Near Neighbor Analysis of the Silurian (Niagaran) Bioherms Near Lagro, Indiana

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Abstract

Spatial relationships among seventeen Silurian (Niagaran) bioherms were analyzed using the near-neighbor statistic. The ratio R between the observed mean distance to the expected mean distance was computed and compared to a random distribution having the same population density. A two-tailed test of significance revealed that the Lagro bioherms exhibit a pattern which is more uniform than random. The majority of the bioherms appear to be distributed in such a way as to maximize their potential for success.

Introduction

Students of Silurian bioherms of northeastern Indiana are continually faced with problems of insufficient surface exposure, limited sub-surface data, and a qualitative view of the Niagaran paleosynecology. Although regional and local paleoenvironmental relationships have been noted frequently, there still exists a need to examine the bioherms with a view toward deriving a quantitative statement which describes their areal variation. Several techniques widely used in other disciplines may contribute to a better understanding of the nature of these mound-like features.

One of these techniques—near-neighbor analysis—was used in this study in order to 1) focus attention on the applicability of the nearest-neighbor statistic to paleobiogeographical investigations, 2) add a new dimension—that of spatial relationships—to the overall study of bioherms; and 3) give workers an added perspective on problems of biohermal paleosynecology. This paper like its predecessor (11) presents the quantitative results of some empirical characteristics of the distribution of bioherms in the Wabash Valley near Lagro, Indiana.

Method

Distance to nearest neighbor as an estimate of the spatial relationships in populations and among communities has been widely used by ecologists, geographers, and biometricians. The spacing of individuals in a community and the spacing of communities themselves is of profound ecological significance. According to Clark and Evans (1), "The pattern of distribution of a population of plants or of animals is a fundamental characteristic of that population, but it is a feature that is extremely difficult to describe in precise and meaningful terms."

In the past, the pattern of distribution of communities or of individuals making up a population has been deduced from the number of individuals per area or the number of communities in a region. Generally no analysis was made of the linear distances separating data points within the area. King (4) noted that these attempts are open to criticism for their generality and for the fact that they are frequently insensitive to important variations in spatial pattern. Moreover, qualitative terms such as "sparse", "dispersed" or "dense" that have been applied to spatial distribution fosters ambiguity. King suggests that actual measurements be used in the analysis of spatial variation. Nevertheless, it is difficult to decide which of the actually measurable differences are due to genuine ecologic forces and which are due to genetic origin or chance geographic factors (8). Many biosociological concepts of earlier workers were founded upon the assumption that real populations are distributed randomly in nature. Today, this idea is tenable only for testing hypotheses against a presumed random distribution. A random distribution is defined as a set of data points in an area for which any point may have the same chance of occurring anywhere in the area as any other point without mutual interference. The assumption of a statistically random distribution is founded upon contemporary probability theory (10).

As suggested by the name, near-neighbor analysis is the linear measurement of the distance separating an object and its nearest neighbor in space, regardless of direction (Table 1). Distances between all subjects in the population may be measured (as in the present

TABLE 1. *Symbols and definitions employed in a measure of spacing based on the mean distance between nearest neighbors (1).*

N	the number of measurements of distance taken in the observed population or sample. When a single sector is employed, N is also equal to the number of individuals used as centers of measurement.
r	the distance in any specified units from a given individual to its nearest neighbor.
ρ	the density of the observed distribution expressed as the number of individuals per unit of area. (The unit of measurement used in the calculation of ρ must be the same as that used in measuring r.)
Σr	the summation of the measurements of distance to nearest neighbor
$\bar{r}_e = \frac{\Sigma r}{N}$	the mean of the series of distances to nearest neighbor.
$\bar{r}_e = \frac{1}{2\sqrt{\rho}}$	the mean distance to nearest neighbor expected in an infinitely large random distribution of density ρ.
$R = \frac{\bar{r}_a}{\bar{r}_e}$	the measure of the degree to which the observed distribution departs from random expectation with respect to the distance to nearest neighbor.
$c = \frac{\bar{r}_a - \bar{r}_e}{\sigma_{\bar{r}_e}}$	the standard variate of the normal curve.
$\sigma_{\bar{r}_e} = \frac{0.26136}{\sqrt{N\rho}}$	the standard error of the mean distance to nearest neighbor in a randomly distributed population of density ρ.

investigation) or a random sample may be chosen. The actual or observed mean distance ($\bar{r}_a$) is computed together with mean distance which would be expected ($\bar{r}_e$) in an infinitely large random distribution having the same density (ρ). The ratio (R) of the observed mean distance to the expected mean distance is termed the near-neighbor statistic and is a measure of the degree to which the observed distribution approaches or departs from random expectation.

The value R has a limited range. In a totally random distribution $R = 1.0$. If the points are agglomerated and therefore all occupy the same locus, the ratio would obviously be equal to 0.0. In a distribution in which spacing of data points is maximized, $R = 2.1491$. Such a perfectly uniform distribution will exhibit data points distributed in an hexagonal pattern about the center of observation, as shown in Figure 1. Thus, the statistic R provides an expression of the two-dimensional spatial pattern of points within a given area. One might expect that an agglomerated pattern of distribution ($R < 1.0$) may indicate particularly favorable locations and local environments for biotic success. A more uniform distribution ($R = 2.15$) may occur where there is a tendency for competition and where the habitat displays considerable heterogeneity (2.7).

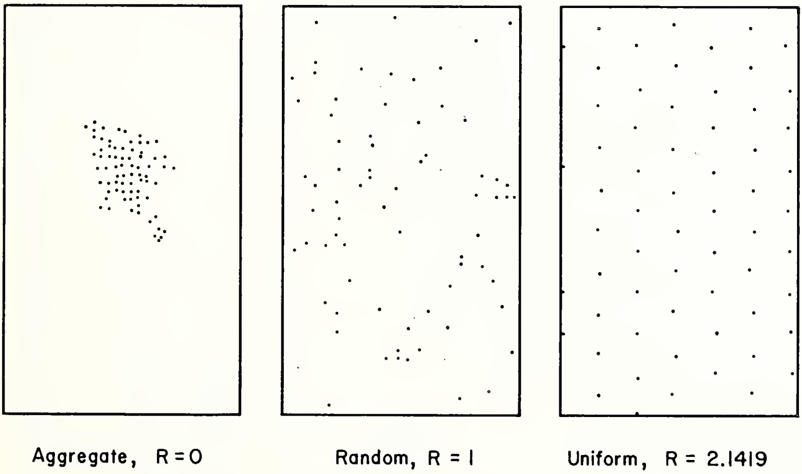

FIGURE 1. *Theoretical patterns of distribution (4).*

Several tests of significance of the departure of the ratio R from a random distribution may be utilized. The method used here was to compute the standard variate of the normal curve (c) using the standard error of the mean. A comparison of the c-value obtained with a table of the normal distribution may establish the significance of the departure under different levels of probability. C-values of 1.96 and 2.58 are significant at the 0.05 and 0.01 levels respectively.

Application

The Wabash River Valley near Lagro, Indiana, with its excellent klintar, was selected as the study area. This area (22.06 km^2) is depicted entirely on the Lagro 7.5′ topographic quadrangle. The right and left margins of the map serve as the east and west boundaries of the study area. The lower slope break between flood plain and right- and left-hand bluffs marks the southern and northern edges (Fig. 2.). Locations of 17 identifiable bioherms were plotted on the map and the

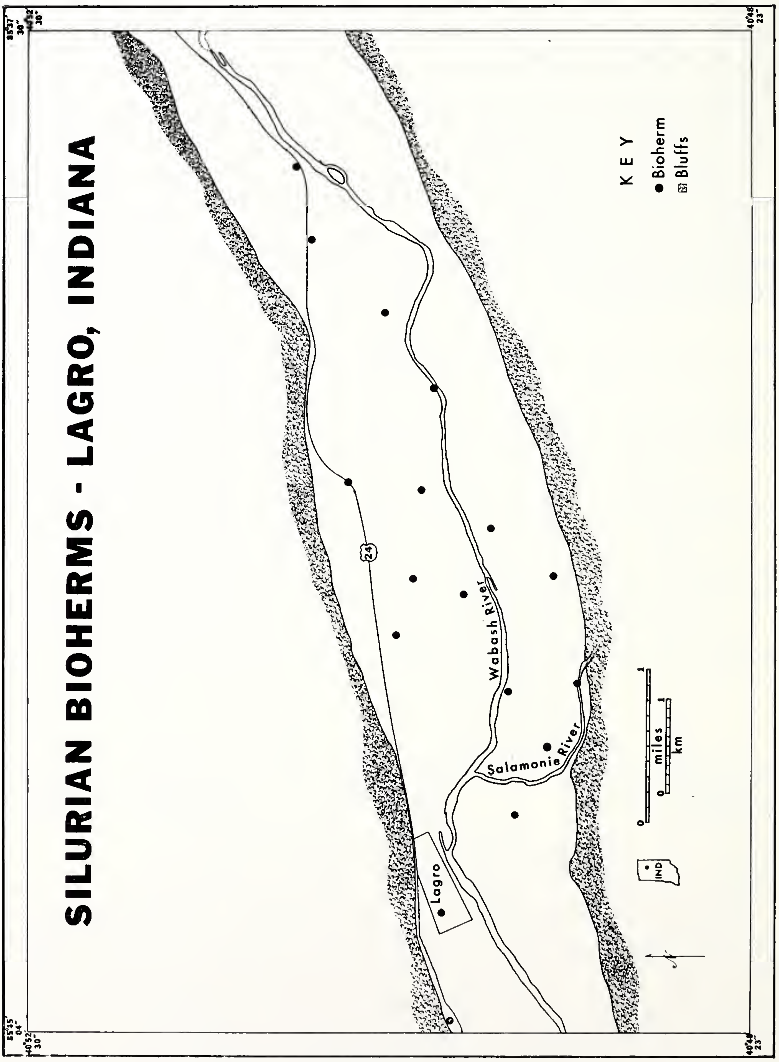

FIGURE 2. *Silurian bioherms—Lagro, Indiana.*

linear distance between the center of each bioherm to its nearest neighbor was measured. Statistics computed are listed in Table 2.

The R-value of 1.46 is significantly greater than 0.0 at the one percent level of significance since $c = 3.69$. This indicates that bioherms in the Lagro area exhibit a tendency to be distributed in a pattern which is more uniform than random. The near-neighbor statistic (R) shows that the observed mean distance ($\bar{r}_a$) is 1.46 times as great as the expected mean distance ($\bar{r}_e$) in a random distribution of the same density.

TABLE 2. *Summary of near-neighbor statistics: Lagro, Indiana bioherms.*

Number of measurements (N)	17
Actual mean distance ($\bar{r}_a$)	0.83 Km
Expected mean distance ($\bar{r}_e$)	0.56 Km
Area	22.06 Km2
Density (ρ)	0.77
Near-neighbor statistic (R)	1.46
Standard error of mean ($\sigma_{\bar{r}_e}$)	0.72
Standard variate of normal curve (c)	3.69

Discussion

Several speculative possibilities may be offered to account for the spatial arrangement of the Lagro bioherms. It is well known among ecologists and geographers studying contemporary biotic and cultural distributions that a regular pattern would be expected in areas of high competition. Both species and communities tend to arrange themselves in order to maximize their potential for success. If one assumes that biohermal communities can "sense" one another's presence (in terms of the effects of food, energy and space; R. L. Anstey, personal communication, 1975), then the spacing of the Lagro bioherms would be expected to be more uniform than random or clustered. On the other hand, the upward and laterally expanding asymmetrical growth (9) may indicate a trend toward coalescence. Thus, although the mathematical trend (R-value) may be in the "direction" of uniform spacing, the growth pattern may have been toward aggregation, if one ignores competition.

Clearly, more work needs to be done on the evolution and distribution of these communities; more bioherms need to be located. A predictive model, perhaps one based upon other known distributions, should be sought in an attempt to help locate buried bioherms. Other unanswered questions include the effects of size (area) occupied by the features, and whether or not there is an hierarchy of sizes of bioherms. Spatial measurements should be taken with regard to an isochronous plane, not merely the exposed "tops", as was done here. Moreover a population model within a fossil community could be derived using nearest neighbor techniques.

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