STATISTICAL ECOLOGY / ECOLOGIE STATISTIQUE

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STATISTICAL MEASUREMENT OF SPATIAL PATTERNS
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1. INTRODUCTION

Although the problems of measuring or describing spatial patterns and of detecting departures from randomness in patterns are important in many fields, most of the work to date has been in the fields of plant and animal ecology. A large number of indices have been proposed in this literature based on a wide variety of underlying concepts and biological interpretations. These motivations are, however, general enough that the applicability of the indices is apparent in many other fields as for example geography, economics, urban planning, etc.

In general, indices of spatial patterns can be classified into two groups—those which are based on a sample of counts for randomly placed plots or quadrats and those based on a sample of distances. We will concentrate here on some of the indices based on plot count data. If we represent by $X$ the number of individuals in a randomly placed plot or quadrat, and let $\mu$ and $\sigma^2$ denote the mean and variance of $X$ respectively, then from a theoretical population viewpoint we can represent many of the indices as functions of $\mu$ and $\sigma^2$.

2. THE INDEX $\omega = \sigma^2/\mu$

Under the assumption of random spatial pattern the random variable $X$ has a Poisson distribution so that $\sigma^2 = \mu$. Intuitively it seems that, at least for plots of "reasonable" size we would have $\sigma^2 > \mu$ for aggregated or contagious patterns and $\sigma^2 < \mu$ for regular patterns, which would lead us to consider the ratio $\omega = \sigma^2/\mu$ as an index of spatial pattern.

Perhaps it is more illuminating to think of $\omega$ as being the ratio of two variances. Since $\mu$ is the average density per unit area times the size of the plot it is clear that it is the same as the parameter which would be obtained for the Poisson distribution if the same population were randomly distributed. That is to say, we are comparing the variance for the population in question against the variance of a random distribution of the same density. If a population has more variability than would be expected for a random distribution we call it aggregated or contagious and if the variability is less we call it regular.

One estimate of $\omega$, the so called "index of dispersion"

$$\omega = \sum \frac{(X_i - \bar{X})^2}{\bar{X}} = (n - 1) S^2 / \bar{X},$$
has been studied by a number of researchers (Batemen, 1950; Bennett, 1956, 1959, 1962, 1964; Bennett and Hsu, 1961, 1962; Darwin, 1957; Fisher, et al., 1922; Hoel, 1943; Kathirgamatamby, 1953; Okamoto, 1955; Selby, 1965; Thomas, 1961).

Student (1919) was probably the first to apply the index of dispersion to the problem of measuring spatial pattern. In another early paper Clapham (1936) calculated the index of dispersion divided by \( n - 1 \) (which he called “relative variance”) for 44 species of grasses and found that for all but two cases \( w/(n - 1) \) was greater than one.

Other researchers have looked at the power of the test of the hypothesis of randomness based on the index of dispersion when the alternative hypothesis specifies various models describing aggregated behavior (Bateman, 1950; Darwin, 1957; Selby, 1965).

A graphical description of \( S^2/X \) as a test of the Poisson model has been given by Gart (1970) in which he uses the relation \( \lambda = ip(i)/p(i - 1), \) \( i = 1, 2, 3, \ldots \) for a Poisson distribution. Denoting by \( f_i \) the observed frequency in the \( i \) th class we obtain the set of estimates \( \hat{\lambda}_i = i f_i/f_{i-1} \). Gart expressed the best estimate of \( \lambda \) which is \( \hat{\lambda} = \bar{X} \) as a weighted mean of the \( \hat{\lambda}_i \)’s.

\[
\hat{\lambda} = \frac{\sum w_i \hat{\lambda}_i}{\sum w_i}
\]

where the weights \( w_i \) are taken to be \( f_{i-1} \).

The set of estimates \( \hat{\lambda}_i \) when plotted against \( i \) on a graph should fall about a horizontal straight line. Gart showed that \( ip(i)/p(i - 1) \) is also a linear function of \( i \) for the negative binomial and binomial distributions but with positive and negative slopes respectively. Hence, as a test of whether a set of data comes from a Poisson distribution one could test the hypothesis that the slope of the regression line is zero. The weighted least squares estimate of the slope \( \beta \) is given by:

\[
\beta = \left[ \sum w_i (i - \bar{x}_w) (\hat{\lambda}_i - \bar{\lambda}_w) \right] / \sum w_i (i - \bar{x}_w)^2
\]

where \( \bar{x} = (\sum w_i \bar{x}_w) / (\sum w_i) \) and \( \bar{\lambda}_w = (\sum w_i \hat{\lambda}_i) / (\sum w_i) \).

If \( w_i = f_{i-1} \) this reduces to:

\[
\beta = 1 - \left[ n/(n - 1) \right] (\hat{X}/S^2),
\]

from which the equivalence of the two tests is apparent.

Another illuminating derivation of \( S^2/X \) for testing the Poisson model is given by Rao and Chakravarti (1956). Let \( X_1, X_2, \ldots, X_n \) be a sample of \( n \) observations from a Poisson distribution. Then given the total \( t = \sum_{i=1}^{n} X_i \) the conditional distribution of \( (X_1, X_2, \ldots, X_n) \) is a singular multinomial. The classical \( \chi^2 \) goodness of fit test is given by

\[
\sum \left[ X_i - E(X_i | t) \right] / E(X_i | t) = \sum (X_i - \bar{X})^2 / \bar{X} = w
\]

since \( E(X_i | t) = t/n = \bar{X} \).
3. THE INDEX $\gamma = (\sigma^2 - \mu)/\mu^2$

The parameter $k$ of the negative binomial distribution has been suggested as a measure of spatial patterns (Waters, 1959). Cassie (1962) chose to use the reciprocal of $k$ and proposed the index $\gamma = (\sigma^2 - \mu)/\mu^2$ which is obtained by expressing the variance of the negative binomial distribution as $\sigma^2 = \mu + (\mu^2/k)$ and solving for $1/k$. It has been suggested by Kuno (1968) that this index is useful as a measure of spatial pattern regardless of the underlying probability distribution. He interprets $\gamma$ as the squared coefficient of variation minus $1/\mu$, the value of the squared coefficient of variation for the Poisson distribution. Then $\gamma$ should be zero for a random distribution, greater than zero for an aggregated distribution, and less than zero for a regular distribution.

Morisita (1959) proposed that the diversity of the numbers of individuals per quadrat be used as a measure of spatial pattern. If $X_i$ is the number of individuals in the $i$th plot ($i = 1, 2, ..., n$) and $t = \sum X_i$, Morisita's index is given by

$$I_4 = n [\sum X_i (X_i - 1)/t(t - 1)].$$

The quantity $\sum X_i (X_i - 1)/t(t - 1)$ is a measure of diversity proposed by Simpson (1949) and in this context is interpreted as the probability that two individuals randomly selected from the total $t$ sampled will be from the same plot. If the sample comes from a Poisson distribution the expected value of this measure of diversity is $1/n$. Therefore Morisita's $I_4$ index measures, as a quotient, the diversity of the sample relative to the diversity expected for a random distribution.

Although $I_4$ was originally introduced as a sample statistic it was given a simple extension to a population concept by Morisita (1964). For this extension it is assumed that the population is distributed over a finite number of distinct habitat units which become the sampling plots. Then if the entire population is censused we have

$$I_4 = E[X(X - 1)]/(E(X))^2 -(1/n) = \gamma + 1.$$

Lloyd (1967) has provided another interpretation for the index $\gamma$ in terms of an index measuring the degree of crowding of individuals of a population. This index, which he calls "mean crowding", is defined as the "mean number per individual of other individuals in the same quadrat" and is computed as

$$\mu^* = \sum X_i (X_i - 1) / \sum X_i,$$

where $X_i$ = the number of individuals in the $i$th quadrat or habitat unit for $i = 1, 2, 3, ..., n$.

In Lloyd's presentation he assumes that all of the habitat units (quadrats) in the region under study have been censused so that a more formal definition
could be given as
\[ \mu^* = \frac{E[X(X - 1)]}{E(X)} = \mu'_0/\mu'(0), \]
where \( \mu'_0 \) refers to the \( r \)th factorial moment of \( X \), the number of individuals in a randomly located plot.

Mean crowding can be expressed in terms of the population mean and variance as:
\[ \mu^* = \mu + \sigma^2/\mu - 1, \]
for which it is clear that for a Poisson distribution \( \mu^* = \mu \). Lloyd has used this fact to provide a new interpretation of the index \( \gamma = (\sigma^2 - \mu)/\mu^2 \) which can be written as \( \mu^*/\mu - 1 \). Lloyd calls \( \mu^*/\mu \) an index of "patchiness" and interprets it as "how many times as 'crowded' an individual is, on the average, as it would have to be if the population had a random distribution".

4. A VECTOR APPROACH TO MEASURING SPATIAL PATTERNS

In this section a new approach to measuring spatial patterns is proposed. This approach uses a vector of indices based on an extension of Lloyd's mean crowding. It will be shown that the proposed indices provide extensions and new interpretations of the indices \( \omega \) and \( \gamma \). A relationship between the proposed vectors of indices and the measurement of spatial pattern as a dynamic concept is examined for a pure birth process.

4.1 An Extension of Lloyd's Mean Crowding

In the preceding section it was noted that Lloyd's mean crowding \( \mu^* \) can be written as the ratio of the second factorial moment to the first. This suggests an extension to \( \varphi_r = \mu'^{r+1}/\mu'(r) \) which could be called the \( r \)th level crowding or the aggregative tendency at level \( r \). To interpret this measure write
\[
\varphi_r = \frac{\mu'^{r+1}/\mu'(r)}{\mu'_0/\mu'(0)} = \frac{\sum X(X - 1) \cdots (X - r)p_X}{\sum X(X - 1) \cdots (X - r + 1)p_X} = \frac{\sum (X - r)X(X - 1) \cdots (X - r + 1)p_X/r!}{\sum X(X - 1) \cdots (X - r + 1)p_X/r!}
\]
\[
= \sum \frac{\binom{X}{r}p_X}{\sum \binom{X}{r}p_X}
\]
which shows that \( \varphi_r \) is the expected number of individuals in excess of a randomly selected group of size \( r \). Extending Lloyd's definition of \( \mu^* = \varphi_1 \) we could call \( \varphi_r \) the mean number per group of size \( r \) of other individuals in the same quadrat.

4.2 Effect of Zero Truncation

It is a desirable property of a measure of \( r \)th order crowding for \( r > 0 \) that it is not affected by ignoring the empty quadrats. That is to say, the number of empty quadrats has nothing to do with the degree to which the individuals in the occupied quadrats are "crowded". On the other hand, the null order crowding \( \varphi_0 \), which is the expected number of individuals in excess of a group of size zero, should depend on the number of empty quadrats.

It is clear that \( \varphi_r \) is not affected by truncation of zeros for \( r > 0 \) since the normalizing constant \( (1 - p_0)^{-1} \) cancels in the ratio. The null level crowding is increased by a multiple of \( (1 - p_0)^{-1} \) reflecting the fact that we no longer have groups of size zero with an excess of zero possible.

4.3 A Vector of Indices for Measuring Spatial Patterns

The manner in which \( \varphi_r \) changes with \( r \) can be interpreted as a measure of spatial pattern. If the crowding at level \( r + 1 \) is the same as the crowding at level \( r \) an indifference among the individuals or a random spatial pattern is implied at that level. If \( \varphi_{r+1} > \varphi_r \) an attractive influence or an aggregated spatial pattern is implied at the \( r \)th level. If \( \varphi_{r+1} < \varphi_r \) a repulsive influence or a regular spatial pattern is implied at the \( r \)th level. This suggests two vectors of indices of spatial pattern; \( R = (R_0, R_1, R_2, ...) \) and \( D = (D_0, D_1, D_2, ...) \) where \( R_r = \varphi_{r+1}/\varphi_r \) and \( D_r = \varphi_{r+1} - \varphi_r \).

The indices \( R_r \) might also be interpreted as the change in attractiveness of a quadrat or habitat unit containing \( r \) individuals to any new individual which might consider entering it.

It is also meaningful to consider as indices of spatial pattern the difference between the \( r \)th level crowding and the null level crowding \( \varphi_0 = \mu \). This is perhaps best interpreted as the difference between the \( r \)th level crowding of the population in question and the \( r \)th level crowding that this same population would have if it were randomly distributed. This is because a Poisson distribution has \( \varphi_r = \varphi_0 = \mu \) for all \( r \). Thus one is comparing the crowding at each level against what it would be for a random distribution to get an overall picture of the spatial pattern.

If \( \varphi_r = \varphi_0 \) an indifference or randomness would be implied at the \( r \)th level. Similarly, \( \varphi_r > \varphi_0 \) implies aggregation and \( \varphi_r < \varphi_0 \) implies regularity at the \( r \)th level. This leads to the two vectors of indices of spatial pattern; \( R' = (R'_1, R'_2, ...) \) and \( D' = (D'_1, D'_2, ...) \) where \( R'_r = \varphi_r/\varphi_0 \) and \( D'_r = \varphi_r - \varphi_0 \).
4.4 Previous Indices as Special Cases

It has been seen in the preceding sections that the two indices \( \sigma^2/\mu \) and \( (\sigma^2 - \mu)/\mu^2 \) can each be derived as measures of spatial patterns in a number of different ways and with different interpretations. In fact, the manner in which they were derived was sometimes so different that it was not immediately recognized that a previously proposed measure was being reintroduced.

These two indices are also special cases of the vectors proposed here since \( \sigma^2/\mu = D_0 + 1 = D'_1 + 1 \) and \( (\sigma^2 - \mu)/\mu^2 = R_0 - 1 = R'_1 - 1 \). Thus the proposed vectors provide not only a new interpretation of these indices but an extension as well.

4.5 \( r \)th Order Crowding for Some Commonly Used Distributions

(1) Poisson, binomial, and negative binomial distributions

For the Poisson, binomial, and negative binomial distributions we have \( \varphi_r \) as linear functions of \( r \) with zero, positive, and negative slopes respectively.

\[
\varphi_r = \begin{cases} 
\lambda & \text{Poisson} \\
(n-r)p & \text{binomial} \\
(k+r)q/p & \text{negative binomial}
\end{cases}
\]

The above property of these distributions was pointed out by Ottestad (1939) who suggested that it be used as a means of differentiating between the three distributions.

The values of the proposed vectors of indices for these three distributions are:

\[
R_r = \varphi_{r+1}/\varphi_r = \begin{cases} 
1 & \text{Poisson} \\
1-1/(n-r) & \text{binomial} \\
1+1/(k+r) & \text{negative binomial}
\end{cases}
\]

\[
D_r = \varphi_{r+1} - \varphi_r = \begin{cases} 
0 & \text{Poisson} \\
-p & \text{binomial} \\
q/p & \text{negative binomial}
\end{cases}
\]

\[
R'_r = \varphi_r/\varphi_0 = \begin{cases} 
1 & \text{Poisson} \\
1-r/n & \text{binomial} \\
1+r/k & \text{negative binomial}
\end{cases}
\]
\[ D' = \phi - \phi_0 = \begin{cases} 0 & \text{Poisson} \\ -rp & \text{binomial} \\ rq/p & \text{negative binomial} \end{cases} \]

It is an interesting property of these three distributions that if we consider \( r \) to be a random variable and assign to it the same distribution as \( X \) we have:

\[
E(\phi_r) = \begin{cases} \lambda = \sigma^2 & \text{Poisson} \\ np(1 - p) = \sigma^2 & \text{binomial} \\ \frac{rq}{p^3} = \sigma^2 & \text{negative binomial}. \end{cases}
\]

So that \( E(R'_i) = \sigma^2/\mu = \omega \), \( i = 1, 2, 3, \ldots \) for all of the three distribution.

(2) Logarithmic series distribution

Another distribution which yields the ratio of factorial moments as a linear function of \( r \) is the logarithmic series distribution with probability distribution

\[ p_x = -\theta^x/x \log(1 - \theta) \quad x = 1, 2, 3, \ldots, \quad 0 < \theta < 1. \]

This distribution has factorial moments

\[ \mu'(r) = a \theta^r(1 - \theta) - r(r - 1)! \]

so that

\[ \phi_r = r\theta/(1 - \theta). \]

The logarithmic series distribution arises as the limit of a zero-truncated negative binomial distribution with parameters \( k \) and \( 1 - \theta \) as \( k \to 0 \). In view of the discussion in section 4.2 we see that the \( \phi_r \) obtained for the logarithmic series distribution is consistent with that obtained in the limit as \( k \to 0 \) for the zero-truncated negative binomial.

It is interesting to note that all of these four distributions yielding straight lines for \( \phi_r \) belong to the class of power series distributions (PSD). This is not, however, a general property of the power series distributions since we have for a PSD with parameter \( \theta \)

\[ \phi_r = \theta^{r+1}/f^{r+1}(\theta) \]

where \( f(\theta) \) is the series function \( \sum_{i=0}^{\infty} a_i \theta^i \). This ratio of power series is not necessarily a straight line.

If we consider \( r \) to be a random variable as for the previous three distributions and assign to it a logarithmic distribution with parameter \( \theta \) we obtain:

\[ E(R'_i) = \mu'(r)/\mu[r] = \mu^* \quad i = 1, 2, 3, \ldots. \]
(3) Neyman type A distribution

The Neyman type A distribution with parameters $\lambda_1$ and $\lambda_2$ arises as a model of spatial patterns through both a clumping model and a heterogeneity model. For the clumping model we take the number of clumps or colonies to have a Poisson distribution with parameter $\lambda_1$, and the size of a colony has a Poisson distribution with parameter $\lambda_2$. For the heterogeneity model the number of individuals in a plot has a Poisson distribution with parameter $\lambda_0$, where $c$ varies over the region as a Poisson random variable with parameter $\lambda_2$.

For this distribution we have the probability generating function

$$g(x) = \exp\{\lambda_1[\exp(\lambda_2(x - 1) - 1)\}.$$

The mean and variance are given by

$$\mu = \lambda_1\lambda_2 \quad \sigma^2 = \lambda_1\lambda_2(1 + \lambda_2).$$

The factorial moments are given by

$$\mu_\nu' = \lambda_2^{\nu} \sum_{i=0}^{\nu} S_{\nu-i}(0)\lambda_1^i$$

where $S$ denotes Stirling numbers of the second kind, so that

$$\phi_r = \mu'_\nu + \mu'_\nu \mu'_\nu = \lambda_2^{\nu+1} \sum_{i=0}^{\nu} S_{\nu-i}(0)\lambda_1^i \mu_\nu'. \sum_{i=0}^{\nu} S_{\nu-i}(0)\lambda_1^i.$$

Note that the vectors $\mathbf{R}$ and $\mathbf{R}'$ do not depend on the parameter $\lambda_2$. For the clumping model this can be interpreted as independence of the quadratic size for it is $\lambda_2$ which varies under this model while $\lambda_1$ remains constant. For the clumping model this means that only the number of colonies is reflected by these two vectors of indices. The vectors $\mathbf{D}$ and $\mathbf{D}'$ are influenced by both $\lambda_1$ and $\lambda_2$.

The first ten elements of the proposed vectors for the Neyman type A distribution with selected values of the parameters are given in Tables 1 and 2. A graph of $\phi$ versus $r$ is given in Figure 2. For a fixed value of the mean we see that the aggregation increases as the parameter $\lambda_1$ decreases. This is expected for the clumping model since small $\lambda_1$ means on the average a small number of large colonies. For the heterogeneity model a decreasing value of $\lambda_1$ also can be interpreted as an increasing aggregation. This is because for a fixed mean value a small value of $\lambda_1$ implies a large value of $\lambda_2$. So in a fixed region we will have the number of individuals following a Poisson distribution with parameter $\nu = \frac{1}{\lambda_2}$. The random variable $\phi$, however, is likely to take small values such as 0, 1, or 2 since $\lambda_1$ is small. If $\lambda_1 = 1$, for example, we have $P(\nu = 0) = .368$, $P(\nu = 1) = .368$, $P(\nu = 2) = .184$, and $P(\nu > 2\lambda_1) = .030$. On the other hand, if $\lambda_1$ is large we have, for a fixed mean, a small value of $\lambda_2$ so that the changes in density from region to region will be less abrupt.
Notice that the change in crowding or attractiveness at the $r$th level, as measured by $R_r$, approaches unity, the value representing indifference. The attractiveness of a quadrate or habitat unit levels off as the number of individuals in the quadrate increases.

(4) Poisson geometric (Polya Aeppli) distribution

The Poisson geometric distribution also arises as a model of spatial patterns through both a clumping model and a heterogeneity model. For the clumping model the Poisson geometric distribution with parameters $\lambda$ and $\theta$ is obtained if the number of colonies or clumps has a Poisson distribution with the parameter $\lambda$ and the colony size is a random variable following a geometric distribution with parameter $1 - \theta$. For the heterogeneity model the Poisson geometric distribution with parameters $\lambda$ and $\theta$ results if the number of individuals in a plot follows a Pascal distribution with parameters $k$ and $1 - \theta$ and $k$ varies over the region according to a Poisson distribution with parameter $\lambda$.

The probability generating function is given by

$$g(z) = \exp\{\lambda[(1 - \theta)z/(1 - \theta z) - 1]\}.$$  

The mean and variance are given by

$$\mu = \lambda/(1 - \theta) \quad \text{and} \quad \sigma^2 = \lambda(1 + \theta)/(1 - \theta)^2 = \mu(1 + \theta)/(1 - \theta).$$

The first six elements of the proposed vector indices are given for selected values of the parameters of this distribution in Tables 3 and 4. A graph of $\varphi_r$ versus $r$ is given in Figure 3. For this distribution we have an increase in aggregation with a decrease in $\lambda$, the mean number of clumps, just as we did for the Neyman type A distribution. In general, the comments made about Tables 1 and 2 apply to Tables 3 and 4 as well.

(5) Log-zero Poisson distribution

The log-zero Poisson distribution with parameters $\lambda$, $p_1$, and $p_2$ is obtained as a clumping model where the number of colonies has a logarithmic series distribution with added zeros with parameters $p_1$ and $p_2$ and the colony size has a Poisson distribution with parameter $\lambda$. This distribution was found to provide a very flexible model of ecological populations by Katti (1965).

The logarithmic series distribution with added zeros is obtained as follows. First let $X$ be zero with probability $\delta$ and with probability $1 - \delta$ let $X$ be an observation from a logarithmic distribution with parameter $\theta$. This gives us a modified logarithmic series distribution having probability generating function

$$g(z) = \delta + (1 - \delta)[\log(1 - \theta z)/\log(1 - \theta)].$$

Now let $p_1 = -(1 - \delta)/\log(1 - \theta)$ and $p_2 = \theta/(1 - \theta)$. This gives us the
log-zero distribution with parameters $p_1$ and $p_2$ having probability generating function
\[ g(z) = 1 - p_1 \log(1 + p_1 - p_2 z). \]

Then the probability generating function of the log-zero-Poisson distribution is given by
\[ g(z) = 1 - p_1 \log(1 + p_1 - p_2 \log(\lambda (z - 1))]. \]

The mean and variance are given by
\[ \mu = \lambda p_1 p_2 \quad \text{and} \quad \sigma^2 = \mu(1 + p_2) + 1 - \mu. \]

The factorial moments are given by
\[ \mu^{(r)} = \lambda^r p_1 \sum_{j=1}^r (j - 1)! \frac{\theta_j p_2}{z_j p_2}. \]

so that
\[ \phi_r = \mu^{(r+1)}/\mu^{(r)} \]
\[ = \lambda \sum_{j=1}^{r+1} (j - 1)! \frac{\theta_j p_2}{z_j p_2} \sum_{j=1}^r (j - 1)! \frac{\theta_j p_2}{z_j p_2}. \]

Note that the $r$th order crowding $\phi_r$ does not depend on the parameter $p_1$ which is a function of $\delta$, the proportion of plots containing no colonies. Also the vector $\mathbf{R}$ depends only on the parameter $p_2$ (except for the first element).

The first ten elements of the proposed vector indices for this distribution with selected values of the parameters are given in Tables 5 and 6. A graph of $\phi_r$ versus $r$ is given in Figure 4. It is interesting to note that the $r$th level crowding appears to be, after some point, a linear function of $r$ with a positive slope as would be obtained for a negative binomial distribution. This perhaps can be explained by the similarity in the two distributions in that the negative binomial distribution arises as a Poisson sum of logarithmic random variables while this distribution arises as a logarithmic (with added zeros) sum of Poisson random variables.

4.6 Role of $\phi_r$ in Pure Birth Processes

Suppose that a population is dispersed over a number of discrete habitat units or in the case of a continuum, suppose that it is partitioned into a grid of cells of equal size. Then various time-dependent stochastic processes are applicable as models of spatial patterns. We will consider only the pure birth process here as it provides us with a motivation for $\phi_r$ as a dynamic measure of spatial patterns.

For the pure birth process we assume that the probability of an individual
entering a particular cell or habitat unit during the time interval \((t, t + h)\)
depends on the number \(x\), of individuals already occupying that cell. This
probability is given by \(\lambda xh + o(h)\). The probability of any other number
of individuals entering the cell in \((t, t + h)\) is given by \(o(h)\).
The number of individuals in a particular cell or habitat unit will depend
on the time of observation so denote by \(P_x(t)\) the probability that \(x\) indi-
viduals are present in the cell at time \(t\). Then under the above assumptions,
\(P_x(t)\) is obtained by solving the system of differential equations:

\[
P_x(t) = -\lambda_0 P_0(t)
\]
\[
P_x(t) = -\lambda_x P_x(t) + \lambda_{x-1} P_{x-1}(t) \quad \text{for } x \geq 1.
\]

The boundary conditions are given by \(P_0(0) = 1\) and \(P_x(0) = 0\) for \(x \geq 1\).
In solving these equations one can first obtain \(P_0(t)\) and then by recursion
the rest of the \(P_x(t)\). Explicit formulae are given by Lundberg (1964) for
computing the \(P_x(t)\).
It is interesting to consider the special case where the \(\lambda_x\) are given as linear
functions \(\lambda_x = \alpha + \beta x\) of the number of individuals already in the cell (see,
for example, Ramakrishnan, 1951; Rogers, 1965). The constants \(\alpha\) and \(\beta\) can
be interpreted as the basic attractive influence of the cell, and the attractive
influence of the individuals, respectively. If \(\beta = 0\), a candidate for entry
into a cell is indifferent to the presence of any individuals already occupying
the cell. This process should lead to a random distribution. If \(\beta > 0\) a cell
becomes more attractive to a candidate for entry as the number of occupant
increases. This process should lead to an aggregated distribution. Finally, if
\(\beta < 0\) a cell becomes less attractive to a candidate for entry as the number of
occupants increases. This should lead to a regular distribution.
The solutions obtained for these three cases are:

(i) \(\beta = 0\)

\[P_x(t) = e^{-\lambda t} (\lambda t)^x / x! \quad x = 0, 1, 2, \ldots\]
a Poisson distribution with parameter \(\lambda t\).

(ii)

\[P_x(t) = \left[\Gamma(k + x) / x! \Gamma(k)\right] p^x (1 - p)^{k-x} \quad x = 0, 1, 2, \ldots\]
a negative binomial distribution with parameters \(k\) and \(p\) where \(k = \alpha / \beta\) and
\(p = e^{-\beta t}\).

(iii)

\[P_x(t) = \binom{n}{x} p^x (1 - p)^{n-x} \quad x = 0, 1, 2, \ldots, n\]
a binomial distribution with parameters \(n\) and \(p\) where \(n = \alpha / \beta\) and \(p =
1 - e^{\beta t}\).
It has been shown by Armitage (1952) and Irwin (1952) that there is a fundamental relationship between the ratio of factorial moments \( \varphi_r \) and the transition probabilities of a pure birth process. They have shown that as the exposure time approaches zero \( \varphi_r \) is asymptotically equivalent to \( \lambda t \). To show this they use an explicit solution obtained by Lundberg (1964)

\[
P_x(t) = \lambda \lambda_1 \cdots \lambda_{x-1} (-1)^x \Delta_x(t),
\]

where

\[
\Delta_x(t) = \sum_{i=0}^{x} \left\{ e^{-\lambda t} / \prod_{j \neq i} (\lambda_j - \lambda_i) \right\}
\]

is the \( x \)th divided difference of \( e^{-\lambda t} \) (see for example Jordan, 1966) with respect to \( \lambda = \lambda_0, \lambda_1, \lambda_2, \ldots, \lambda_r \).

Then as \( t \to 0 \) this expression reduces to

\[
P_x(t) = (\lambda \lambda_1 \cdots \lambda_{x-1} t^x) / x! + o(t^x).
\]

Now writing

\[
\varphi_r = \frac{\sum_{x=r+1}^{\infty} P_x(t) x(x-1) \cdots (x-r)}{\sum_{x=r}^{\infty} P_x(t) x(x-1) \cdots (x-r+1)}
\]

we have (as \( t \to 0 \))

\[
\varphi_r = \frac{\sum_{x=r+1}^{\infty} \left[ \frac{\lambda \lambda_1 \cdots \lambda_{x-1} t^x}{x!} + o(t^x) \right] \frac{x!}{(x-r+1)!}}{\sum_{x=r}^{\infty} \left[ \frac{\lambda \lambda_1 \cdots \lambda_{x-1} t^x}{x!} + o(t^x) \right] \frac{x!}{(x-r)!}}
\]

\[
= \frac{\sum_{x=r}^{\infty} \left[ \frac{\lambda \lambda_1 \cdots \lambda_{x-1} t^{x+1}}{(x+1)!} + o(t^{x+1}) \right] \frac{(x+1)!}{(x-r)!}}{\sum_{x=r}^{\infty} \left[ \frac{\lambda \lambda_1 \cdots \lambda_{x-1} t^x}{x!} + o(t^x) \right] \frac{x!}{(x-r)!}}
\]

\[
= \frac{x!}{(x-r)!} \lambda t + o(t).
\]

This relationship gives us another interpretation of \( \varphi_r \) and provides insight into its meaning as a measure of spatial patterns showing how it is related to the attractiveness of a habitat unit which contains \( r \) individuals.
SUMMARY

A number of indices of spatial pattern which have been proposed in the ecological literature are examined. These indices are based on a sample of counts from randomly placed plots or quadrats and while they were motivated by a variety of different concepts and biological interpretations they all employ, either implicitly or explicitly, a relationship between the variance, \( \sigma^2 \), and the mean, \( \mu \), of the plot counts. From a theoretical viewpoint, each of the indices is essentially expressing either \( \omega = \sigma^2/\mu \) or \( \gamma = (\sigma^2 - \mu)/\mu^2 \).

A new approach to measuring or describing spatial patterns based on vectors of indices is proposed in this paper. These vectors are based on an index of crowding or aggregative tendency measured by the ratio of successive factorial moments. This index is interpreted by writing

\[
\phi_r = \mu'(r+1)/\mu'(r) = \sum \left[ (r-r) \left( \begin{array}{c} x \ \n \end{array} \right) p_x / \sum \left( \begin{array}{c} x \ \n \end{array} \right) p_x \right]
\]

as the mean number per randomly selected group of size \( r \) of other individuals in the same quadrat or habitat unit. The manner in which the crowding changes with the level \( r \), measured as either the ratio or difference of successive values of \( \phi_r \), provides a description of spatial pattern. It is also meaningful to consider as a description of spatial pattern the difference between the crowding at each level for the population being studied and the crowding which the population would have if it were randomly distributed. Since for a random distribution we have \( \phi_r = \phi_0 \) for all \( r \), where \( \phi_0 \) is the mean number per plot, it is proposed that the difference between \( \phi_r \) and \( \phi_0 \) as measured by either a ratio or a difference, be used to describe spatial patterns. The proposed vectors provide both extensions and new interpretations for the indices \( \omega = \sigma^2/\mu \) and \( \gamma = (\sigma^2 - \mu)/\mu^2 \). These vectors are examined for various probability distributions used as models of spatial patterns.

A relationship between the measure of crowding \( \phi_r \) and the transition probabilities of a pure birth process provides an interpretation of \( \phi_r \) in terms of the attractiveness of a habitat unit which contains \( r \) individuals and provides insight into the use of the proposed indices based on \( \phi_r \) for measuring or describing spatial patterns.

RESUME

Dans cette étude sont examinés quelques indices de distribution spatiale proposés en littérature écologique. Ces indices sont basés sur un échantillon de comptes faits sur des morceaux de terrain ou bien sur des individus choisis à l’hasard.

Bien que motivés par nombre de actions différentes et par plusieurs interprétations biologiques, tous ces indices exploitent plus ou moins implicitement une relation entre la variance, \( \sigma^2 \), et la moyenne, \( \mu \), des comptes faits sur des \( \omega = \sigma^2/\mu \) soit \( \gamma = (\sigma^2 - \mu)/\mu^2 \).

L'auteur propose une nouvelle technique à mesurer ou décrire les distributions spatiales, basée sur des vecteurs d'indices. Ces vecteurs sont dérivés d'un in-facteurielles successives. La relation

\[
\phi_r = \mu'(r+1)/\mu'(r) = \sum \left[ (r-r) \left( \begin{array}{c} x \ \n \end{array} \right) p_x / \sum \left( \begin{array}{c} x \ \n \end{array} \right) p_x \right]
\]

montre l'interprétation de cet indice comme la moyenne calculée par groupes de \( r \) individus sur le même terrain. Une description de la distribution spatiale est fournie par la manière dont l'agglutination change avec le niveau \( r \), mesuré comme soit la proportion soit la différence des valeurs successives de \( \phi_r \). Il est également intéressant de décrire la distribution spatiale en considérant la différence entre l'agglutination à chaque niveau pour la population étudiée et l'agglutination de la population distribuée à l'hasard. Puisque dans cette distribution on a pour chaque \( r \) \( \phi_r = \phi_0 \) étant le nombre moyen par morceau de
terrain, l'auteur propose de décrire les distributions spatiales par l'écart entre $\varphi$ et $\varphi_0$ mesure par leur différence ou leur proportion. Les vecteurs proposés fournissent des extensions et des interprétations nouvelles des indices $\omega = \sigma^2/\mu$ et $\gamma = (\sigma^2 - \mu)/\mu^2$. Ces vecteurs sont examinés pour plusieurs distributions de probabilité employées comme modèles de distributions spatiales.

Une relation entre la mesure de l'agglutination $\varphi$, et les probabilités de transition d'un processus de naissance pure fournit une interprétation de $\varphi$, en termes de l'attractivité d'un domicile habité par $r$ individus et facilite la compréhension de l'usage des indices proposés et basés sur $\varphi$, pour mesurer ou décrire des distributions spatiales.

REFERENCES

2. Bateman, G. I. [1950]. The power of the $\chi^2$ index of dispersion test when Neyman's contagious distribution is the alternative hypothesis. *Biometrika* 37, 59-63.
Figure 1. $q_r$ for Poisson, Binomial, and Negative Binomial Distributions
Figure 2. $\Phi_2$ for Neyman Type A Distributions
Figure 3. $\varphi_r$ for Poisson-Geometric Distributions
Figure 4. \( q_z \) for Log-Zero-Poisson Distributions
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| 1 | 24.0000 | 1.1389 | 1.2000 | 3.3333 | 4.0000 |
| 2 | 27.3333 | 1.1101 | 1.3667 | 3.0081 | 7.3333 |
| 3 | 30.3415 | 1.0920 | 1.5171 | 2.7904 | 10.3415 |
| 4 | 33.2318 | 1.0794 | 1.6566 | 2.6308 | 13.2318 |
| 5 | 35.7624 | 1.0701 | 1.7881 | 2.5062 | 15.7624 |
| 6 | 38.2686 | 1.0629 | 1.9134 | 2.4054 | 18.2686 |
| 7 | 40.6740 | 1.0571 | 2.0337 | 2.3213 | 20.6740 |
| 8 | 42.9953 | 1.0523 | 2.1598 | 2.2498 | 22.9953 |
| 9 | 45.2451 | 1.0484 | 2.2623 | 2.1879 | 25.2451 |
| 10 | 47.4330 | 1.0451 | 2.3716 | 2.1260 | 27.4330 |

| \( \lambda_1 \) = 1 | \( \lambda_2 \) = 20 |
|---|---|---|---|---|---|
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| 2 | 50.0000 | 1.7000 | 2.5000 | 10.0000 | 30.0000 |
| 3 | 60.0000 | 1.1556 | 3.0000 | 9.3333 | 40.0000 |
| 4 | 69.3333 | 1.1261 | 3.4667 | 8.7436 | 49.3333 |
| 5 | 78.0769 | 1.1067 | 3.9038 | 8.1270 | 58.0769 |
| 6 | 86.4039 | 1.0927 | 4.3202 | 7.5088 | 66.4039 |
| 7 | 94.4128 | 1.0821 | 4.7206 | 7.7466 | 74.4128 |
| 8 | 102.7594 | 1.0737 | 5.1080 | 7.9252 | 82.7594 |
| 9 | 109.8846 | 1.0669 | 5.4842 | 8.1355 | 89.8846 |
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TABLE 3
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