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T. FREY

THE PATTERN FIELD

Abstract

This paper is concerned with the development of certain ideas introduced in an earlier (Frey, 1965) paper as the Pattern Field. Here the attempt is made to define the co-ordinates of the Pattern Field by means of the population characteristics — density (p) and variance (v^2), both expressed as a proportion of the maximum possible. For the maximum possible variance a new formula has been derived.

The determining of the co-ordinates of the Pattern Field is found to be satisfactory for practical purposes. The fitting of data to any of distributions seems to be a question connected with detailed investigations only. However, the mathematical character of the Pattern Field needs future discussion.

Introduction

The spatial pattern of plant units within a plant community is one of the main concepts in modern plant ecology. It should be emphasized that this subject, though of considerable fundamental importance, is not without practical interest. Surveys of grasslands, forests, freshwater communities etc. involve a lot of unsolved and often barely recognizable problems, especially in connection with the measurement of their biological productivity, various effects of ecological factors, indicator value of a particular species in different habitats etc.

Progress made heretofore towards understanding the principles of the quantitative distribution of plants was reviewed by Goodall in detail in 1952 and Greig-Smith in 1964. Considerable contributions on this topic were also made by Curtis and McIntosh (1950), Kershaw (1964), and Pielou (1964). Since the reader may refer to these sources, I prefer to omit the discussion of quite a bulk of literature in this article.

However, some difficulties with terminology have arisen. First, the English-speaking authors do not separate the p a t t e r n t y p e, shown by any particular species, and the d i s t r i b u t i o n as a purely mathematical term indicating any function type fitting the field data. Here I attempt to separate them.

Further, the terms "under-dispersion" and "over-dispersion" are often used, but, unfortunately, as in their reverse, as well as in different senses, referring to the pattern type — a physical, and to distribution — a statistical concept. The latter confusion becomes manifest also in connection with the term "contagious", that is a special case of distributions (math.), introduced originally by Pólya (1931). Somewhat later, Neyman (1939), Beall (1940) etc. used this term in a wider sense.

Finally, Gurland (1958) suggested quite an appropriate "generalized family of contagious distributions". So that it might be better to avoid the use of the term "over-dispersed" in general and that of "contagious" in a physical sense, replacing them by the term a g g r e g a t e d. Instead of "under-dispersion" the usage of r e g u l a r is widely accepted. To indicate the physical aspect of the normally distributed population the term r a n d o m seems quite appropriate.

Hereafter these terms are used in the meanings indicated above.

Pattern Field

The greatest of interest should be paid to the problem of correlation of differences in certain microenvironmental factors in the cases of certain kinds of spatial pattern shown by the species under consideration. This approach has been discussed by Greig-Smith (1964). With the view of avoiding artifacts, the basic methods of any attempt at making an objective determination of the pattern type should remain applicable under any conditions. Unfortunately, none are recommended as universal. One of the important reasons for this might be the fact that the influence of the density is ignored and the pattern types are regarded as successive levels of aggregation only. These two variables were used together in definition of the Pattern Field, a new concept (Frey, 1965).

The well-known parametres of a statistical population are the mean $(\bar{x})$, the variance $\left(v^2 = \frac{\Sigma\,(x_i - \bar{x})^2}{n-1}\right)$ and the amount of samples (n). It is not very surprising therefore that they all have some influence on the possible pattern type. The increase in v^2 is reflected by the succesive pattern types as regular, random and aggregated, so that the maximum possible variance appears at the stage of highest aggregation. However, the maximum possible variance could not be considered as an independent variable. It is easily understood that the maximum possible variance $(\hat{v}^2)$ is related to the density. Namely, if the population density (p) is very low, the $\hat{v}^2$ does not exceed $\bar{x}$ noticeably (Poisson expectation; sporadic pattern). An alternative Poisson expectation should hold good when the density increases towards the maximum possible $(\bar{x} \rightarrow \hat{x})$, until the probability of any point *not* occupied by a plant falls on the Poisson expectation. In other words, the variance of such a Poisson series does not equal $\bar{x}$, but $\hat{x} - \bar{x}$ (closed pattern). For this extreme it does not seem likely that the aggregation could be marked. Consequently, it is doubtful that Poisson series fits well the data drawn from a true random population with the mean about $^1/_2\ \hat{x}$. To illustrate the dependence of intrapopulation aggregation on population density these variables $(\hat{v}^2,\ \hat{x})$ are best regarded as co-ordinates at right angle. Such an approach leads us to five categories of pattern (see fig. 1 and 2).

The goodness of fit to various (discrete or continuous) distributions is dependent on the level of significance, the number of observations, the sample size and the specific character of the species under consideration (i. e. the $\hat{x}$), although the degree of aggregation is most important (see

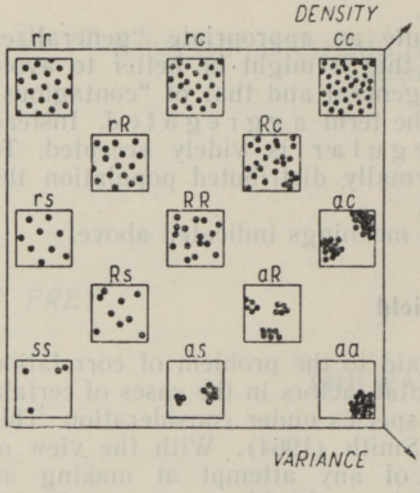

Fig. 1. The pattern types. Abbreviations: r — regular, R — random, a — aggregated, s — sporadic, c — closed pattern.

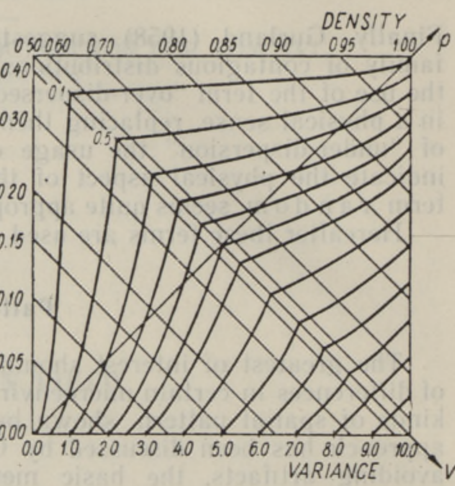

Fig. 2. The Pattern Field (see text).

below). Thus, if a measure is required, this can be obtained best by determining the co-ordinates of the Pattern Field and the subsequent fitting of data against the possible distributions. It is often, of course, sufficient to use only the two co-ordinates, e. g. for the same sampling procedure and species under investigation.

The Density Co-ordinate

It seems to be desirable to compare all the species on the same scale. The species under investigation differ in their mean projective area per individual (φ) and respectively, in the possible number of individuals ($\hat{x}$) per unit area (a), because

$$\hat{x} = \frac{1}{\varphi}. \tag{1}$$

Thus the actual number of individuals per unit area has different response to the distributions and the goodness of fit to, for example, Poisson expectation. "If the mean number per quadrat is, say, 10 or a hundred, Poisson expectation still applies if the maximum possible number that could occur in a quadrat is very much higher" (Greig-Smith, 1964).

Hence the important conclusion results in the actual densities being regarded as relative to the maximum possible for any particular species. This way it is possible to examine all species on the same scale, p, or the density co-ordinate:

$$p = \frac{\bar{x}}{a\hat{x}}. \tag{2}$$

The density relative to maximum possible in a quadrat of any specified size is a theoretical concept. A rough estimate may be possible if the morphology and behaviour of a species are known. Determination of this characteristic in the field imposes evident difficulties, as the $\hat{x}$ applies to the inverse relationship with the average size of an individual of the species, i. e. somewhat like a constant for any habitat, the performance. This constant is in fact a phytocoenological variable, showing the maximum value for a community where the species under investigation reaches its optimum.

Here several possible approaches are outlined to the estimation of $\hat{x}$:

1) The determination of the mean projective area of an individual, defined by the circle around the midpoint of an individual or plant unit within which the chance of another individual occurring is depressed because two individuals cannot be superimposed. However, if individuals vary widely in size the situation is quite complicated (Pielou, 1960).

2) Examination of distances between individuals in dense clumps.

3) Counting the number of individuals on a number of small samples located in dense clumps.

4) Estimation of maximum possible weight above ground. In cases 2), 3) and 4) it is useful to subdivide the plots with the purpose to obtain an evidence of markedly decreased variance in clumps reaching the maximum possible density. Then the data may be handled in a way that permits to test the skewness and to ascertain the mode. An appropriate estimate of $\hat{x}$ would be the mode provided the negative skewness and positive curtosis are significant.

In connection with the Pattern Field the maximum possible density turns out to be a fundamental characteristic of a plant population, being not only of theoretical interest as usually stated. Therefore the methods of determining $\hat{x}$ require full attention and future development.

On the other hand, it is often pointed out that the application of the number of individuals per unit area as the measure of quantity is not ideal at all. For example, Goodall wrote: "Accordingly, instead of density a continuous variable representing the quantity of the species has been preferred — an estimate of ground cover, in fact" (Goodall, 1961 : 165).

It is evident that the question dealt with here can be approached in terms of cover as well.

The Maximum Possible Variance

The maximum possible variance appears provided the degree of aggregation of plant units reaches its maximum.

Let the area under consideration, having a defined density, p, be sampled by means of n random quadrats, each of a square metre. The area investigated, S, is then

$$S = na. \tag{3}$$

The maximum possible density on S square metres, M equals (1), (3)

$$M = S\hat{x}. \tag{4}$$

Suppose the aggregation results in the clusters, within each the density reaches the maximum possible ($p_{cluster} = 1$). If the aggregation is the maximum indeed, we may consider all the individuals (2), (4)

$$\Sigma x = S\hat{x}p \tag{5}$$

growing in one dense cluster only. In such circumstances we have (3), (5)

$$\bar{x} = \frac{\Sigma x}{n} = a\hat{x}p \tag{6}$$

regardless of the a being large enough to contain Σx individuals. In case it does not, a proportion of quadrats, nq, tend to be absolutely empty and another proportion, np, to contain the maximum possible number of plant units (i. e. $a\hat{x}$). Accordingly, the samples tend to contain $\frac{\Sigma x}{np}$, or none, plant units. The maximum possible sum of squares, $\Sigma\hat{D}^2$, is given by

$$\Sigma\hat{D}^2 = \Sigma x^2 - \frac{(\Sigma x)^2}{n} = np\left(\frac{\Sigma x}{np}\right)^2 - \frac{(\Sigma x)^2}{n} = \frac{(\Sigma x)^2}{n}\cdot\left(\frac{1}{p} - 1\right) = n\bar{x}^2\frac{q}{p},$$

or from (3), (6)

$$\Sigma\hat{D}^2 = Sa(\hat{x})^2\ pq. \tag{7}$$

When applied to the definition of pattern, we may consider the variance of a binomial series $(p+q)^M$ as belonging to regular pattern. In other words, this variance can be regarded as residual (heterogeneity at any level of aggregation and therefore, without biological interest). It may be designated as C (4):

$$C = pqM = pqS\hat{x} \tag{8}$$

and the (7) can be rewritten as

$$\Sigma\hat{D}^2 = C\hat{x}a.$$

Consequently, the maximum possible variance, $\hat{v}^2$, is given by (7), (8)

$$\hat{v}^2 = C\frac{a}{n-1}\hat{x}, \tag{9}$$

from which some conclusions can be drawn, namely:

1) The maximum possible variance to be expected for any given data may be regarded as consisting of a "unity" of heterogeneity, C, in spite of the degree of actual aggregation. Due to certain analogy I suggest to term this "unity" as residual heterogeneity. The other parts of the maximum variance are: the population parameter $\hat{x}$ and the ratio $\frac{a}{n-1}$. The latter may be considered as a characteristic of sampling applied, K.

2) From (9) it results that the maximum possible variance for an observed series with parameter $\hat{x}$, on the area investigated, S, depends not only on the degree of aggregation shown by the given population, but on the density of this population as well. In fitting data to rather numerous possible distributions this point is usually overlooked. That means, the pq determines the character and significance of the skewness.

3) The ratio K is inversely related to the efficiency of sampling. At first it is to be stressed that the size of sampling unit, a, applies to the direct, and the amount of samples, n, to the inverse relationship with maximum possible variance. Evidently this is in good accordance with one's experience in field studies. For example, Goodall (1961) demonstrated the log relationship between sample size and variance. The number of records, n, needs no comments.

4) The consideration of the ratio $\frac{a}{n-1}$ will support the conclusions of many students with respect to the increased effectiveness of the sampling when the area investigated, S, is divided into a comparable large number of relatively small quadrats.

5) Likewise, the maximum possible variance depends on the mean projective area, φ (resp. $\hat{x}$) of a plant unit (individual). Consequently, the smaller the plant units the greater the possible variance, and the greater the actual variance belonging to any specified degree of aggregation. The latter conclusion is in line with experience of many earlier workers (see, for example, Družinina, 1963) who have considered the data on the significance of mean quantities for different species, computed on the basis of the same number of observations (in relation to the size of plant units).

Therefore, the assumption can be made that the suggested formula for $\hat{v}^2$ should be appropriate.

The Variance Co-ordinate

As indicated in previous sections, the maximum possible variance depends on a series of variables and the value of $\hat{v}^2$ is specifical for any species under consideration.

Actually we have the observed variances for various populations to be evaluated to indicate the degree of aggregation reached as the result of intermingled biological and ecological factors. The observed variances should occur no greater than $\hat{v}^2$ and no smaller than our speculative residual variance, C. The best way to determine the position of any actual variance on the latter scale seems to be the ratio of the observed (v_x^2) to the corresponding maximum possible $(\hat{v}^2)$ variance. Thus the variance co-ordinate, V^*, represents the same scale for whatever species similarly to the density co-ordinate, p:

$$V^* = \frac{(v_x^2)}{(\hat{v}^2)}. \tag{10}$$

Usually the sampling procedure remains unchanged during a period, and therefore, $S_{(a,n)}$ remains constant. For a given sample-area the $\hat{x}$ does not vary substantially either. In such circumstances it results from (7) that the maximum sum of squares is directly related to pq. As the maximum value for $pq = {}^1/_4$, the true maximum possible variance did appear when $p = 1 - q = {}^1/_2$. Putting this value into (10), we have

$$V^* = \frac{\Sigma D^2}{n-1} : \frac{\Sigma \hat{D}^2}{n-1} = \frac{4\,\Sigma D^2}{Sa(\hat{x})^2}. \tag{11}$$

Let us denote by R the scale constant $R = 10$ to enter it into formula of V^* for simplifying calculations and by K_m all the constant values (R, S, a, $pq = {}^1/_4$)

$$K_m = \frac{4R}{Sa}. \tag{12}$$

The variance co-ordinate, V, is now given by

$$V = RV^* = w \Sigma D^2, \quad (13)$$

where

$$w = \frac{K_m}{(\hat{x}_B)^2} = \frac{40}{Sa(\hat{x}_B)^2} \quad (14)$$

and $(\hat{x}_B)$ is the value of $\hat{x}$ for a species B.

Some Further Comments

Let us consider the appropriateness of the main phytocoenological characteristics. The application of density needs a restriction of higher values, $\hat{x}$, as stated above. The frequency has such a restriction by itself — the number of samples, n, or 100 per cent of occurrence. Likewise, of continuous characteristics (see table), the cover has well defined limitations, but to assess the biological value or meaning of any given weight value

CHARACTERISTIC	DISCRETE	CONTINUOUS
RELATIVE (Limited from 0 to 100)	FREQUENCY (Per cent of occurrence in samples)	COVER (Per cent of ground cover)
DIRECT (No upper limit)	DENSITY (Number of plant units per unit area)	WEIGHT (g per unit area)

needs an upper limit, say $\hat{w}$, in relation to which the actual values are to be evaluated. In this respect, the restricted relative characteristics in phytocoenological investigations are to be preferred, since there arise no problems in estimating the maximum possible quantities. On the other hand, the discrete measures have a serious disadvantage in that actually the precise determination of density is impossible, and if the frequency is employed, the exactness of records is to a great extent dependent on the number, size and shape of samples used.

However, of continuous characteristics the cover is timeconsuming to measure with sufficient exactness. Often the data estimated could not in fact present a continuous measure. So it may be concluded that the measurement of the weight of aerial parts of the plants is the best approach in spite of the difficulties in determination of the upper limit, $\hat{w}$.

The Pattern Field is applicable to whatever characteristics provided the upper limits and replicate measurements are available. Even more, the possible patterns to be expected in quantities are similar as well. Unfortunately, at the present moment it is yet impossible to show the interrelations of different distributions projected on the Pattern Field. Possibly, the third co-ordinate is required for this purpose. The one point I have to emphasize here is that the possible distributions have no well-defined boundaries, and so many of them are related as special cases of each other.

In literature the Poisson distribution is applied to the random patterns. Not very surprisingly the goodness of fit observed is usually high since the size of the samples used is relatively small. For example, Greig-Smith (1964) suggests as a practical criterion the usage of quadrats of size which does not result in more blank quadrats than those occupied by one individual. Accordingly, there is no place for a high degree of aggregation to occur. On the other hand, being a special case of Gaussian distribution, the Poisson series with relatively high mean is very similar to normal distribution indeed. So the mathematical character of the Pattern Field needs further discussion and development.

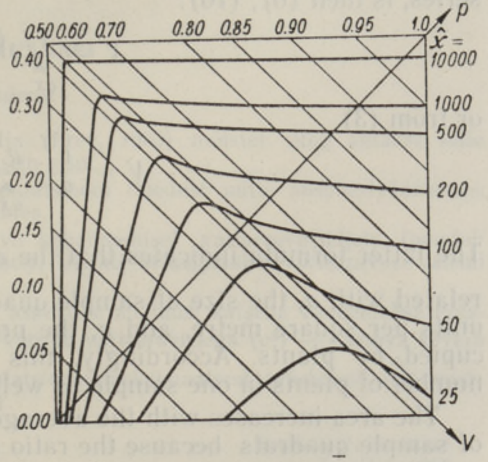

Fig. 3. The dependence of the $\bar{x} = v^2$ line on plant size (on $\hat{x}$). $n = 20$; $a = 0.1$; $q = 1 - p$.

An attempt towards clarification of problems of this kind may be the following. Let us consider the area on Pattern Field which can be referred to as fitting the Poisson expectation. The variance of Poisson distribution equals to its mean

$$v^2 = \bar{x}.$$

From (11), (13)

$$\bar{x} = V^* \frac{\Sigma \hat{D}^2}{n-1} = \frac{V \Sigma \hat{D}^2}{R(n-1)}, \tag{15}$$

and (7)

$$\bar{x} = \frac{V}{R} \cdot \frac{Sa(\hat{x})^2 pq}{n-1}. \tag{16}$$

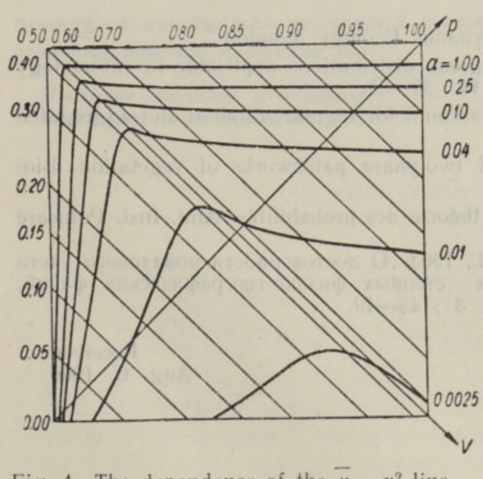

Fig. 4. The dependence of the $\bar{x} = v^2$ line on plot size (a in square metres). $n = 20$; $\hat{x} = 1000$; $q = 1 - p$.

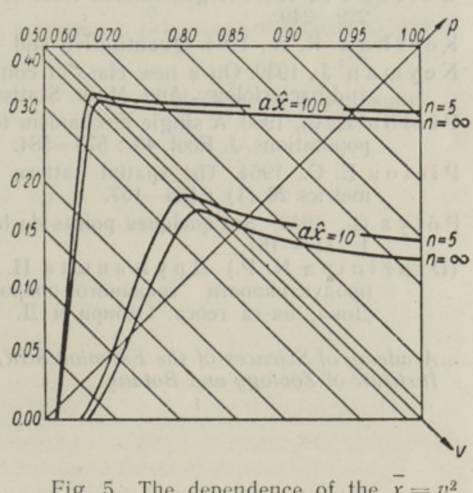

Fig. 5. The dependence of the $\bar{x} = v^2$ line on sample size (n).

The relationship of the co-ordinates V and p, corresponding to a Poisson series, is then (6), (16):

$$V = \frac{1}{a\hat{x}} \cdot \frac{R\,(n-1)}{S}, \tag{17}$$

or from (3)

$$V = \frac{1}{q} \cdot \frac{R}{a\hat{x}} \cdot \frac{(n-1)}{n}. \tag{18}$$

The latter formula indicates that the area under consideration is inversely related with a, the size of sample quadrat, $\hat{x}$, the possible number of plant units per square metre, and q, the proportion of area investigated, unoccupied by plants. Accordingly, this applies to the maximum possible number of plants in one sample as well.

The area increases with the average size of plants and with the number of sample quadrats because the ratio of $(n-1)$ to n increases then.

In figs 3—5 the influence of some variables to the topography on Pattern Field of the line, satisfying $v^2 = \bar{x}$, is indicated.

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Academy of Sciences of the Estonian SSR,
Institute of Zoology and Botany

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T. FREY

JAOTUMUSVÄLI

Resümee

Artiklis arendatakse edasi jaotumusvälja (Frey, 1965) mõistet ning antakse selle koordinaatidele bioloogilises mõttes konkreetsem sisu.

Tiheduse telg kirjeldab vaadeldava populatsiooni tihedust mitte absoluutväärtustes, vaid bioloogiliselt maksimaalse võimaliku suhtes.

Raskus, mis tekib samasuguse suhtarvu kohandamisel varieeruvusteljele (puudub maksimaalse varieeruvuse hindamise võimalus), ületati maksimaalse varieeruvuse valemi tuletamisega.

Jaotumusvälja (joon. 2) matemaatiliste aspektide analüüsi katsena vaadeldakse Poisson' jaotuse põhitunnusele — keskmine ($\bar{x}$) võrdub varieeruvusega (v^2) — vastava kõvera paiknevust (vt. joon. 3—5) sõltuvana populatsiooni maksimaalsest tihedusest ($\hat{x}$), vaatluste arvust (n) ja proovipinna suurusest (a).

Eesti NSV Teaduste Akadeemia
Zooloogia ja Botaanika Instituut

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Т. ФРЕЙ

ПОЛЕ РАЗМЕЩЕНИЯ

Резюме

В статье уточняется понятие «поле размещения» (Frey, 1965), более конкретно определяются, с биологической точки зрения, координаты последнего.

Ось плотности характеризует обилие данной популяции не в абсолютных величинах, а в отношении к биологически максимально возможному.

Возникающие трудности при применении такой же относительной оценки для оси варьирования — максимально возможная изменчивость неизвестна — преодолеваются путем применения соответствующей формулы.

Делается попытка анализа математических аспектов поля размещения (рис. 2) путем изучения расположения линии, соответствующей основному признаку распределения Пуассона — среднеарифметическая ($\bar{x}$) равняется дисперсии (v^2) — в зависимости от максимально возможной густоты популяции ($\hat{x}$), числа наблюдений (n) и величины пробной площадки (a).

Институт зоологии и ботаники
Академии наук Эстонской ССР

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