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ABSTRACT

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The spatial heterogeneity of plants influences the ecology of plant communities. This paper examines the spatial distribution pattern of plants in a simulated grassland colony. A circular quadrat sampling method was used to construct the colony. Edge problems arose because circular quadrats were placed randomly in a square area. We developed a simple mathematical correction to eliminate the shortcomings of the edge effect of the circular colony. Spatial heterogeneity of binary characteristics such as occurrence or non-occurrence of plants was studied. We addressed the heterogeneity of within and between sampling units. Binomial distribution (BD) and beta-binomial distribution (BBD) were used to represent the spatial pattern within and between sampling units. The BBD described the frequency distribution of the occurrence of plants aggregated between sampling units more accurately than the BD. It was found that the heterogeneity within a colony is of an under-dispersion type. Therefore, the required number of sampling units to achieve a level of accuracy of 20% variation was determined.

Key words: colony, beta-binomial distribution, binomial distribution, heterogeneity

INTRODUCTION

Spatial pattern in a plant community population is an important aspect of the community ecology. Energy inputs, disturbances, and species interactions are the main causes of the formation of such spatial patterns, and these patterns often influence the diversity of the plant communities. The size of individual plant species, spatial heterogeneity in biomass, and species diversity can thus be measured if the distribution of the spatial patterns is known. In grassland, plants or species form a continuum with different patterns of heterogeneity. In general, heterogeneity in the grassland continuum is classified as patterns that are regular, random, or aggregated. In a regular pattern, plants are more or less equally spaced, and a completely regular pattern has no heterogeneity. However, in a random pattern, plant spacing in the continuum are not related to one another, and individual plants exist at any place with the same probability. In an aggregated pattern, plants tend to form clusters in particular places. As spatial heterogeneity of a species increases, the spatial patterns randomly change from regular to aggregate.

The number of individual plants per unit area can be estimated assuming the negative binomial distribution (Fisher 1941) or the Poisson distribution (Greig-Smith 1983) for the spatial pattern of individual plants. The number of plant occurrences is also estimated assuming binary counts (presence or absence) using beta-binomial distribution (BBD; Skellam 1948) and binomial distribution (BD; Greig-Smith, 1983). Similarly, the gamma distribution (May 1973; Shiyomi *et al.* 1984) and the beta distribution (Chen *et al.* 2006) are assumed to model the biomass and species (plant) coverage, respectively. Recent studies have demonstrated that BBD is more appropriate for estimating the number of plant occurrences since the data on plant occurrence are binary (Chen *et al.* 2005). The BBD is a mixture of binomial distribution and beta distribution that accounts for the over-dispersion; the two parameters of the distribution are the expected probability of a plant occurrence $(\hat{p})$ and the aggregation index (θ). The BBD model has been used successfully in the study of, for example, chromosomes, market research, toxicology, plant disease incidence, and teratology (Skellam 1948; Haseman and Kupper, 1979; Williams 1975; Paul 1982).

In this paper, we aim to implement the BBD model to determine the distribution of the spatial pattern of plants in grassland. The main objective is to quantify the spatial pattern of plant species in a grassland colony. Using a computer simulation, fictitious vegetation (considered to be a colony) was sampled using a circular quadrate method to test the adequacy of the BBD model in such environmental situations. A simple mathematical correction for circular edge adjustment is also suggested to overcome the shortcomings of the edge effect of the colony. For simulated data on a specified species A, both BD and BBD were used to determine heterogeneity among colonies. The heterogeneity within each colony was also characterized.

MATERIALS AND METHODS

Sampling

A cluster sampling method can directly measure heterogeneity or variability of any binary variable (e.g., pest or plant disease or occurrence of plants) compared to other methods such as simple random samples, systematic samples, and stratified samples. In cluster sampling, each sampling unit contains *n* individuals, and all individuals in a sampling unit are observed. Using a computer simulation, hypothetical grassland was sampled with a circular quadrat. For this purpose, a fictitious square area was created in which the sampling units (circular quadrats) were randomly placed. These sampling quadrats were considered to be colonies (Fig. 1).

Let X_i be the number of observed plants of a species A per sampling unit and N be the number of sampling units ($i = 1,2,......,N$). A large population (e.g.- a field) is assumed in the sampling process, so that most individuals were not considered as sampling units, i.e.- N is small relative to the total population size. As a result no finite population correction is needed in the formulas presented in this paper. Let each sampling unit contain n_i individuals, i.e. - the number of counted plants per sampling unit X_i varies from 0 to n_i.
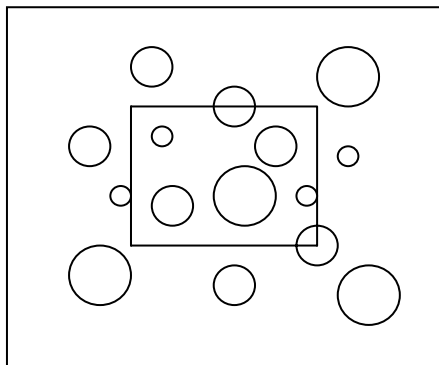

Fig. 1. Square boundary (inside square) intersecting the colonies of different sizes

Edge Correction

It is considered that the colonies have almost circular boundaries. The probability of selecting a plant from a colony of size R is $P = R/A$, where A is the area of the considered square area. Using a similar concept, it could be found that the probability of a random line intersecting the colony is proportional to the colony's diameter. Assuming that a randomly drawn line intercepts the ith colony in the represented area, the estimated frequency of plants in the ith colony is as follows:

$$f_i^* \propto d_i f_i \qquad (1)$$

where f_i^* is the observed frequency in the ith colony, d_i is the diameter of the ith colony, and f_i is the true or corrected frequency in the ith colony.

After introducing a normalizing factor, the normalized unbiased estimate of frequency of the ith colony can be found as (from equation 1):

$$f_i = \frac{\dfrac{f_i^*}{d_i}}{\displaystyle\sum_{i=1}^{N} \dfrac{f_i^*}{d_i}} \qquad (2)$$

where the denominator of the equation is the normalization factor that ensures $\displaystyle\sum_{i=1}^{N} f_i = 1$. Now the above equation (2) can be written as:

$$f_i = \frac{w_i f_i^*}{\displaystyle\sum_{i=1}^{N} w_i f_i^*} \qquad (3)$$

where:

$w_i = \dfrac{1}{d_i}$ is the correction term.

Let us consider that a square is randomly placed in a represented area, intercepting the colony. The correction term can be defined as (Kerscher 1999):

$$w_i = \frac{A}{area(A \cap R_i)}$$

where A is the area of the square and R_i is the size of ith colony. The denominator is the "effectively" sampled area.

Binomial Distribution (BD)

Let us assume that the *i*th colony contains n_i plants of species A. If the number of plants of species A in the *i*th colony has a common probability of occurrence and the plants are independent, then X_i follows a BD. If p_i is the estimated probability of occurrence of the plant of species A in the *i*th colony then the probability mass function (pf) of X_i will be given by:

$$\Pr\left(X_i = x_i\right) = \binom{n_i}{x_i} p_i^{x_i} \left(1 - p_i\right)^{n_i - x_i};$$

$$\forall \, i = 1, 2, \ldots, N, \, x = 0, 1, \ldots, n$$

By the binomial rule, the mean and the variance of X_i are given, respectively, by $n_i p_i$ and $n_i p_i\left(1 - p_i\right)$. Consequently, the proportion of the occurred plants of species A per sampling unit will have a p_i and variance $p_i\left(1 - p_i\right)/n_i$.

Beta-Binomial Distribution (BBD)

The BBD is used for accounting for any possible over-dispersion in BD. It plays a role in binomial regression similar to that played by the negative binomial distribution in Poisson regression. Both are mixture distributions that accommodate variances if they exceed the usual variance functions for the binomial and Poisson distributions. To clarify the issue, the BD theoretically requires the variance to be smaller than the mean of the distribution, but this condition does not prevail under all practical situations. The BBD can be used to model such situations in which, under binomial circumstances, the variance could exceed the mean of the distribution.

Under the BBD, the probability p_i varies across the observational units for which the variables X_i s are observed and hence p_i is taken to be a random variable and is assumed to follow a beta distribution with the pf:

$$f\left(p_i\right) = \frac{1}{Be}\left(\alpha_i, \beta_i\right) p_i^{\alpha_i - 1} \left(1 - p_i\right)^{\beta_i - 1}$$

$$\forall \, 0 \leq p_i \leq 1$$

where α and β are the parameters of the beta distribution and *Be* is the beta function.

Since p_i is a random variable in BBD, it can take values between 0 and 1, and for its flexibility, the beta distribution is a promising way for characterizing this parameter's heterogeneity. Our primary interest is on the effects of the variation of this parameter on the observed X_i. The pf of BBD is as follows:

$$\Pr\left(X_i = x_i\right) = \binom{n_i}{x_i} \frac{Be\left(\alpha_i + x_i, \beta_i - x_i + n_i\right)}{Be\left(\alpha_i + \beta_i\right)}$$

where α_i and β_i are positive parameters.

The mean and variance of BBD are defined (Ennis and Bi, 1998) as $\mu = \alpha_i n_i \left(\alpha_i + \beta_i\right)^{-1}$ and $v = \alpha_i \beta_i n_i \left(\alpha_i + \beta_i + n_i\right)\left(\alpha_i + \beta_i\right)^{-2}\left(\alpha_i + \beta_i + 1\right)^{-1}$, respectively. It is evident that μ and v are both functions of α_i and β_i, and simultaneous solution of the equations will produce the values of α_i and β_i.

For BBD, $\theta_i = 1/\left(\alpha_i + \beta_i\right)$ is the index of heterogeneity or aggregation. If $\theta_i = 0$, the distribution of occurrence is binomial, and over-dispersion increases with increasing values of θ_i. The maximum likelihood estimates of p_i and θ_i can be obtained using an iterative Newton-Raphson procedure (Smith 1983).

We used Tarone's Z test, the most powerful test to test the null hypothesis $\theta = 0$ (Tarone 1979). Tarone's Z statistics can be defined as:

$$Z = \frac{S - \sum_{i=1}^{N} n_i}{\sqrt{2 \sum_{i=1}^{N} n_i\left(n_i - 1\right)}}$$

with

$$S = \frac{\sum_{i=1}^{N}(x_i - n_i p)^2}{p(p-1)} \quad \text{and} \quad p = \frac{\sum_{i=1}^{N} x_i}{\sum_{i=1}^{N} n_i}$$

where N is the total number of colonies, p is the overall number of occurred plants, x_i is the number of occurred plants of the species A, and n_i is total plants in the ith colony, respectively. The statistics were scaled to have a standard normal distribution.

Because of the non-constant number of plants per quadrat, it is not possible to calculate expected frequencies. Therefore, χ^2 goodness-of-fit (GOF) could not be used in calculating BBD. In this paper, we used another GOF test for BBD, proposed by Neerchal and Morel (1998). In this process, these authors first divided the unit interval into r mutually exclusive intervals A_s ($s = 1, 2,\ldots, r$). Now the GOF test statistics are as follows:

$$\chi^2 = \sum_{s=1}^{r} \frac{(O_s - E_s)^2}{E_s}$$

where:

$$O_s = \sum_{i=1}^{N} I\left(\frac{x_i}{n_i} \in A_s\right)$$

and

$$E_s = \sum_{i=1}^{N} \sum_{j=0}^{n_i} \Pr(X_i = x) I\left(\frac{x_i}{n_i} \in A_s\right)$$

where I (.) is an indicator function.

The above χ^2 is the usual Pearson's χ^2 statistics. This statistical test is used for testing the adequacy of the model.

Internal Heterogeneity

Let X_{ij} be the variable of interest of the jth species in the ith colony. p_{ij} is the probability of selecting of the jth species in the ith colony.

Again let us consider that X_i is the total of C_i clusters of the component binary variable. Each cluster has its own response probability p_{ij}. Now we assume that each of the C_i clusters have m equal number of plants and $m = n_i / C_i$. The mean of p_{ij} for an observed x_i is denoted as $\bar{p}_i$. $\bar{p}_i$ is the variable response (occurred) probability having mean $\tilde{p}$ and variance $\phi_i \tilde{p}_i (1 - \tilde{p}_i)$, where ϕ_i is the correlation coefficient of any two components in the ith colony.

The conditional expectation and variance of X_i can be found as follows:

$$E\left(X_i | p_{ij}\right) = \sum_{j=1}^{C_i} m p_{ij} = n_i \bar{p}_i$$

and

$$V\left(X_i | p_{ij}\right) = \sum_{j=1}^{C_i} m p_{ij} \left(1 - p_{ij}\right)$$

$$= \sum_{j=1}^{C_i} m p_{ij} - \sum_{j=1}^{C_i} m p_{ij}^2$$

$$= n_i \bar{p}_i \left(1 - \bar{p}_i\right) - m(C_i - 1)\sum_{j=1}^{C_i} \frac{(p_{ij} - \bar{p}_i)^2}{C_i - 1}$$

When there is only one cluster, the conditional variance is equal to the binomial variance. The above conditional variance is less by the amount of the second term from the conditional variance when there is only one cluster.

The mean is

$$E(X_i) = E\big(E(X_i|p_{ij})\big) = n_i \tilde{p}$$

We know that,

$$V(X_i) = E\big(V(X_{ij}|p_{ij})\big) + V\big(E(X_i|p_{ij})\big) \qquad (4)$$

Now, $E\big(V(X_{ij}|p_{ij})\big)$ of equation (4) can be calculated as:-

$$E\big(V(X_i|p_{ij})\big) =$$

$$E\left[n_i \bar{p}_i(1-\bar{p}_i) - m(C_i-1)\sum_{j=1}^{C_i} \frac{(p_{ij}-\bar{p}_i)^2}{C_i-1} \right]$$

$$= n_i \tilde{p}_i(1-\tilde{p}_i)(1-\phi_i) \qquad (5)$$

The $V\big(E(X_i|p_{ij})\big)$ of equation (4) can be calculated as:-

$$V\big(E(X_i|p_{ij})\big) = V(mC_i\bar{p}_i)$$

$$= mn_i\phi_i\tilde{p}_i(1-\tilde{p}_i) \qquad (6)$$

Using the values from equations (5) and (6) in equation (4) we found that,

$$V(X_i) = n_i\tilde{p}_i(1-\tilde{p}_i)(1-\phi_i) + mn_i\phi_i\tilde{p}_i(1-\tilde{p}_i)$$

The simplified value is

$$V(X_i) = n_i\tilde{p}_i(1-\tilde{p}_i)\big(1+(m-1)\phi_i\big)$$

Now, if $C_i = n_i$, the effective cluster size $m = 1$, then X_i follows BD.

Again assume that each of the X_{ij} have different p_{ij}.

The conditional expectation and variance of X_i can be found as follows (Feller 1968):

$$E(X_i|p_{ij}) = \sum_{j=1}^{n_i} p_{ij} = n_i\bar{p}_i$$

and

$$V(X_i|p_{ij}) = \sum_{j=1}^{n_i} p_{ij}(1-p_{ij})$$

$$= n_i\bar{p}_i(1-\bar{p}_i) - \sum_{j=1}^{n_i}(p_{ij}-\bar{p}_i)^2$$

$$= n_i\bar{p}_i(1-\bar{p}_i)(1-\gamma_i) \qquad (7)$$

where

$$\gamma_i = \frac{\sum_{j=1}^{n_i}(p_{ij}-\bar{p}_i)^2}{n_i\bar{p}_i(1-\bar{p}_i)} .$$

Here γ_i is the relative measure of the internal parameter heterogeneity, which can take the values from 0 to 1. If any internal heterogeneity is present, i.e., $\gamma_i > 0$, $V(X_i|p_{ij})$ will be less than the binomial variance.

Determination of Sampling Units

Using a standard error of $\hat{p}$ (estimated occurrence) and a level of heterogeneity identical to that used in the Karandinos study (1976), we calculated N for sampling other than cluster sampling of insect density or binary data. Here we develop the methods for determining N.

Let $p_i = X_i/n$, for $i = 1, 2,..., N$, is the proportion of occurred plants in the i th colony.

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Now, $\hat{p}$ can be defined as:

$$\hat{p} = \frac{\sum_{i=1}^{N} p_i}{nN}.$$

The estimated variance of $\hat{p}$ is as follows (Bi *et al.* 2000)

$$v(\hat{p}) = \frac{\hat{p}(1-\hat{p})}{nN}\{1 + \rho(n-1)\}$$

where

$\rho = \dfrac{\theta}{1+\theta}$ is the intra-cluster correlation.

The coefficient of variation (C_V) is a useful statistic for characterizing precision in relative terms. Here C_V is defined as

$$C_V = \frac{se(\hat{p})}{\hat{p}} \qquad\qquad (8)$$

where

$$se(\hat{p}) = \sqrt{\left[\frac{\hat{p}(1-\hat{p})}{nN}\right]\left[1 + \rho(n-1)\right]}.$$

Now using equation (8) we found

$$N = \frac{\{1-\hat{p}\}\{1+\rho(n-1)\}}{n\hat{p}C_V^{\,2}}. \qquad\qquad (9)$$

For the BD, $\rho = 0$ and equation (9) reduces to $(1-\hat{p})/n\hat{p}C_V^2$. Again if $n = 1$, i.e., for sampling other than cluster sampling, the equation further reduces to the well-established formula for the binomial distribution, $(1-\hat{p})/\hat{p}C_V^2$.

The value of ρ may vary with cluster size (n). Hence, it is preferable to retain the same n in the preliminary stage. For uncontrolled constant cluster size, it is better to use the mean cluster size, which is why we used mean cluster size in the present paper.

RESULTS AND DISCUSSION

Edge Correction

To demonstrate the outcomes with the suggested corrections, we simulated a hypothetical population of grasses. In the simulation, the plants were scattered over the grassland. For sampling, an area of 50 by 50 units was selected. This area was sampled randomly with circular quadrats (considered to be a colony) based on a diameter of 0.05 units. The simulated results show that the observed distributions differed significantly ($p \leq 0.05$, Kolmogorove-Simrnov test) from the true frequency distribution. By applying the correction term (equation 3), we found that the corrected distributions retrieved the true frequencies for species A (Fig. 2). This result demonstrates that the correction is significant and it changes the interpretation of the results dramatically.
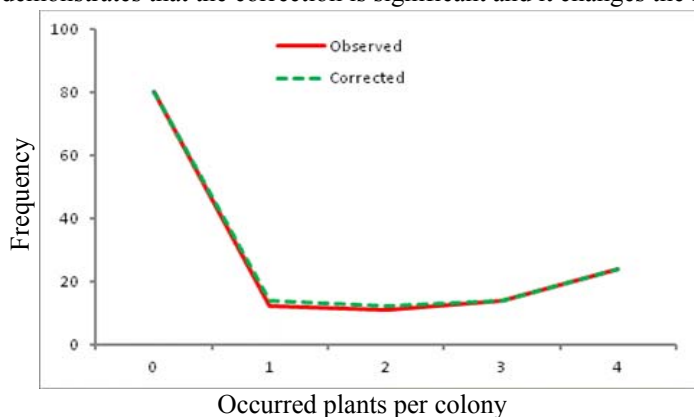

Fig. 2. After edge correction, corrected frequency distributions are found in the simulation for the observed data The graph represents data from species A.

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Identifying the Distribution

The corrected proportion and the predicted probabilities of a small group of occurred plants are shown in Table 1 for the BD and the BBD, respectively. The data in this table indicates that the BBD fits better than the BD.

Table 1. Corrected proportions and estimated probabilities

Frequency	Corrected	BD	BBD
0	0.803	0.993	0.998
1	0.019	0.694	0.011
2	0.009	0.003	0.032
3	0.009	0.002	0.372
4	0.158	0.000	0.490

BD =binomial distribution, BBD =beta-binomial distribution

The maximum likelihood estimator (MLE) of p and θ are $\hat{p}$ = 0.1, 0.2, and 0.4 and $\hat{\theta}$ = 0.20, 0.11, and 0.14 for n = 4, 6, and 8, respectively (Table 2). Here the MLE of θ of the BBD is larger than zero, indicating that the occurred plants showed over-dispersion. Therefore, it could be concluded that the distribution of the data departed from the BD.

The Tarone's Z scores together with the results of fitting BBDs are presented in Table 2. Tarone's Z test confirms the necessity of using the BBD, i.e., the plants demonstrated over-dispersion. The existence of over-dispersion in the data causes the BD to be unreliable. The GOF indicated that the BBD improved the description of the frequency distribution of occurred plants (Table 2).

Table 2. Tarone's Z statistics and results of fitting the BBD for assessing aggregation of plants

n	p-value of Z	MLE of θ	MLE of p	p-value of GOF of BBD
4	< 0.05	20.5	0.1	=0.22
6	< 0.05	11.2	0.2	=0.24
8	< 0.05	14.4	0.4	=0.27

n = mean cluster size; MLE = maximum likelihood estimator; BD = binomial distribution, BBD = beta-binomial distribution, GOF = goodness of fit

Internal Heterogeneity

As shown in Table 3, the conditional variance (using equation 7) is smaller than the binomial variance for different numbers of observations, e.g., when n = 3, binomial variance is 0.712 and conditional variance is 0.472. Therefore, we can observe that the heterogeneity at the individual level is of the under-dispersion type.

Table 3. Binomial variance with conditional variance for different numbers of observations

Number of observations	Binomial variance	Conditional variance
2	0.375	0.25
3	0.712	0.472
4	0.998	0.659
5	1.241	0.819
6	1.449	0.958
7	1.632	1.081

Sampling Units Determination

To achieve $C_V = 0.2$, one needs more sampling units for over-dispersed data than for randomly distributed (binomial) data. For instance, at $\hat{p}$ = 0.1, the required N is ~10 (n = 4) for the binomial case and ~12 for the over-dispersed case (Table 4).

Table 4. Sampling unit with sample size

n	N	
	BD	BBD
4	10	12
6	17	25
8	29	61

n = mean cluster size; N = number of colonies; BD = binomial distribution, BBD = beta-binomial distribution

The choice of which combination should be used depends on the relative costs of n and N.

CONCLUSION

This study focused on spatial distribution problems of plants in colonies having a circular boundary. The circular quadrat method was used for sample collection, and problems of the edge with respect to frequency distribution evaluations were addressed. Ignoring colonies intersected by the edge of the square leads to a underestimation of heterogeneity. In contrast, considering all the observations of the intersected colonies leads to overestimation. This means that the edge effect on sampling biases frequency distribution estimates. The edge effect may result in erroneous nature reserve management policies, and the suggested correction of the edge effect can eliminate these types of sampling errors (Figure 2).

Our results indicated that the plants were distributed in an aggregative pattern between the simulated colonies and thus the BD cannot adequately describe the observed data (Table 1). The BBD captured the observed heterogeneity (over-dispersion) in the plant occurrence as indicated by Tarone's Z test for the θ (Table 2). All the values of MLE of θ are greater than zero (Table 2). The results for BBD were in high agreement with the GOF test (Table 2). Our data demonstrated that the plant occurrence within a colony showed underestimated heterogeneity (Table 3).

It is necessary to determine the number of sampling units that would be equally applicable over the whole range of the mean plant occurrence. The BBD (Table 4) was shown to require more sampling units than the BD.

Finally, it could be concluded that the distribution of plant occurrence between simulated colonies was clearly aggregated, indicating an over-dispersed, non-random variability among groups of plants. In contrast, within groups of plants, plant occurrence showed an under-dispersed heterogeneity.

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