_{i2}, n_{i3}, \ldots, n_{ik}$ (k = number of small quadrats contained in a large quadrat) will be larger than the mean at least on an average. In general, though the intra-clump distribution of individuals is at random, and a fixed value of I_δ is obtained from a series of the quadrat sizes up to certain extent, the value will begin to decrease after the quadrat would have attained the size which is not much smaller than the clump sizes. The larger the quadrat size becomes, the more the I_δ value will approach unity in this case. On the contrary, if the individuals are distributed uniformly within each clump, and the size of each clump is much larger than the size of the large quadrat, the I_δ value obtained from the small quadrats will be smaller than that from the large ones. Therefore, the change

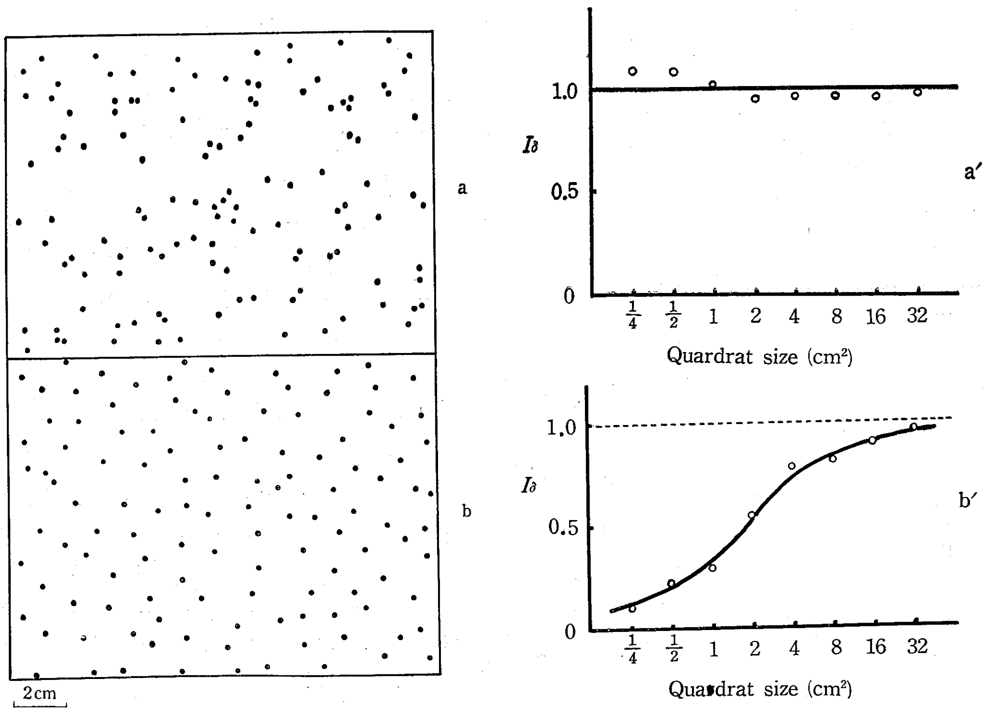


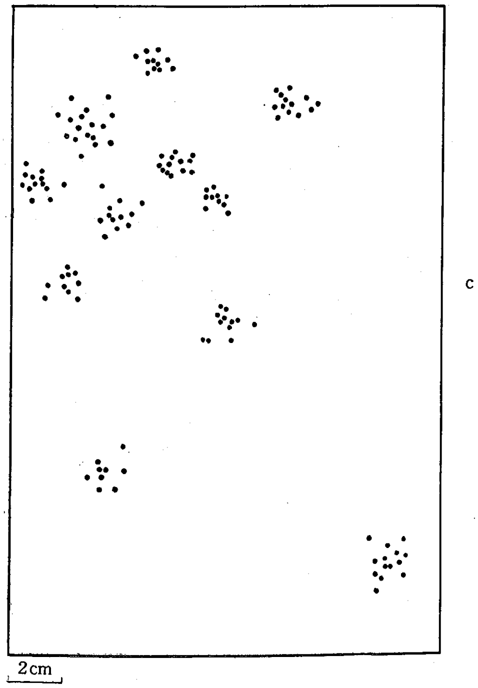
Fig. 2. Artificial populations and corresponding I_δ-quadrat size relations.
a, a′ ・・・・ Randon distribution b, b′ ・・・・ Uniform distribution

of the I_δ value with the change of quadrat size may be utilized for the analysis of the distributional patterns of populations.

From the above considerations, several types of the I_δ–quadrat size relations, each corresponding to each of several distributional patterns, are theoretically presumed. They are shown in Fig. 1.

Application of the distribution analysis by the I_δ index to the artificial populations.

For the comparison of the theoretical types of the I_δ-quadrat size relations with the actual distributional patterns of populations, the maps of various artificial populations, which had been made plotting 120 (Fig. 2 a, b, c, d) and 1942 (Fig. 2 e) dotts on 16×12 cm (Fig. 2 a, b) and 16×24 cm (Fig. 2 c, d, e) areas, were subdivided into a series of the quadrats of 1/4, 1/2, 1, 2, 4, 8, 16 and 64 cm², and the number of dotts occurring in each quadrat of each size was counted. The I_δ values computed from the frequency distributions of individuals thus obtained are shown in Fig. 2 a′, b′, c′, d′, e′. It will be seen from Fig. 1 and 2 that the distributional patterns analysed through the I_δ-quadrat size relations are in good harmony with the inspections of the mapped distributional patterns of populations.



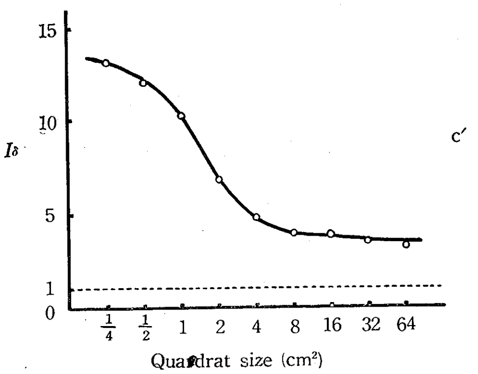


Fig. 2. c, c′ · · · · Contagious distribution with small clumps

In Table 2, the I_δ values from various quadrat sizes for the artificial population mapped in Fig. 2 d are compared with the values of other indices hitherto proposed. As the artificial population examined has a large clump within which the individuals are distributed rather randomly, the I_δ values are almost unchanged for various quadrat sizes except the largest one, while much difference among the values with the difference of quadrat size is seen in other indices indicating that these indices are not free from the effect of the average number of individuals per quadrat.

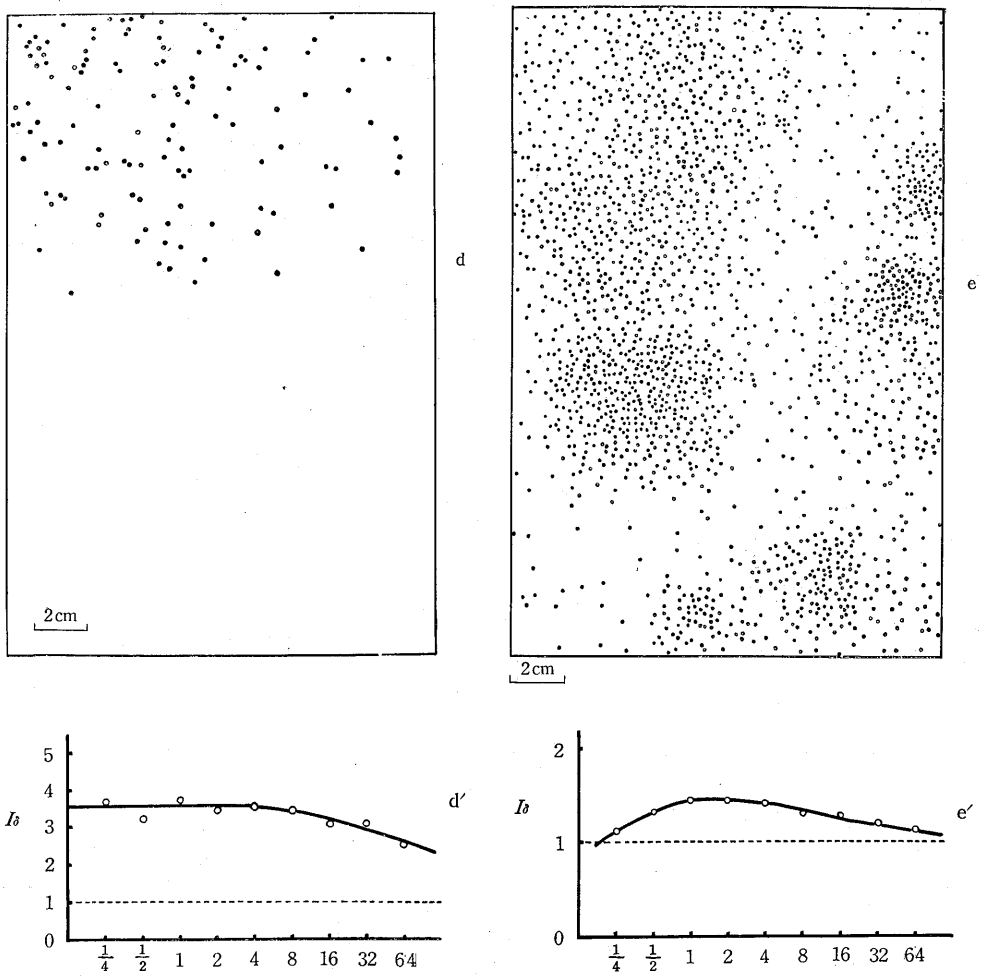


Fig. 2. d, d′ • • • • Contagious distribution with large clumps (intra-clump distribution is at random)

Fig. 2. e, e′ • • • • Contagious distribution with large clumps (intra-clump distribntions are uniform)

Table 2. Effects of quadrate size on various indices of dispersion for the artificial population shown in Fig. 2 d.

Quadrat size (cm²)	Number of quad-rats	McGinnies (1934) D/d	Blackman (1942) V/D	Fracker Brischle (1944) $(D-d)/d^2$	Whitford (1949) 100 D/F^2	Numata (1949) $\frac{\tau\sqrt{V}}{D\sqrt{q}}$	Kato (1952) n_0/n'_0	Moore (1953) $2n_0n_2/n_1^2$	David Moore (1954) $V/D-1$	I_δ
0.25	1536	1.100	1.206	1.389	0.1672	0.197	1.009	3.938	0.206	3.656
0 5	768	1.184	1.345	1.378	0.1025	0.208	1.025	3.589	0.345	3.232
1	384	1.481	1.842	2.269	0.0865	0.243	1.106	5.205	0.842	3.672
2	192	1.703	2.505	1.913	0 0662	0.274	1.295	5.377	1.505	3.415
4	96	2.660	4.025	3.531	0.0889	0.358	2.178	14.815	3.025	3.550
8	48	4.348	4.477	5.823	0.1306	0.390	6.128	4.320	3.477	3.460
16	24	7.215	11.757	6.213	0.2000	0.645	74.18	6.000	10.757	3.078
32	12	14.430	23.527	19.379	0.4000	0.967	1101.3	∞	22.527	3.082
64	6	28.860	37.380	40.204	0.8000	1.367	—	∞	36.380	2.528

V=unbiased estimate of variance
F=frequency
D=actual mean density per quadrat
d=expected mean density per quadrat
n_0, n_1, n_2=number of quadrats containing 0, 1, 2 individuals
n'_0=expected number of empty quadrats
τ=value of t when the level of significance is α (in this example α=0.05)
$I_\delta=q\delta$, where

$$\delta=\frac{\sum n(n-1)}{N(N-1)},$$ n=number of individuals occurred in each quadrat
$N=\sum n$=total number of individuals sampled

Index of uniformity and analysis of intra-clump distribution

The independence of the I_δ value from the effect of mean population density per quadrat considered in the previous chapters is based on the random distribution of individuals on each of the subareas. If the individuals in each clump or on the whole area examined are uniformly distributed, the I_δ value will rise with the increase of the quadrat size being influenced by the increase of mean density per quadrat as has been shown in Fig. 1 B. Therefore, a correction of the I_δ value is needed to express the degree of uniformity of distribution independently of the effect of mean density.

Consider that the distribution of individuals over an area is perfectly uniform, then the numbers of individuals occurred in the quadrats taken at random from the area will be equal to each other at least approximately, and if each of the quadrats of total q_1 is divided into k small quadrats of equal size, the numbers of individuals found in the small quadrats will also be equal to each other at least approximately being $1/k$ of that of large quadrat. Let the number of individuals in the large quadrat be n, and δ of the large and small quadrats be δ_1 and δ_2 respectively, then we will have approximately

$$\delta_1 = \frac{q_1 n(n-1)}{N(N-1)} = \frac{n-1}{N-1} \tag{11}$$

and

$$\delta_2 = \frac{kq_1 \frac{n}{k}\left(\frac{n}{k}-1\right)}{N(N-1)} = \frac{\frac{n}{k}-1}{N-1}. \tag{12}$$

Therefore,

$$I_{\delta_1} = \frac{q_1(n-1)}{N-1} = \frac{N-q_1}{N-1} \tag{14}$$

$$I_{\delta_2} = \frac{kq_1\left(\frac{n}{k}-1\right)}{N-1} = \frac{N-q_2}{N-1} \tag{13}$$

where $q_2 = kq_1$, and I_{δ_1} and I_{δ_2} are the values of I_δ of the large and small quadrats respectively.

Hence, it is known that the I_δ index takes the value of

$$\frac{N-q}{N-1}$$

approximately when the distribution of individuals is perfectly uniform and $N \geqq q$ where q is the number of quadrats sampled.

Then by putting

$$I_{\delta_0} = \frac{N-q}{N-1} \tag{15}$$

and

$$H_\delta = \frac{I_\delta - I_{\delta_0}}{1 - I_{\delta_0}}, \tag{16}$$

the H_δ may be used as the uniformity index when I_δ is smaller than unity.

However, there is a problem that the numbers of individuals in the quadrats will not always be exactly equal to each other. For example, when N is larger than nq but smaller than $(n+1)q$, the quadrats of at least two groups, the one containg n individuals and the other $(n+1)$ individuals, will be sampled, although the distribution of individuals is perfectly uniform. Therefore, on the assumption of the occurrence of these two quadrat groups a corrected form of I_{δ_0} is obtained as:

$$I'_{\delta_0} = \frac{2nq}{N(N-1)}\left\{N - \frac{1}{2}(n+1)q\right\}. \tag{17}$$

Then, a corrected form of H_δ is written as;

$$H'_\delta = \frac{I_\delta - I'_{\delta_0}}{1 - I'_{\delta_0}} \tag{18}$$

When N is large, I'_{δ_0} and H'_δ are nearly equal to I_{δ_0} and H_δ respectively. When $N = kq$, I'_{δ_0} equals I_δ and accordingly H'_δ equals H_δ.

Analysis of intra-clump distribution

If the distribution of individuals is contagious but the intra-clump distribution is uniform, the I_δ value will increase with the increase of quadrat size up to certain extent which is larger than unity as has been shown in Fig. 1 Ca_2 and Cb_2. If the intra-clump distribution is perfectly uniform, using the notations mentioned before, we have approximately

$$\delta_2 = \frac{k \sum_{i=1}^{q_1} \frac{n_i}{k}\left(\frac{n_i}{k} - 1\right)}{N(N-1)} = \frac{1}{k}\delta_1 - \frac{k-1}{(N-1)k} . \tag{19}$$

Hence,

$$I_{\delta_2} = kq_1\delta_2 = I_{\delta_1} - \frac{q_2(k-1)}{(N-1)k} . \tag{20}$$

Then,

$$I_{\delta_1} - I_{\delta_2} = \frac{q_2(k-1)}{(N-1)k} . \tag{21}$$

Therefore, if we put

$$h_\delta = 1 - (I_{\delta_1} - I_{\delta_2})\frac{(N-1)k}{q_2(k-1)} , \ (N \geqq q_2), \tag{22}$$

the h_δ will be a measure expressing the degree of uniformity of intra-clump distribution which takes the value of unity when the intra-clump distribution is at random, and the value of zero when it is perfectly uniform. If the individuals are distributed uniformly over an area without forming clump, the h_δ value may approximately be equal to the H_δ value. In this case, if the whole area examined is treated as a quadrat, the relation $h_\delta = H_\delta$ is easily proved.

In Table 3, the values of H_δ and h_δ obtained from the artificial population mapped in Fig. 2 b are compared, taking the I_δ values from the largest quadrat (32 cm^2) and those from the other quadrats as I_{δ_1} and I_{δ_2} respectively. It is shown in this table that the values of h_δ are almost equal to the corresponding H_δ values as is expected, and that the values from the quadrats of 8 and 16 cm^2 are much smaller than those from 2 and 4 cm^2 indicating that the inter-large quadrat (or inter-subarea) distribution is much more uniform than the intra-large quadrat (or intra-subarea) distribution in this population.

Table 3. Comparison of H_δ, H'_δ and h_δ values for the uniformly distributed population mapped in Fig. 2 b.

Size of quadrats (cm^2)	Number of quadrats ($=q_2$)	k	$I_{\delta 0}$	$I_{\delta 1}$	$I_{\delta 2}$	H_δ	H'_δ	h_δ
2	96	16	0.2017	0.9634	0.5513	0.438	0.289	0.454
4	48	8	0.6050	〃	0.7800	0.443	0.341	0.480
8	24	4	0.8067	〃	0.8368	0.156	0.156	0.163
16	12	2	0.9076	〃	0.9174	0.106	0.106	0.088
32	6	1	0.9580	〃	0.9634	0.129	0.129	—

Table 4. The h_δ values of 2 cm^2 quadrat using the I_δ values from the quadrats of various sizes as $I_{\delta 1}$, for the population used in Table 3.

Quadrat size for $I_{\delta 1}$ (cm^2)	Number of quadrats ($=q_2$)	k	$I_{\delta 1}$	$I_{\delta 2}$	h_δ
4	96	2	0.7800	0.5513	0.433
8	〃	4	0.8368	〃	0.528
16	〃	8	0.9174	〃	0.481
32	〃	16	0.9634	〃	0.454
192 (=whole area)	〃	96	1.0000	〃	0.438

The h_δ values, taking the I_δ value from the quadrat of 2 cm^2 and the values from the other quadrats as I_{δ_2} and I_{δ_1} respectively, are shown in Table 4.

As the h_δ values are almost fixed in spite of the change of quadrat size used in the computation of the I_{δ_1} value, it is known that the structure of intra-quadrat distribution is not changed by the increase of the quadrat size indicating a high degree of uniformity of the distribution of individuals over the whole area as has been analysed through Table 3.

The analysis of intra-clump distribution using the h_δ index has been applied to the artificial population mapped in Fig. 2 e, in which the I_δ value from the quadrats of the smallest size, 1/4 cm^2, has been used as I_{δ_2} and each of the values from 1/2, 1 and 2 cm^2 quadrats as I_{δ_1}. The results are given in Table 5.

The h_δ value of 1/2 cm^2 quadrat using the I_δ value from 1 cm^2 quadrat as I_{δ_1} is 0.490 which is almost equal to the h_δ values of 1/4 cm^2 quadrat shown in Table 5. From these results, it can be seen that the degree of intra-clump distribution of this population is about 0.5 which indicates considerable uniformity of the distribution.

The use of the above method to find out the degree of uniformity of intra-clump distribution will be confined to the case of $N \geqq q_2$. When $N < q_2$, it is difficult to determine the exact degree of uniformity at present. However, if the smallest I_δ value is taken as I_{δ_2} and the largest I_δ value obtained from the quadrat larger than that of I_{δ_2} is taken as I_{δ_1}, the value of $I_{\delta_2}/I_{\delta_1}$ may give a rough indication about the uniformity of the intra-clump distribution when I_{δ_2} is larger than unity.

For the population of Fig. 2 e, the smallest $I_{\delta_2}/I_{\delta_1}$ value is $1.133/1.450=0.774$. Though the value is considerably larger than 0.5 of the h_δ value, yet it may enough to indicate the uniformness of the intra-clump distribution of the population.

Table 5. Analysis of intra-clump distribution for the artificial population mapped in Fig. 2 e.

Size of quadrats for $I_{\delta 1}$ (cm^2)	Number of quadrats (q_2)	k	$I_{\delta 1}$	$I_{\delta 2}$*	h_δ
0.5	1536	2	1.328	1.133	0.507
1	〃	4	1.429	〃	0.501
2	〃	8	1.450	〃	0.542

* 1/4 cm^2 quadrat was used.

Analysis of clump size

As has been shown in Fig. 1, the I_δ-quadrat size curve begins to fall at smaller quadrat size in accordance with the smaller size of clumps, and it is clear that the change of the decrease rate of the I_δ value is related to the sizes and distribution of clumps.

From the data of the contagious distributions mapped in Fig. 2 c, d, e, the values of $I_{\delta(s)}/I_{\delta(2s)}$, where $I_{\delta(s)}$ is the I_δ value of the quadrat size s, and $I_{\delta(2s)}$ is that of the quadrat size $2s$, have been computed and plotted for each quadrat size taken as $2s$ in Fig. 3 a, b, c. In Fig. 3 a, a peak is seen in $I_{\delta(s)}/I_{\delta(2s)}$ curve at the quadrat size of 2~4 cm^2, and the existence of another peak at the quadrat size larger than 64 cm^2 is supposed. As the corresponding actual distribution shown in Fig. 2 c has several clumps with the mean size of about 2~4 cm^2 and an aggregation of these clumps covering an area about 150 cm^2, it is known that a quadrat size at a peak of the $I_{\delta(s)}/I_{\delta(2s)}$ curve coincides well with the size of clump or with the size of aggregation of clumps. Similar relation is also seen in Fig. 3 b suggesting the existence of a large clump with the size larger than 64 cm^2, which is actually seen in

Fig. 2 d. As to the population in Fig. 2 e, the clumps have various sizes, and the $I_{\delta(s)}/I_{\delta(2s)}$ curve corresponding to this distribution has a slow rise with the increase of quadrat size (Fig. 3 c).

Thus, the clump size may be analysed through the use of $I_{\delta(s)}/I_{\delta(2s)}$-quadrat size relation, although further investigations may still be needed for the accurate estimation of clump size.

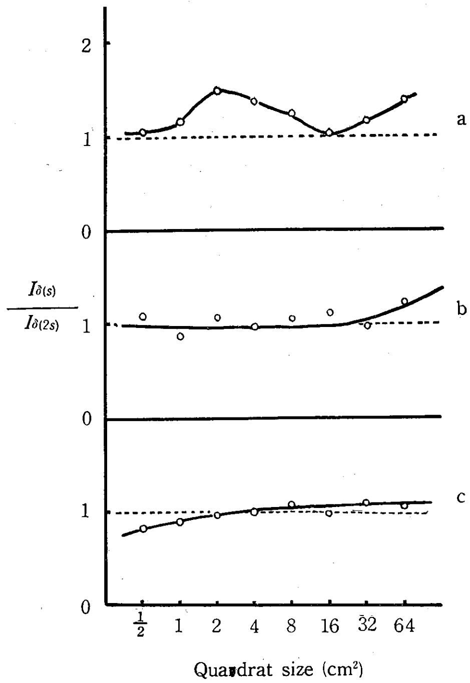


Fig. 3. $I_{\delta(s)}/I_{\delta(2s)}$ curves for the artificial populations mapped in Fig. 2.

a. · · · The population in Fig. 2 c.
b. · · · Tne pupulation in Fig. 2 d.
c. · · · The population in Fig. 2 e.

Application of the distribution analysis by the I_δ index to natural populations

The methods of distribution analysis using the I_δ index have been applied to the natural populations of three species of plants studied by Cain and Evans (1952) and by Evans (1952). The results are shown in Fig. 4 and 5, from which several characters of the distributional structures of these plants may be suggested. They are as follows:

(1) Among the three species, *Solidago*'s distribution is much less contagious than the distributions of the other two (Fig. 4) as has been analysed by Evans (1952) and Thomson (1952) through the use of several measures.

(2) All of the three species have small clumps. The clumps with the size of $1/4\sim1/2$ m^2 in these populations represented by the peaks in $I_{\delta(s)}/I_{\delta(2s)}$ curves (Fig. 5) may be the aggregations of a few individuals, supposing from their very small size. Besides these small clumps, *Solidago* and *Liatris* seem to have somewhat larger clumps with the size of $2\sim4$ m^2. The proportions of the individuals forming the small clumps in the populations of *Lespedeza* and *Liatris*, however, may be small, since the corresponding peaks in $I_{\delta(s)}/I_{\delta(2s)}$ curves are not conspicuous in these species.

The existence of major clumps with the sizes larger than 16 m^2 is suggested by the rise of $I_{\delta(s)}/I_{\delta(2s)}$ curves for all of the three populations (Fig. 5).

(3) The intra-clump distributions of teh three species are known to be more or less uniform (Fig. 4) indicating that the individuals in each clump have a tendency to keep some distance from each other. The degrees of uniformity of intra-clump distributions measured by the smallest $I_{\delta_2}/I_{\delta_1}$ values are 0.914, 0.628 and 0.814 in *Lespedeza, Solidago* and *Liatris* respectively. Though the h_δ values are not obtained as the numbers of small quadrats are much larger than the numbers of individuals, the above figures may suggest an obvious uniformity in *Solidago*'s intra-clump distribution, and at least slight uniformness in the clumps of *Liatris and Lespedeza.*

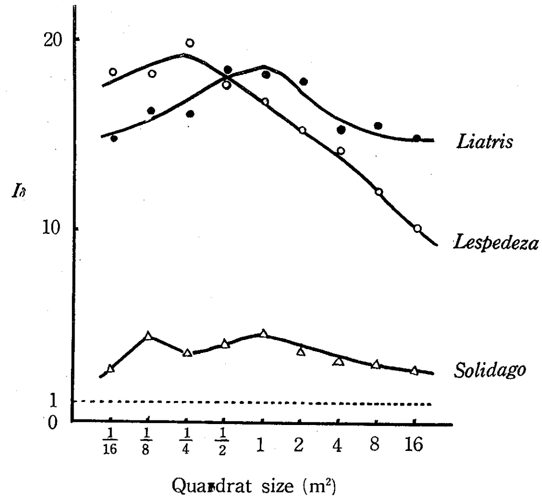


Fig. 4.

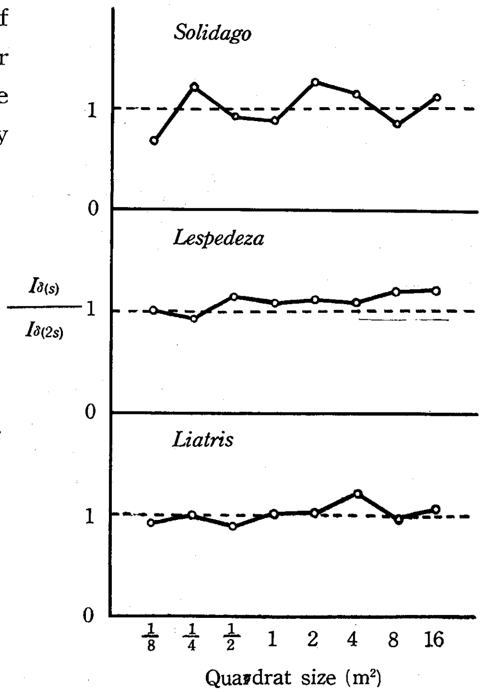


Fig. 5.

Fig. 4. I_δ-quadrat size relations in the populations of three species of plants studied by Evans (1952).

Fig. 5. $I_{(\delta s)}/I_{(\delta 2s)}$ curves for three species of plants studied by Evans (1952).

These characters, except the character (1), have not been analysed by the measures heretofore in use, though much of the character (2) has been known by the field observation (Evans, 1952).

Then, it may be said that the methods of distribution analysis using the I_δ-quadrat size relations give much more exact informations about the distributional patterns of populations than the indices hitherto proposed do.

Summary

1. A new index of dispersion of individuals, which is influenced neither by the average number of individuals per quadrat nor by the number of quadrats at least when the latter is not very small, was proposed.

2. Using this index, I_δ, the distributional patterns of several artificial and natural populations were examined. The I_δ-quadrat size relations theoretically presumed for various patterns of populations well agreed with the actual relations obtained from the corresponding artificial populations, and it was demonstrated that, through the use of this method, and of the methods developed further, not only the quantitative expression of the degree of contagiousness of a population, but the analysis of the intra-clump distribution of individuals and also the estimation of the clump sizes in a population, might be possible.

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