ANALYSIS OF SPATIAL ASSOCIATION BETWEEN TWO SPECIES BASED ON THE INTERSPECIES MEAN CROWDING

Syun'iti IWAO

Laboratory of Applied Entomology and Nematology, Faculty of
Agriculture, Nagoya University, Nagoya 464, Japan

INTRODUCTION

In ecological studies, it is often necessary to measure the degree of overlapping or correlation between distributions of two species, such as competitors, prey and predator, or even different subclasses within one species. Many indices have hitherto been proposed to meet such a requirement, and some of them are currently referred to as indices of 'niche overlap' (e.g., DICE, 1945; COLE, 1949; WHITTAKER, 1952; MORISITA, 1959; LEVINS, 1968; PIELOU, 1972; PIANKA, 1973). Each of these indices has its own merit but seems not to be sufficient as a tool of analyzing various features of interspecies relationship in some way or the other.

Here, I attempt to develop more systematically a method of analysis of spatial association between two species based on LLOYD's (1967) concept of interspecies mean crowding. Such an approach may be advantagious because interspecies mean crowding by itself can be a meaningful parameter from ecological point of view. Firstly, it will be shown that several incices of interspecies association, some of them are newly proposed and others are essentially identical with the existing ones, can be derived using the inter- and intraspecies mean crowdings. Then, the method of analysis based on the inter- and intraspecies $\overset{*}{m}-m$ relationships will be illustrated using artificially constructed distributions as well as data of insect distributions. Finally, possible application of the method to more general cases including continuous distributions will be briefly mentioned in relation to the wider implication of the parameters involved.

INTERSPECIES MEAN CROWDING AND MEASURES OF ASSOCIATION BETWEEN TWO SPECIES

Basic relations

Let assume that the individuals belonging to species X and Y are distributed over the same space. According to LLOYD (1967), the mean crowding on sp. X by sp. Y can be given by

$$\overset{*}{m}_{XY} = \sum_{j=1}^{Q} x_{Xj} x_{Yj} / \sum_{j=1}^{Q} x_{Xj} \tag{1}$$

and mean crowding on sp. Y by sp. X by

$$\overset{*}{m}_{YX} = \sum_{j=1}^{Q} x_{Xj}x_{Yj} / \sum_{j=1}^{Q} x_{Yj} \tag{2}$$

where x_{Xj} and x_{Yj} are the numbers of individuals of sp. X and sp. Y in the jth quadrat respectively, and Q is the total number of quadrats contained in the whole area. The sample estimates of these parameters $\overset{*}{x}_{XY}$ and $\overset{*}{x}_{YX}$, can be obtained by replacing Q with q, the number of quadrats sampled, in the above equations, though they are liable to sampling error of unknown magnitude. Interspecies mean crowding indicates the average number of individuals of the other species per individual of the subject species per quadrat. It serves, therefore, as a measure of association between species, but it does not necessarily indicate the effect of crowding or intensity of competition upon one species by the other, as pointed out by IWAO (1968) for mean crowding within a species.

When the mean crowding within each species is denoted by

$$\overset{*}{m}_X = \sum_{j=1}^{Q} x_{Xj}(x_{Xj}-1) / \sum_{j=1}^{Q} x_{Xj} \tag{3}$$

and

$$\overset{*}{m}_Y = \sum_{j=1}^{Q} x_{Yj}(x_{Yj}-1) / \sum_{j=1}^{Q} x_{Yj}, \tag{4}$$

the mean crowding on sp. X by both species X and Y is shown as

$$\overset{*}{m}_{X, X+Y} = \overset{*}{m}_X + \overset{*}{m}_{XY}. \tag{5}$$

Similarly, the mean crowding on sp. Y by spp. X and Y as

$$\overset{*}{m}_{Y, X+Y} = \overset{*}{m}_Y + \overset{*}{m}_{YX}. \tag{6}$$

If we disregard the distinction between species X and Y, the overall mean crowding including both species is expressed by

$$\overset{*}{m}_{X+Y} = p(\overset{*}{m}_X + 1 + \overset{*}{m}_{XY}) + (1-p)\,(\overset{*}{m}_Y + 1 + \overset{*}{m}_{YX}) - 1 \tag{7}$$

where $p = \sum_{j} x_{Xj} / (\sum_{j} x_{Xj} + \sum_{j} x_{Yj})$.

These simple relations will be convenient if we want to separate or combine the mean crowding for some purpose.

Measurement of overlapping

If there is no spatial overlapping between species X and Y, obviously $\overset{*}{m}_{XY}$ and $\overset{*}{m}_{YX}$ equal 0. If the distributions of both species are completely overlapped (i.e., the proportional relation $x_{Yj} = a\,x_{Xj}$, where a is a constant, exactly holds for every quadrat), we have the following relations:

$$\overset{*}{m}_{XY(prop)} = \frac{\sum_{j}(x_{Xj}\,ax_{Xj})}{\sum_{j} x_{Xj}} = \overset{*}{m}_Y + 1 \tag{8}$$

and

$$\overset{*}{m}_{YX(prop)} = \frac{\sum_{j}(x_{Xj}\,ax_{Xj})}{\sum_{j} ax_{Xj}} = \overset{*}{m}_X + 1 \tag{9}$$

respectively. Then the ratios

$$\eta_{XY} = \frac{\overset{*}{m}_{YX}}{\overset{*}{m}_X+1} = \frac{\sum_j x_{Xj} x_{Yj}}{\sum_j x_{Xj}^2} \cdot \frac{\sum_j x_{Xj}}{\sum_j x_{Yj}} \qquad (10)$$

and

$$\eta_{YX} = \frac{\overset{*}{m}_{XY}}{\overset{*}{m}_Y+1} = \frac{\sum_j x_{Xj} x_{Yj}}{\sum_j x_{Yj}^2} \cdot \frac{\sum_j x_{Yj}}{\sum_j x_{Xj}} \qquad (11)$$

may indicate the degree of overlapping of Y on X and *vice versa*; their values equal 1 if the distributions of two species are completely overlapped, and equal 0 if no overlapping occurs. In other cases, however, η_{XY} will not equal η_{YX} unless $\sum x_{Xj}= \sum x_{Yj}$ and $\overset{*}{m}_X=\overset{*}{m}_Y$, and either of them will exceed 1.0 under certain conditions of high degrees of overlapping.[1] It can be seen from eqs. (10) and (11) that η_{XY} and η_{YX} are similar to the regression coefficient of x_{Yj} on x_{Xj} and that of x_{Xj} on x_{Yj} under *a priori* assumption of a linear regression passing through the origin, though they are adjusted by the ratio of abundance of the two species. It is also noted that η_{XY} and η_{YX} are equivalent to the index of niche overlap α proposed by Levins (1968) which is derived using the proportional abundance of each species over the resource units on the basis of Volterra-Gause competition equations. (Putting $p_{Xj} = x_{Xj}/\sum_j x_{Xj}$ and $p_{Yj}=x_{Yj}/\sum_j x_{Yj}$, we can get the same equations).

By taking the geometric mean of η_{XY} and η_{YX}, we have a more appropriate index of overlapping:

$$r=\sqrt{\eta_{XY} \eta_{YX}}=\sqrt{\frac{\overset{*}{m}_{XY} \overset{*}{m}_{YX}}{(\overset{*}{m}_X+1)(\overset{*}{m}_Y+1)}} = \frac{\sum_j x_{Xj} x_{Yj}}{\sqrt{\sum x_{Xj}^2 \sum x_{Yj}^2}} \qquad (12)$$

which takes the maximum value of 1.0 when the distributions of both species are completely overlapped and the minimum value of 0 when the distributions are completely exclusive with each other.

The index r may correspond to a sort of correlation coefficient between x_{Xj} and x_{Yj} which measures the closeness to the linear relation $x_{Yj}=a\,x_{Xj}$. On this basis, Kuno (1968) has obtained the same index in his study on rice leafhoppers. The index is also essentially identical with Pianka's (1973) measure of niche overlap which is derived from Levin's α. Thus the same index is derived from different theoretical backgrounds.

Measurement of spatial correlation between species

Eq. (12) can be rewritten as

$$r=\sqrt{\left(\frac{\overset{*}{m}_{YX}}{m_X} \frac{\overset{*}{m}_{XY}}{m_Y}\right)\bigg/\left(\frac{(\overset{*}{m}_X+1)}{m_X} \frac{(\overset{*}{m}_Y+1)}{m_Y}\right)} . \qquad (12')$$

It is apparent from the above expression that the degree of overlapping indicated by

---

[1] For example, suppose that 10 individuals of Spp. X and Y are distributed among 5 quadrats in the following manner: (10 ; 6), (0 ; 1), (0 ; 1), (0 ; 1), (0 ; 1). Then we have $\eta_{YX}=0.6$ and $\eta_{XY}=1.5$. See p. 259 for additional comments.

γ will change with mean densities m_X and m_Y even if the relative degrees of aggregation in respective species, $\overset{*}{m}_X/m_X$ and $\overset{*}{m}_Y/m_Y$, remain the same. Then, one may be more interested to know how the observed value of γ is different from the degree of overlapping expected from independent occurrence of both species.

If two species are distributed independently of each other, the following relation would be expected whatever the distribution patterns of respective species:

$$\sum_{j=1}^{Q} x_{Xj} x_{Yj} \approx \frac{1}{Q} \sum_{j=1}^{Q} x_{Xj} \sum_{j=1}^{Q} x_{Yj},$$

and hence

$$\overset{*}{m}_{XY(ind)} \approx \frac{\sum_j x_{Yj}}{Q} = m_Y \tag{13}$$

and

$$\overset{*}{m}_{YX(ind)} \approx \frac{\sum_j x_{Xj}}{Q} = m_X. \tag{14}$$

These relations have already been suggested by LLOYD (1967).

Substituting these relations into eq. (12), we have the γ expected for independent distributions of two species as follows:

$$\gamma_{(ind)} = \sqrt{\frac{m_X}{(\overset{*}{m}_X+1)} \frac{m_Y}{(\overset{*}{m}_Y+1)}} = \frac{1}{\sqrt{\frac{(\overset{*}{m}_X+1)}{m_X} \frac{(\overset{*}{m}_Y+1)}{m_Y}}} \tag{15}$$

Then, as a measure of the degree of spatial correlation or the degree of overlapping relative to the independent distributions, we have

$$\omega_{(+)} = \frac{\gamma - \gamma_{(ind)}}{1 - \gamma_{(ind)}} = \sqrt{\frac{\overset{*}{m}_{XY} \overset{*}{m}_{YX} - m_X m_Y}{(\overset{*}{m}_X+1)(\overset{*}{m}_Y+1) - m_X m_Y}} \quad \text{for } \gamma \geq \gamma_{(ind)}$$

or

$$\omega_{(-)} = \frac{\gamma - \gamma_{(ind)}}{\gamma_{(ind)}} = \sqrt{\frac{\overset{*}{m}_{XY}}{m_X} \frac{\overset{*}{m}_{YX}}{m_Y}} - 1 \quad \text{for } \gamma \leq \gamma_{(ind)} \tag{16}$$

The value of ω changes from its maximum of $+1$ for complete overlapping, through 0 for independent occurrence, to the minimum of -1 for complete exclusion.

Also, it is noted that the ratio

$$\kappa = \frac{\overset{*}{m}_{XY}}{m_Y} = \frac{\overset{*}{m}_{YX}}{m_X} = \frac{Q \sum_j x_{Xj} x_{Yj}}{\sum_j x_{Xj} \sum_j x_{Yj}} \tag{17}$$

is equal to 1 if both species are distributed independently, and greater or smaller than 1 (min. 0) if there is positive or negative association between species. Since the values of $\overset{*}{m}_{XY}/m_Y$ and $\overset{*}{m}_{YX}/m_X$ expected for complete overlapping are $(\overset{*}{m}_Y+1)/m_Y$ and $(\overset{*}{m}_X+1)/m_X$ respectively and they are usually different from each other, the ratio κ does not serve as a quantitative measure. From eq. (12′), it is known that γ index can be interpreted as the geometric mean of the κ ratios adjusted for their expected values at the complete overlapping.

Morisita's indices C_δ and R_δ and their modifications

Morisita (1959) proposed indices of interspecies association C_δ and R_δ based on Simpson's (1949) measure of diversity. Lloyd (1967) showed the relation of C_δ to intra- and interspecies mean crowdings as

$$C_\delta \approx \left(\frac{\overset{*}{m}_{XY}}{m_Y} + \frac{\overset{*}{m}_{YX}}{m_X}\right) \bigg/ \left(\frac{\overset{*}{m}_X}{m_X} + \frac{\overset{*}{m}_Y}{m_Y}\right). \tag{18}$$

More strictly, the relation should be written as

$$C_\delta = \left(\frac{\overset{*}{m}_{XY}}{m_Y} + \frac{\overset{*}{m}_{YX}}{m_X}\right) \bigg/ \left[\left(\frac{\sum x_{Xj}}{\sum x_{Xj}-1}\right)\frac{\overset{*}{m}_X}{m_X} + \left(\frac{\sum x_{Yj}}{\sum x_{Yj}-1}\right)\frac{\overset{*}{m}_Y}{m_Y}\right]. \tag{18'}$$

According to Morisita, C_δ varies from 0 when no overlapping exists to about 1 when the density ratio between two species does not change between subareas. A characteristic feature of this index is that its value is almost free from the influence of mean densities, provided that the distribution patterns of both species in terms of $\overset{*}{m}/m$ do not change with mean densities (though this proposition is satisfied in rather limited cases as pointed out by Iwao, 1968). On the other hand, C_δ will take an indefinite value greater than 1.0 if the distribution of two species are highly overlapped. For the case of complete overlapping, we have from eqs. (8) and (9)

$$C_{\delta(prop)} \approx \left(\frac{\overset{*}{m}_X+1}{m_X} + \frac{\overset{*}{m}_Y+1}{m_Y}\right) \bigg/ \left(\frac{\overset{*}{m}_X}{m_X} + \frac{\overset{*}{m}_Y}{m_Y}\right) = 1 + \frac{m_X+m_Y}{m_Y\overset{*}{m}_X + m_X\overset{*}{m}_Y} \tag{19}$$

It is apparent that $C_{\delta(prop)}$ is greater than 1 and varies with mean densities m_X and m_Y (approaching 1.0 as m_X and m_Y become large).

R_δ as a measure of interspecies correlation can be expressed as

$$\begin{matrix} R_{\delta(+)} \approx \left(\dfrac{\overset{*}{m}_{XY}}{m_Y} + \dfrac{\overset{*}{m}_{YX}}{m_X} - 2\right) \bigg/ \left(\dfrac{\overset{*}{m}_X}{m_X} + \dfrac{\overset{*}{m}_Y}{m_Y}\right) \quad \text{for } R_\delta \geq 0, \\[2em] \text{or} \\[1em] R_{\delta(-)} \approx \dfrac{1}{2}\left(\dfrac{\overset{*}{m}_{XY}}{m_Y} + \dfrac{\overset{*}{m}_{YX}}{m_X}\right) - 1 \qquad \text{for } R_\delta \leq 0. \end{matrix} \tag{20}$$

For more strict expression, the denominator of $R_{\delta(+)}$ should be corrected as in eq. (18'). R_δ becomes -1 when the two species are distributed with no overlapping, 0 when they are distributed independently, and positive when the distributions are more overlapped. The upper limit of R_δ is again affected by mean densities and its value approaches 0 as m_X and m_Y become large, for its maximum in the complete overlapping is given by

$$R_{\delta(prop)} \approx \left(\frac{\overset{*}{m}_X+1}{m_X} + \frac{\overset{*}{m}_Y+1}{m_Y} - 2\right) \bigg/ \left(\frac{\overset{*}{m}_X}{m_X} + \frac{\overset{*}{m}_Y}{m_Y}\right). \tag{21}$$

Morisita (1971) proposed the corrected forms of both indices, C_δ' and R_δ', but the problems mentioned above are similar in them also. The influence of mean densities on C_δ and R_δ is illustrated by the following simple examples where the relation $x_{Yj}=2x_{Xj}$ holds for every quadrat:

quadrat (jth) :	Set A				Set B			
	1	2	3	4	1	2	3	4
x_{Xj}:	1	2	3	4	100	200	300	400
x_{Yj}:	2	4	6	8	200	400	600	800
C_δ :		1.236				1.002		
R_δ :		0.206				0.167		
C_δ' :		1.175				0.998		
R_δ' :		0.196				0.166		
γ :		1.000				1.000		
ω :		1.000				1.000		

C_δ can be modified in the following way to remove such a defect:

$$C_\mu = \left(\frac{\overset{*}{m}_{YX}}{m_X} + \frac{\overset{*}{m}_{XY}}{m_Y} \right) \Big/ \left(\frac{\overset{*}{m}_X + 1}{m_X} + \frac{\overset{*}{m}_Y + 1}{m_Y} \right) \tag{22}$$

The upper limit of C_μ for complete overlapping is exactly 1 as apparent from eqs. (8) and (9). From comparison of this equation with eq. (12'), it can be seen that C_μ and ω contain the same component ratios in both numerator and denominator, though the former index is additive and the latter is multiplicative. C_μ is very similar in behaviour to ω, because the former corresponds the weighted arithmetic mean and the latter the geometric mean of the ratios $\left(\frac{\overset{*}{m}_{XY}}{m_Y} \Big/ \frac{\overset{*}{m}_Y + 1}{m_Y} \right)$ and $\left(\frac{\overset{*}{m}_{YX}}{m_X} \Big/ \frac{\overset{*}{m}_X + 1}{m_X} \right)$. It should be noted that C_μ index derived here is formally identical with HORN's (1966) modification of C_λ which is a version of C_δ for measurement of similarity between communities (MORISITA, 1959).

For independent distributions of two species, C_μ becomes

$$C_{\mu(ind)} = 2 \Big/ \left(\frac{\overset{*}{m}_X + 1}{m_X} + \frac{\overset{*}{m}_Y + 1}{m_Y} \right) \tag{23}$$

Then the index of interspecies correlation can be derived as similar to eq. (14):

$$R_{\mu(+)} = \frac{C_\mu - C_{\mu(ind)}}{1 - C_{\mu(ind)}} = \left(\frac{\overset{*}{m}_{YX}}{m_X} + \frac{\overset{*}{m}_{XY}}{m_Y} - 2 \right) \Big/ \left(\frac{\overset{*}{m}_X + 1}{m_X} + \frac{\overset{*}{m}_Y + 1}{m_Y} - 2 \right)$$

for $C_\mu \geq C_{\mu(ind)}$

or

$$R_{\mu(-)} = \frac{C_\mu - C_{\mu(ind)}}{C_{\mu(ind)}} = \frac{1}{2} \left(\frac{\overset{*}{m}_{YX}}{m_X} + \frac{\overset{*}{m}_{XY}}{m_Y} \right) - 1 \qquad \text{for } C_\mu \leq C_{\mu(ind)}$$

$$\tag{24}$$

As can be seen, $R_{\mu(-)}$ is equivalent to $R_{\delta(-)}$.

ANALYSIS OF INTERSPECIES RELATION BASED ON THE UNIT-SIZE $\overset{*}{m} - m$ RELATIONSHIP

If the complete census data for two species are available for a specified area, we can detect the distributional interrelationship between species as well as distribution patterns of respective species by calculating m_X, m_Y, $\overset{*}{m}_X$, $\overset{*}{m}_Y$, $\overset{*}{m}_{XY}$ and $\overset{*}{m}_{YX}$ for several different quadrat sizes. Then, it may be convenient to show the result in an

extended form of the $\overset{*}{m}-m$ graph (IWAO, 1972) where the relations of $\overset{*}{m}_{XY}$ on m_Y and/or m_{YX} on m_X are shown together with $\overset{*}{m}_X-m_X$ and $\overset{*}{m}_Y-m_Y$ relations. As apparent from eqs. (13) and (14), $\overset{*}{m}_{XY}-m_Y$ and $\overset{*}{m}_{YX}-m_X$ points would fall around the line passing through the origin with the slope of 1 if both species are distributed independently of each other. Conveniently, this line also indicates the random distribution of individuals within one species (refer to as the *random line* hereafter). If there is positive or negative association between species, the points, of course, would fall above or below the random line. For the intraspecies relation, the points in the upper left of the line indicate the aggregated distributions and those in the lower right the regular (uniform) patterns and we can distinguish more detailed patterns of distributions using the unit-size $\overset{*}{m}-m$ relation as shown by IWAO (1972). A graph or table showing the change of γ and ω (or C_μ and R_μ) with successive changes of quadrat size is to be attached to show more quantitative information on the pattern of interspecies relationship.

Analysis of artificial populations

Applicability of the method presented in the foregoing pages is testified by constructing the 9 kinds of mixed-population maps illustrated in Fig. 1. Three different quadrat sizes are used for each case; the smallest size is denoted by $u=1$ (1×1 square), the medium size by $n=4$ (2×2), and the largest size by $u=6$ (4×4).

A. *Independent mixture of random distributions* (Fig. 1, A): As expected, all the values of intra- and inter-species $\overset{*}{m}-m$ points fall along the random line and ω index also suggests independent distributions of two species at any quadrat size (Fig. 2, left). The value of γ becomes large as quadrat size increases, because the degree of overlapping gradually approaches to its maximum as mean densities increase.

B. *Independent distributions of two populations comprizing randomly distributed colonies* (Fig. 1, B): As shown in Fig 2 right, the intraspecies $\overset{*}{m}-m$ regressions for both species are curvilinear and they become parallel with the random line at large quadrat sizes, which indicate the random distributions of loose colonies (see IWAO, 1972). In spite of positive association between individuals of the same species, the interspecies $\overset{*}{m}-m$ points are well within a small range of deviation from the random line, indicating rightly the independent distributions of two populations. Upward deviation of points and hence a small positive value of ω at the largest quadrat size may reflect the real existence of deviation by chance in the process of preparing the map.

C. *Independent mixture of a random distribution of individuals with that of colonies* (Fig. 1, C): In this case, one species denoted by X shows a weakly aggregated distribution at the largest quadrat size as indicated by the intraspecies $\overset{*}{m}-m$ relation, while the other species Y is distributed randomly in colonies (Fig. 3 left). Again, the interspecies $\overset{*}{m}-m$ relation and ω index indicate that both species are distributed independently, as is anticipated.
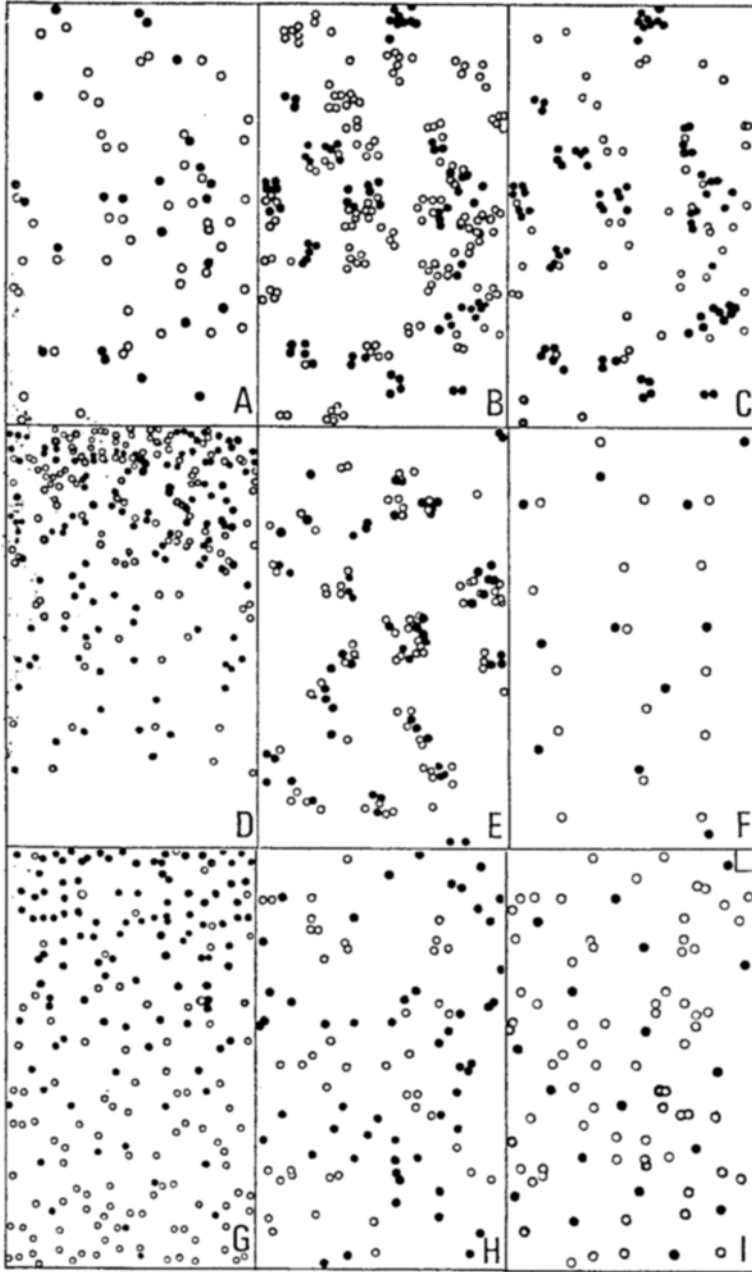
250

Fig. 1. Maps of artificially constructed populations showing various patterns of interspecies association. ◯ : species X ; ● : species Y.

A: Independent mixture of random distributions; B: Independent distributions of two populations comprizing randomly distributed colonies, C : Indepenent mixture of a random distribution of individuals with that of colonies ; D : Positive association of two species due to density gradients in the same drection ; E : Positive association of two species in clumps ; F : Positive association of two species being distributed uniformly; G: Negative association of two species due to density gradients in the opposite directions ; H: Negative association of two species being segregated in a irregular pattern ; I : Negative association due to a spaced-out distribution of one of the two species. A square in the upper right corner in I indicates the smallest quadrat size ($u=1$) used for the analysis.
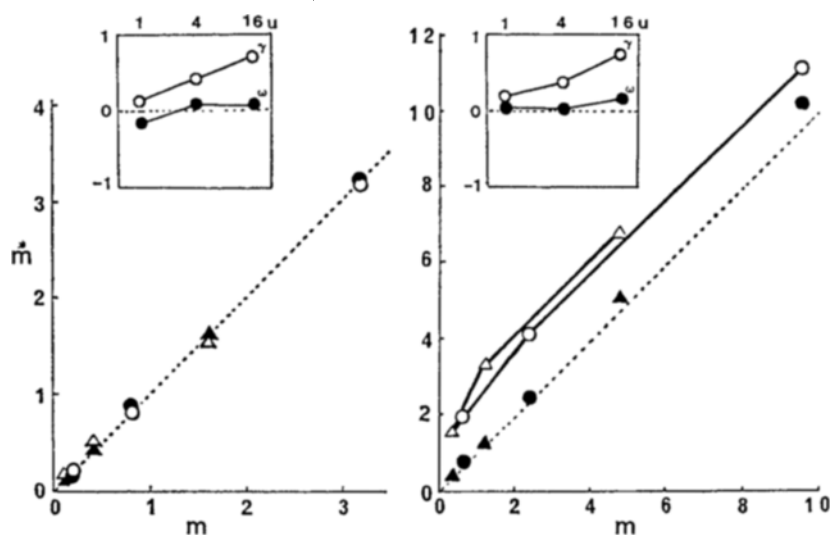
Fig. 2. Analysis of interspecies association by successive changes of quqdrat size. Showing the intraspecics and interspecies $\overset{*}{m}\text{-}m$ relations for distribution maps A (left) and B (right) in Fig. 1, with the changes of γ and ω indices in the upper graphs. $\bigcirc$: $\overset{*}{m}_X$ plotted against m_X; $\triangle$: $\overset{*}{m}_Y$ against m_Y; $\bullet$: $\overset{*}{m}_{YX}$ against m_X; $\blacktriangle$: $\overset{*}{m}_{XY}$ against m_Y.
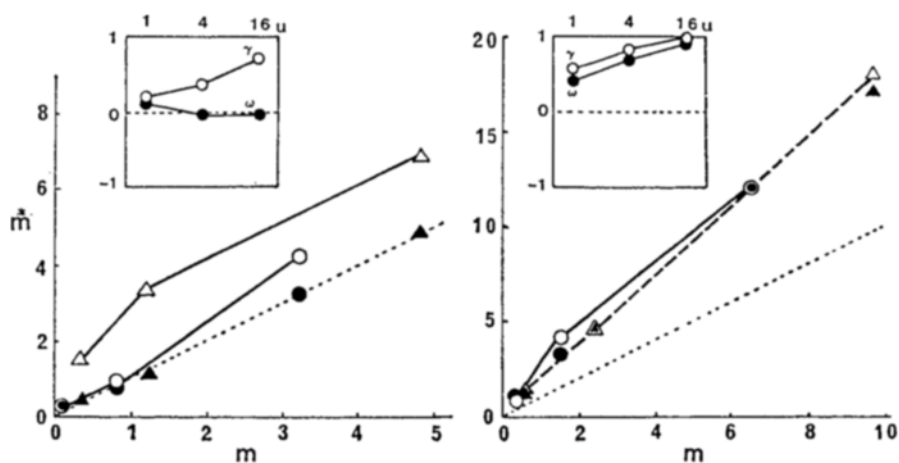
Fig. 3. The intraspecies and interspecies $\overset{*}{m}\text{-}m$ relations and changes in γ and ω indices for distribution maps C (left) and D (right). Symbols as in Fig. 2.

D. *Positive association of two species due to density gradients in the same direction* (Fig. 1, D): Both species are distributed nearly at random within any small part of the area but their densities change gradually from one end to the other. The $\overset{*}{m}-m$ rleation within each species, therefore, is approximately fitted to a regression line passing through the origin with a slope steeper than 1 (Fig. 3, right). The interspecies $\overset{*}{m}-m$ points also fall into upper zone and approximately fitted to the

regression for the intraspecies relation, indicating that both species are positively associated with each other and there is little difference in their distribution patterns. Both of γ and ω indices show relatively high positive values even at the smallest quadrat size and they increase towards the maxima as quadrat size becomes large.

E. *Positive association of two species in clumps* (Fig. 1, E): This kind of distribution overlap may be expected in such a case where two species prefer the same spots of habitat in response to common environmental factor(s) or where predators concentrate to high density patches of their prey. As shown in Fig. 4 left, the intraspecies $\overset{*}{m}-m$ rleation indicates that distribution of sp. X is more clumpy
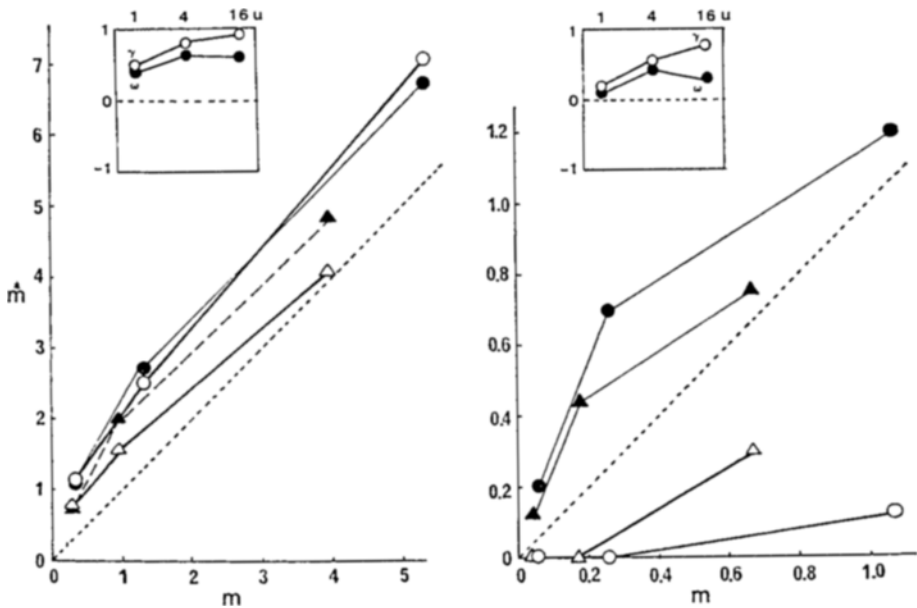

Fig. 4. The intraspecies and interspecies $\overset{*}{m}$-m relations and changes in γ and ω indices for distribution maps E (left) and F (right), For symbols, see Fig. 2.

than that of sp. Y. Comparison of $\overset{*}{m}_{YX}$ with $\overset{*}{m}_{Y}$ for the same quadrat size (except for $u=1$) suggests that individuals of sp. Y tend to live together with individuals of sp. X rather than other individuals of their own. Little increase of ω value from medium to large quadrat size indicates that the spatial unit of positive association is not large.

F. *Positive association of two species being distributed uniformly* (Fig. 1, F): This is a rather special model in which individuals of either species are distributed uniformly but the nearest neighbours are mostly individuals of the other species. In such a case, the intraspecies $\overset{*}{m}-m$ points, of course, lie below the random line while the interspecies $\overset{*}{m}-m$ points are in the opposite side (Fig. 4, right). This example shows more clearly the existence of spatial unit at which positive association is strongest.

G. *Negative association of two species due to density gradients in the opposite directions* (Fig. 1, G): Density gradients in the opposite directions may be caused by either differential preference to environmental cline or a tendency for interactive segregation between two species, or both. As shown in Fig. 5 left, sp. Y has a slightly stronger tendency for aggregation than sp. X. Since densities of two species gradually change from one side to the other, the degree of overlapping indicated by γ does not change markedly within the range of quadrat sizes used, and the interspecies $\overset{*}{m}-m$ relation as well as ω index shows a rather consistent pattern of negative association over different quadrat sizes.
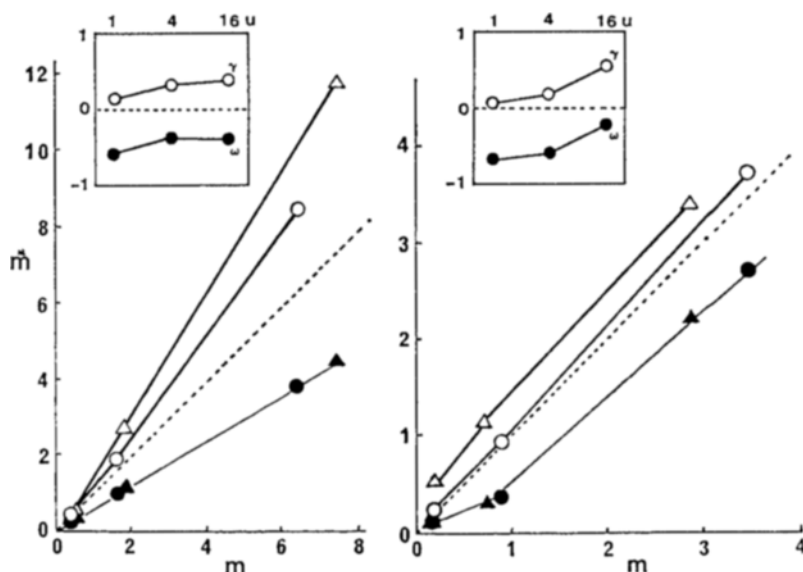

Fig. 5. The intraspecies and interspecies $\overset{*}{m}-m$ relations and changes in γ and ω indices for distribution maps G (left) and H (right). Symbols as in Fig. 2.

H. *Negative association of two species being segregated in an irregular pattern* (Fig. 1, H): Two populations are spatially segregated from each other in a more irregular pattern than in the preceding example. Distribution of each species is nearly at random within its territory but the presence of subareas from which it is excluded makes the distribution pattern in the whole area weakly aggregative (Fig. 5, right). As indicated by ω index, the intensity of negative association becomes weaker at large quadrat size because of the smaller patchwork of their distributions.

I. *Negative association due to a spaced-out distribution of one of the two species* (Fig. 1, I): Individuals of sp. X are distributed nearly at random but excluded from the neighbourhood of individuals of sp. Y that distribute themselves uniformly. As anticipated from the map, the complete exclusion occurs in a small spatial unit ($u=1$) but the intensity of negative association diminishes quickly as quadrat size increases
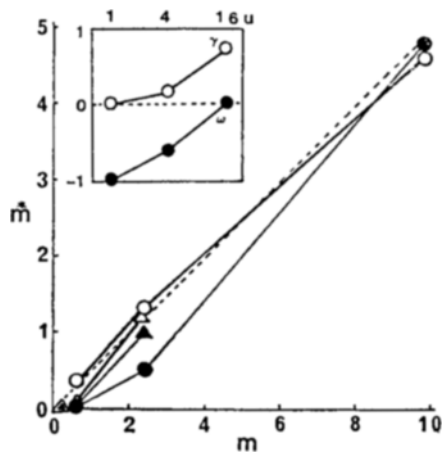
Fig. 6. The intraspecies and interspecies $\overset{*}{m}$-m relations
and changes in γ and ω indices for distribution map I.
Symbols as in Fig. 2.

towards almost independent distributions at $u=16$. Such a case may be expected when repulsive interaction or competition takes place locally between individuals of two species.

These examples may be sufficient to show the validity of the method for analyzing the interspecies association. Table 1 shows the vslues of the aforementioned indices of interspecies overlapping and correlation that are calculated for the distribution maps A~I being depicted at the smallest quadrat size. As can be seen, either combination of γ and ω or C_μ and R_μ give rise similar values. On the other hand, C_δ and R_δ behave differently and they cannot apply when both species are distributed uniformly (i. e., $\overset{*}{m}_X=\overset{*}{m}_Y=0$) as in F. As mentioned previously, R_δ becomes identical with R_μ when there is a negative association.

Table 1. Comparison of association indices when applied to artificial
distribution maps A~I in Fig. 1. ($u=1$)

Map	Overlap index			Correlation index		
	γ	C_μ	C_δ	ω	R_μ	R_δ
A	0.099	0.094	0.594	−0.166	−0.167	−0.167
B	0.185	0.178	0.277	0.034	0.032	0.042
C	0.185	0.182	0.424	0.052	0.053	0.103
D	0.559	0.555	1.193	0.399	0.395	0.625
E	0.475	0.475	1.013	0.382	0.382	0.690
F	0.158	0.154	infinitive	0.111	0.108	—
G	0.116	0.116	0.369	−0.624	−0.625	−0.625
H	0.050	0.046	0.168	−0.678	−0.678	−0.678
I	0	0	0	−1.000	−1.000	−1.000

Application to biological data

The method mentioned above is applied to detect the pattern of spatial association between stem borers attacking rice plants, based on the distribution maps given by KOJIMA and OKAMOTO (1957).

Relation between the paddy borer and the purplish stem borer: KOJIMA and OKAMOTO presented in their Fig. 1 a map showing the distributions of larvae of the paddy borer, *Tryporyza (Schoenobius) incertulas* and the purplish stem borer, *Sesamia inferens*, on a rice field comprizing 2500 (50×50) hills. This was analyzed using the quadrat sizes of 1, 4, 25, and 100 hills. The result is shown in Fig. 7 left. The intraspecies $\overset{*}{m}-m$ relations indicate that larvae of both species are distributed in loose colonies, though the colony size seems to be much larger in the paddy borer than in the purplish stem borer. Such a difference may surely be related with the difference in egg-mass size between both species, 30-100 eggs per mass in the former and 5-20 eggs in the latter.
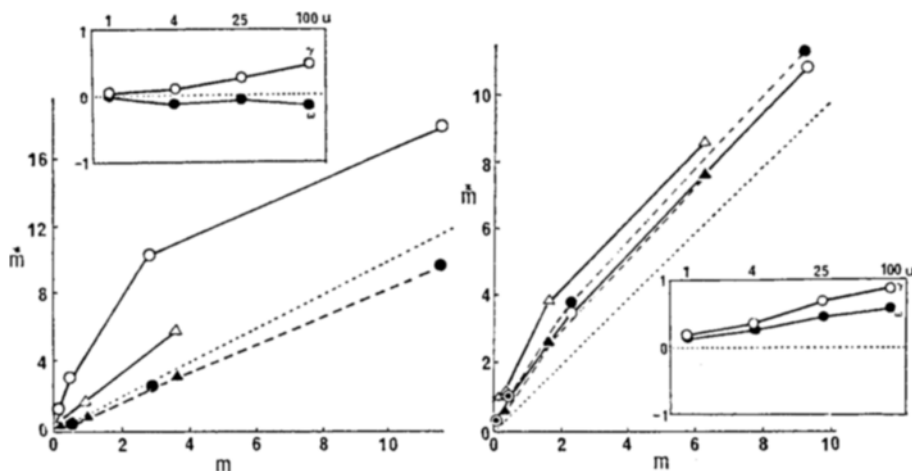

Fig. 7. Analysis of interspecies association between lepidópterous stem borers in paddy fields. Left: Relation between the paddy borer, *Tryporyza (Schoenobius) incertulas* (*X*), and the purplish stem borer, *Sesamia inferens* (*Y*); Right: relation between purplish stem borer (*X*) and the rice stem borer, *Chilo suppressalis* (*Y*). ○: $\overset{*}{m}_X-m_X$; △: $\overset{*}{m}_Y-m_Y$; ●: $\overset{*}{m}_{Y.X}-m_X$; ▲: $\overset{*}{m}_{X.Y}-m_Y$. (Original data from KOJIMA and OKAMOTO, 1957).

The interspecies $\overset{*}{m}-m$ relation suggests a weak tendency for negative association except for 1-hill unit. Although the deviation from the random line seems to be too small to be meaningful, it might suggest a minor difference in the preference for micro-habitat conditions between two species. Possibility of competitive interaction between larvae of both species can be denied, because ω value at the smallest unit ($u=1$) indicates the independent occurrence.

Relation between the purplish stem borer and the rice stem borer: Analysis was done using Fig. 3 of KOJIMA and OKAMOTO's paper on the relation between the

larvae of the purplish stem borer and the rice stem borer, *Chilo suppressalis*, in a plot of 50×40 hills of rice plants. As shown in Fig. 7 right, both species are distributed colonially and spatial disposition of colonies is nearly at random. In contrast with the preceding example, there is a definite tendency for positive association. Since ω value increases from 0.13 at 1-hill unit to 0.57 at 100-hill unit, positive association observed may be due to similar preference for local habitat conditions in both species.

ANALYSIS OF INTERSPECIES ASSOCIATION BASED ON THE SERIES $\overset{*}{m}-m$ RELATIONSHIP: AN EXAMPLE

For a single species, the relation of $\overset{*}{m}$ on m in a series of populations being depicted by a fixed quadrat size is known to be fitted to a linear regression in a wide variety of organisms, and intercept (α) and slope (β) of the regression indicate the pattern of distribution characteristic of the species (IWAO, 1968; IWAO and KUNO, 1971; etc.).

It is, however, difficult to develop a theoretical framework for the series relation of interspecies mean crowding to other variable such as mean density, except for the case where two species are distributed independently. Yet, empirical examination of the interspecies $\overset{*}{m}-m$ relation in a set of distribution data would yield useful information on the interrelationship between species as in the unit-size relation.

As an example, the relation between females and males of the flour beetle, *Tribolium confusum*, is shown below based on the re-analysis of NAYLOR's (1959) experimental work. As already shown by IWAO (1968) and IWAO and KUNO (1971), females of this insect tend to be distributed uniformly among the flour-filled tubes that are arranged to form a ring in the experimental arena, whereas males are distributed contagiously. According to NAYLOR, males tend to be attracted by females, which results in a superficially random distribution of mixed-sex population (IWAO and KUNO, *l. c.*).

In Fig. 8, mean crowding on males by females $(\overset{*}{m}_{XY})$ as well as female's mean crowding $(\overset{*}{m}_Y)$ are plotted against female density (m_Y). The relation of $\overset{*}{m}_{XY}$ on m_Y seems to change from positive to neutral (independent) as m_Y increases, and this relation can be approximated by a linear regression empirically. The same trend can be seen even more clearly by change of ω value with increase of m_Y. Then, it can be inferred that at low densities females would occupy only some of the tubes and males tend to be attracted to such tubes that contain females, but at higher densities females spread over many of the tubes and the effect of females to attract males is masked or diminished. As a consequence, a near-random distribution of the total population could be produced. From the data used here (NAYLOR's Table IV), we have the following regressions:

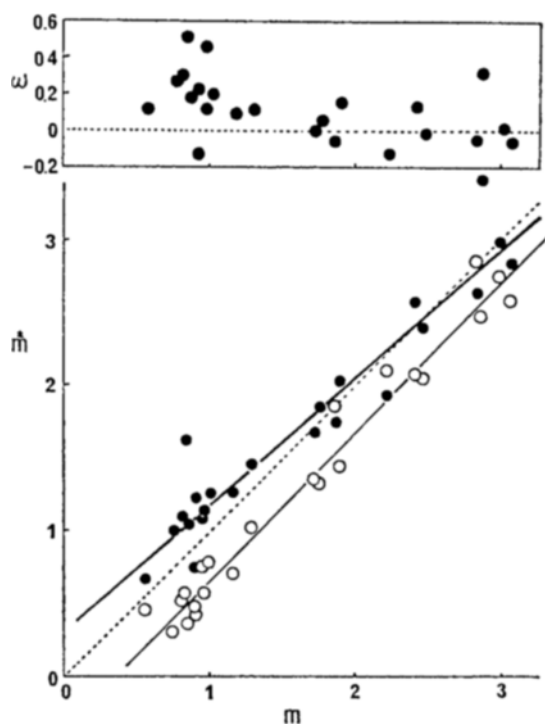$\overset{*}{m}_X = 0.36 + 1.09m_X \ (r^2 = 0.72); \ \overset{*}{m}_Y = -0.36 + 1.02m_Y \ (r^2 = 0.97);$

Fig. 8. Analysis of association of males (X) and females (Y) of
the flour beetle, *Tribolium confusum*, in an experimental arena.
$\overset{*}{m}_{XY}$ (●) and $\overset{*}{m}_{Y}$ (○) are plotted against m_{Y} in the lower
graph. Upper graph shows the change of ω index with increasing
density. (Original data from NAYLOR, 1959).

$\overset{*}{m}_{XY} = 0.31 + 0.88 m_{Y}$ $(r^2 = 0.96)$; $\overset{*}{m}_{YX} = 0.22 + 0.88 m_{Y}$ $(r^2 = 0.97)$.

Then, we can estimate from eq. (7) the $\overset{*}{m} - m$ relation for the total population:

$\overset{*}{m}_{X+Y} = p\,(1.67 + 1.09 m_{X} + 0.88 m_{Y}) + (1-p)(0.86 + 1.02 m_{X} + 0.88 m_{X}) - 1.$

If we assume $1:1$ sex ratio (i.e., $p = 0.5$), the above equation becomes

$\overset{*}{m}_{XY} = 0.27 + 0.97 m_{X+Y}.$

This is very close to the regression for the total population calculated from the data:

$\overset{*}{m}_{X+Y} = 0.20 + 0.96 m_{X+Y}$ $(r^2 = 0.97)$,

in spite of the fact that both variation in sex ratio and deviation of observed points
from the regression are not negligible in the actual data.

EXTENSION OF THE METHOD TO MORE GENERAL CASES

In this paper, our direct concern is the spatial association between species, but
the parameters and indices described here would also be applicable to compare the
temporal distribution patterns between species, similarity between communities, etc.
For such a wider application, it may be necessary to change definition and inter-
pretation of the parameters involved. IWAO (1976) pointed out that the parameter

$(\overset{*}{m}+1)$, defined by Lloyd (1967) as the mean number of individuals per individual per quadrat, can be a more general measure of concentration in both continuous and discrete distributions, and proposed the term 'mean concentration' (symbol $\overset{*}{c}$) for such a general usage which defined as the ratio of the second to the first moment about the origin. In a similar way, the interspecies mean crowding $(\overset{*}{m}_{XY}, \overset{*}{m}_{YX})$ can be formally defined as the ratio of the product moment μ'_{11} to the first moment μ'_{10} or μ'_{01} about the origin, and it may be called the *mean concentration on X by Y* or *vice versa* (symbolized by $\overset{*}{c}_{XY}$ and $\overset{*}{c}_{YX}$):

$$\overset{*}{c}_{XY} = \overset{*}{m}_{XY} = E\,(x_{Xj}x_{Yj})/E\,(x_{Xj}) = \mu'_{11}/\mu'_{10}$$

and

$$\overset{*}{c}_{YX} = \overset{*}{m}_{YX} = E\,(x_{Xj}x_{Yj})/E\,(x_{Yj}) = \mu'_{11}/\mu'_{01}.$$

Then, for example, eq. (12) can be rewritten as

$$r = \sqrt{(\overset{*}{c}_{XY}\overset{*}{c}_{YX})/(\overset{*}{c}_X\overset{*}{c}_Y)}$$

in a general expression which is applicable not only to discrete variables but also to continuous variables such as proportion, biomass, etc. The concept and terminology of intra- and interspecies mean crowdings, however, should be retained as far as they are appropriate because of their clearer ecological meanings.

Summary and Conclusion

The measurement of spatial association between two species is considered on the basis of interspecies mean crowding. Two indices of overlapping, r and C_μ, are derived as geometric and weighted arithmetic means of the same component ratios related to inter- and intraspecies mean crowdings. Both indices behave in a similar way, ranging from 1 when the distributions of two species are completely overlapped to 0 when they are completely exclusive with each other. The former is essentially identical with indices proposed by Kuno (1968) and Pianka (1973), and the latter is a modified form of Morisita's (1959) C_λ index. Indices to measure the degree of spatial correlation between species, ω and R_μ, are then derived for both kinds of overlapping indices, which vary from 1 in complete overlapping, through 0 in independent occurrence, to -1 in complete exclusion.

Various kinds of interspecies association are analyzed using these indices and an extended form of the $\overset{*}{m}-m$ regression graph which provides a convenient way of indicating the spatial interrelation between two species as well as distribution patterns of respective species.

The method presented in this paper may also be applicable to compare temporal distribution patterns between species, similarity between communities, etc. For such a wider application which includes continuous as well as discrete distributions, the interpretation of intra- and interspecies mean crowdings is not necessarily appropriate, and hence the concept of mean concentration with the symbols $\overset{*}{c}_X\,(=\overset{*}{m}_X+1)$ and $\overset{*}{c}_Y$ $(=\overset{*}{m}_Y+1)$ for intraspecies relation and $\overset{*}{c}_{XY}\,(=\overset{*}{m}_{XY})$ and $\overset{*}{c}_{YX}\,(=\overset{*}{m}_{YX})$ for interspecies

relation is suggested.

REFERENCES

COLE, LA MONT, C. (1949)   The measurement of interspecific association. *Ecology* 30: 411-424.

DICE, L. R. (1945)   Measures of the amount of ecologic association between species. *Ecology* 26: 297-302.

HORN, H. S. (1966)   Measurement of "overlap" in comparative ecological studies. *Amer. Nat.* 100: 419-424.

IWAO, S. (1968)   A new regression method for analyzing the aggregation pattern in animal populations, *Res. Popul. Ecol.* 10: 1-20.

IWAO, S. (1972)   Appilcation of the $\overset{*}{m}-m$ method to the analysis of spatial patterns by changing the quadrat size. *Res. Popul. Ecol.* 14: 97-128.

IWAO, S. (1976)   A note on the related concepts 'mean crowding' and 'mean concentration'. *Res. Popul. Ecol.* 17: 240-242.

IWAO, S. and E. KUNO (1971)   An approach to the analysis of aggregation pattern in biological populations. In *Statistical Ecology, Vol. 1* (ed. by G. P. PATIL *et al.*), pp. 461-513. Penn. State Univ. Press. University Park and London.

KOJIMA, K. and M. OKAMOTO (1957)   Distribution pattern of the paddy borer, the rice stem borer and the purplish stem borer in the paddy field. *Res. Rept. Kochi Univ.* 6: (29): 1-6. (In Japanese with English summary)

KUNO, E. (1968)   Studies on the population dynamics of rice leafhoppers in a paddy field. *Bull. Kyushu Agric. Expt. Sta.* 14: 131-246. (In Japanese with English summary)

LEVINS, R. (1968)   *Evolution in Changing Environments.* 120 pp. Princeton Univ. Press, Princeton.

LLOYD, Monte (1967)   'Mean crowding'. *J. anim. Ecol.* 36: 1-30.

MOSISITA, M. (1959)   Measuring of interspecific assosiation and similarity between communities. *Mem. Fac. Sci., Kyushu Univ., Ser. E (Biol.),* 3: 65-80.

MORISITA, M. (1971)   Composition of the I_δ-index. *Res. Popul. Ecol.* 13: 1-27.

NAYLOR, A. F. (1959)   An experimental analysis of dispersal in the flour beetle, *Tribolium confusum. Ecology* 42: 231-237.

PIANKA, E. R. (1973)   The structure of lizard communities, *Ann. Rev. Ecol. Syst.* 4: 53-74.

PIELOU, E. C. (1972)   Niche width and niche overlap: A method for measuring them. *Ecology* 53: 687-692.

SIMPSON, E. H. (1949)   Measurement of diversity. *Nature* 163: 688.

WHITTAKER, R. H. (1952)   A study of summer foliage insect communites in the Great Smoky Mountains. *Ecol. Monogr.* 22: 1-44.

Supplementary Note

As mentioned on page 245, η_{XY} or η_{YX} can be greater than unity under certain conditions of positive association between two species. This happens in such a case where disproportionately large numbers of one species (say, Y) concentrate on high density patches of the other species (X). Thus, the local density dependence in terms of the density ratio x_{Yj}/x_{Xj} against x_{Xj} can be detected by η_{XY} index or by $\overset{*}{m}-m$ graphic method. A superproportional relation of Y on X means a subproportional relation of X on Y, and hence the overlapping index γ or C_μ cannot distinguish such a case from weak, positive association between species.

種間平均こみあい度に基づく種間関係の解析

厳　　俊　一

　種間の分布重なり度や分布相関の指数はこれまでにもいくつか提案されているが，それぞれ一長一短がある。ここでは種間平均こみあい度の概念に基づいて一連の解析法を提案した。

　種Xに対する種Yの平均こみあい度（$\overset{*}{m}_{XY}$）およびYに対するXの平均こみあい度（$\overset{*}{m}_{YX}$）と，それぞれの種内の平均こみあい度（$\overset{*}{m}_X$, $\overset{*}{m}_Y$），平均密度（m_X, m_Y）との間には次の基本的関係がある。

　　　2種の分布が全く重ならないとき：$\overset{*}{m}_{XY}=\overset{*}{m}_{YX}=0$;

　　　2種が独立に分布するとき：$\overset{*}{m}_{XY}\approx m_Y$, $\overset{*}{m}_{YX}\approx m_X$;

　　　2種の分布が完全に重なるとき：$\overset{*}{m}_{XY}=\overset{*}{m}_Y+1$, $\overset{*}{m}_{YX}=\overset{*}{m}_X+1$。

これらの関係から分布重なり度の指数としてrとC_μが導かれる。前者は久野（1968）やPIANKA（1973）の指数と結果的には同じであり，後者は森下（1959）のC_δ指数の変形に相当する。また，2種が独立に分布するときを基準にした相対的な重なり度，すなわち分布相関の指数としては，上記2つの重なり度指数に対応するωとR_μを新たに提案した。

　2種それぞれの分布様式と種間の相互関係をより具体的に示すには$\overset{*}{m}-m$グラフを用いるのが便利である。m_Xに対し$\overset{*}{m}_{YX}$, m_Yに対し$\overset{*}{m}_{XY}$をプロットするとき，原点を通り勾配1の直線は2種の分布が独立のとき期待される関係を示すが，同じ直線は種内の分布に対してはランダム分布を示す基準線となるので，同じグラフに種内の分布様式と種間関係についての情報を同時に示すことができる。

　種々の分布様式と種間の相互関係を示す2種人工個体群の分布図や昆虫の実例によって，上述の方法の有効性を例証した。なお，連続量を用いたデータや群集構成の比較などより広汎な問題にもこれらの方法を適用することが可能であるが，その際には平均こみあい度の概念は必ずしも適切ではないので，より一般的に定義される平均集中度（$\overset{*}{c}$）の概念を用いるべきことを指摘した。