

Fig. 6.28 Frequency distribution of the resistance of *Trifolium repens* to the pathogens (a) *Cymadothea trifolii* and (b) *Pseudopeziza trifolii*. Resistance was assessed on a 10-point scale, with highly resistant individuals scoring low values and highly susceptible individuals scoring high values. The horizontal bars above the histogram indicate which values are not significantly different at $P = 0.01$ on the basis of a Student-Newman-Keuls test; clones with disease-ratings which fall under a common bar are not significantly different. (From Burden, 1980b, courtesy of the *J. Ecol.*)

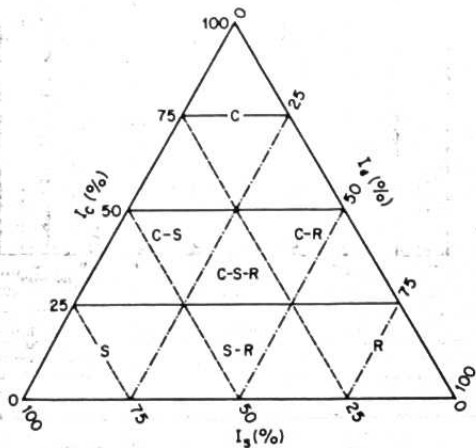


Fig. 6.29 A triangular ordination of the strategies developed by plants in relation to competition, stress and disturbance. I_c , relative importance of competition (—); I_s , relative importance of stress (---); I_d , relative importance of disturbance (---). (From Grime, 1979; courtesy of John Wiley and Sons.)

The Poisson Series and the Detection of Non-randomness

In addition to the detection of non-randomness in species distributions by correlation methods discussed in the last chapter, a number of approaches have been made to the non-random distribution of individuals of the same species. This, in part, can be accounted for in similar terms as correlation between species, but several other methods of detecting departure from randomness are available.

Historical

The earliest accounts of the non-random nature of the distribution of plants in a community are those of Gleason (1920) and Svedberg (1922) who independently showed that several species were markedly non-random. Svedberg's approach to the problem has since become one of the standard methods of detecting non-randomness in vegetation and consisted of relating the observed number of individuals per quadrat to the expected number derived from the Poisson series e^{-m} , $m e^{-m}$, $m^2/2! e^{-m}$, $m^3/3! e^{-m}$, $m^4/4! e^{-m}$, ..., where m is the mean density of individuals. Successive figures of the series give the probability of quadrats containing 0, 1, 2, 3, 4, ... individuals respectively, and the expected number of quadrats thus falling into each of these classes can be readily calculated. The nature of the non-randomness was termed as 'overdispersed' when individuals tended to be clumped together, and 'underdispersed' when individuals were scattered very evenly over the area. Overdispersion is thus characterized by large numbers of both empty quadrats and quadrats containing a large number of individuals, and similarly underdispersion by the majority of quadrats containing an intermediate number of individuals. Svedberg showed that dispersal of a number of species agreed satisfactorily with the Poisson series which indicated random dispersion, but also that several species showed either 'overdispersion' or 'underdispersion'. The terms 'overdispersed' and 'underdispersed' refer to the distribution curve of the data and *not* to the pattern of individuals on the ground. This has led to some confusion and it has been suggested by Greig-Smith (1957) that the terms 'contagious' and 'regular' should replace 'overdispersion' and 'underdispersion'. In a Poisson series the variance is equal to the mean and thus the ratio of these two values is equal to 1. Svedberg used this ratio as a measure of randomness; when the values were greater than 1 the distribution was assumed to be contagious, when less than 1 it was assumed to be regular.

Tests of significance

The use of variance:mean as an index of contagion in vegetation has since been used by a number of workers (Clapham, 1936, Archibald, 1948, Dice, 1952, etc.) usually employing a significance test for the difference between the observed and expected variance:mean ratio (Blackman 1942) or a χ^2 -test to compare the terms of the Poisson series with the observed data (Blackman 1935). In addition to the test of goodness of fit, and variance:mean ratio (sometimes termed the Coefficient of Dispersion (Blackman 1942) or relative variance (Clapham, 1936)) several

additional tests for non-randomness have been devised which are adequately described by Greig-Smith (1957) (see also Moore, 1953; Ashby, 1935; David and Moore 1954; Whitford, 1949) and are not discussed here. However, as Evans (1952) has pointed out the variance:mean ratio may give a widely different estimate of non-randomness from a χ^2 -test of goodness of fit and it may be necessary to use more than one test for non-randomness. Evans gives the following hypothetical case with a mean and variance of 1.00 and hence a variance:mean ratio of 1 which indicates a random distribution within the population:

Table 7.1 The observed and expected number of quadrats containing 0, 1, 2, ... individuals in a hypothetical case, where the variance and mean of the population equal 1.

Number per quadrat	Observed number of quadrats	Expected number of quadrats
0	20	36.79
1	76	36.79
2	—	18.40
3	—	6.13
4	—	1.53
5	5	0.31
>5	—	0.05

Obviously there is a considerable discrepancy between the observed and expected data ($\chi^2 = 63.24$, $p \ll 0.1$ per cent) and in general the χ^2 -test of goodness of fit is a more reliable indication of non-randomness than the variance:mean ratio.

The method of testing departure from randomness is illustrated below. The data are taken from two communities, one consisting entirely of random individuals (Fig. 7.1) and one with hypothetical offspring grouped around the 'parents' (Fig. 7.2). The data have been obtained from randomly placed quadrats located by pairs of co-ordinates,

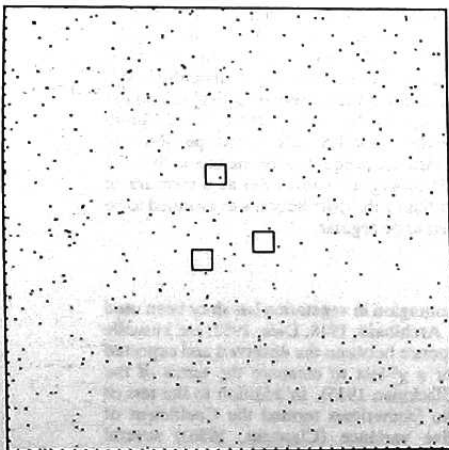


Fig. 7.1 A random 'community' with sample quadrats positioned by pairs of random co-ordinates.

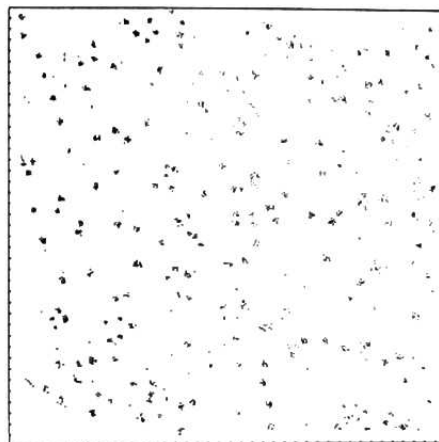


Fig. 7.2 A contagious distribution of individuals.

taken from tables of random numbers. Thus the first quadrat is located by co-ordinates 240.200 (the bottom-left hand corner of the quadrat), the second by co-ordinates 163.187 and third 179.241 and so on (a procedure identical with that used to position the 'individuals' (Fig. 7.1) in the 'community'.

Random population (Fig. 7.1)

The data for 100 random samples are given below:

Table 7.2 The observed number of quadrats containing 0, 1, 2, ... individuals taken from a random population.

Number of individuals in each quadrat (a)	0	1	2	3
Frequency of occurrence in 100 quadrats (f)	46	34	14	6

(a) χ^2 goodness of fit

$$\text{Mean density of the population, } m = \frac{\sum af}{100} = 0.8$$

Thus from the series e^{-m} , $m e^{-m}$, $m^2/2! e^{-m}$, $m^3/3! e^{-m}$, ..., the expected number of quadrats containing 0, 1, 2, ... individuals can be calculated:

$$e^{-m} = e^{-0.8} = 0.4493$$

(see Greig-Smith, 1983; Table 3)

$$m e^{-m} = 0.4493 \times 0.8 = 0.3594$$

$$\frac{m^2}{2!} e^{-m} = 0.4493 \times \frac{0.64}{2} = 0.1438$$

$$\frac{m^3}{3!} e^{-m} = 0.4493 \times \frac{0.512}{6} = 0.0383$$

Thus the expected distribution should be:

$$0.4493 \times 100, \quad 0.3594 \times 100, \dots \text{ and thus:}$$

Number of individuals per quadrat	0	1	2	3
Expected frequency	44.9	35.9	14.4	3.8
Observed frequency	46	34	14	6
Difference	1.1	1.9	0.4	2.2

The goodness of fit is calculated as the sum of the differences squared divided by the expected frequency:

$$= \frac{(1.1)^2}{44.9} + \frac{(1.9)^2}{35.9} + \frac{(0.4)^2}{14.4} + \frac{(2.2)^2}{3.8}$$

$$= 0.0269 + 0.1006 + 0.0111 + 1.2737$$

$$= 1.4123$$

The χ^2 -table is entered with 2 degrees of freedom (2 less than the number of terms used to calculate the χ^2 total) which shows a value of 1.386 when $p=0.5$. Thus the chance of this difference between the two sets of data arising fortuitously is 50:50 and we can regard the observed data as showing a very good fit with the expected series and the population sampled was randomly distributed. (When the chance of a difference between two sets of figures arising completely fortuitously, falls as low as 0.05 (1 in 20 or a 5 per cent level of significance) it is usually considered that such a level of odds necessitates some other hypothesis, and the difference can be safely regarded as 'real' rather than 'accidental').

(b) *Variance:Mean ratio*

From the data above:

$$N = 100, \quad x = \frac{\Sigma(x)}{N} = \frac{80}{100} = 0.8$$

$$\Sigma(x)^2 = 144$$

$$(\Sigma x)^2 = 6400$$

$$\therefore \frac{(\Sigma x)^2}{N} = 64$$

The variance of the population is given by

$$\frac{\Sigma(x)^2 - \frac{(\Sigma x)^2}{N}}{N-1} = \frac{144 - 64}{99} = \frac{80}{99} = 0.8080$$

$$\text{Thus the variance:mean ratio} = \frac{0.8080}{0.8000} = 1.01$$

The variance:mean ratio shows the population to have apparently some degree of contagion, and this difference from the expected ratio of 1 must be tested by a *t*-test:

Standard error of the variance:mean ratio is given by

$$\sqrt{[2/(N-1)]} = \sqrt{\frac{2}{99}} = 0.1421$$

$$t = \frac{\text{Observed} - \text{Expected}}{\text{Standard Error}}$$

$$= \frac{0.01}{0.1421}$$

$$t = 0.0704, \quad p < 0.9$$

Again this difference is not significant, for such a difference could arise by chance very frequently, and the distribution of the population can be regarded as random.

Contagious population (Fig. 7.2)

The data for 100 random samples is given below, the sampling procedure being identical to that used above:

Table 7.3 The observed number of quadrats containing 0, 1, 2, ... individuals taken from a contagious population.

Number of individuals in each quadrat	0	1	2	3	4	5	6	>7
Frequency of occurrence in 100 quadrats	47	6	5	8	5	6	7	16

(a) χ^2 goodness of fit

$$\text{Mean density of the population, } m = 2.44$$

The Poisson series with this mean value is given by the probabilities:

$$e^{-m} = e^{-2.44} = 0.0872$$

$$m e^{-m} = 0.2128$$

$$\frac{m^2 e^{-m}}{2!} = 0.2596$$

$$\frac{m^3 e^{-m}}{3!} = \frac{2.44^3}{6} 0.0872 = 0.2111$$

$$\frac{m^4 e^{-m}}{4!} = \frac{2.44^4}{24} 0.0872 = 0.1288$$

$$\frac{m^5 e^{-m}}{5!} = \frac{2.44^5}{120} 0.0872 = 0.0628$$

$$\frac{m^6 e^{-m}}{6!} = \frac{2.44^6}{720} 0.0872 = 0.0256$$

$$\frac{m^7 e^{-m}}{7!} = \frac{2.44^7}{5040} 0.0872 = 0.0089$$

Number of individuals per quadrat	0	1	2	3	4	5	6	7	≥7
Expected frequency	8.7	21.3	26.0	21.1	12.9	6.3	2.6	0.9	
Observed frequency	47	6	5	8	5	6	7	16	
Difference	38.3	15.3	21.0	13.1	7.9	0.3	4.4	15.1	

$$\chi^2 = \frac{(38.3)^2}{8.7} + \frac{(15.3)^2}{21.3} + \dots + \frac{(15.1)^2}{0.9}$$

$$= 470.334, \quad p < 0.001$$

The difference between the observed and expected numbers of occurrences is highly significant, the chances of this difference arising accidentally are very much greater than 1000:1.

(b) *Variance:mean ratio*

$$N = 100, \quad m = \bar{x} = 2.44$$

$$\Sigma(x)^2 = 1364.0$$

$$(\Sigma x)^2 = 59\,536.0$$

$$\frac{(\Sigma x)^2}{N}$$

$$t = \frac{\Sigma(x^2) - \frac{(\Sigma x)^2}{N}}{N - 1} = \frac{768.64}{99} = 7.7640$$

$$\therefore \text{Variance:mean ratio} = \frac{7.7640}{2.44} = 3.182$$

Standard error = 0.1421

$$\therefore t = \frac{3.182}{0.1421}$$

$$= 22.3927 \text{ with } 99 \text{ degrees of freedom, } p < 0.001$$

Again the probability of this difference arising by chance is very much less than 1000:1.

Various criticisms of the variance: mean ratio have been made, in addition to the case outlined by Evans (1952) described previously. Thus Jones (1955-6) suggests the interpretation of variance: mean ratios is very unreliable when the mean density of individuals is very high or very low, and Skellam (1952) has criticized this approach on the grounds that the success of the ratio as an indicator of non-randomness is dependent on the size of the quadrat used for sampling. This latter criticism is, in fact, applicable to all of the methods used in the detection of non-randomness of vegetation. This effect of size of quadrat can be very useful in gaining information on the scale of the non-randomness present and is discussed below. In general the χ^2 -test for goodness of fit gives a reliable indication of the occurrence of non-randomness relative to the choice of quadrat size, provided very abundant and very rare species are not included in the investigation. Both these tests and others which have appeared are not applicable to distributions where an individual is not an obvious entity, and work on grassland for instance has accordingly been severely handicapped (see below).

Several attempts at deriving a method for detecting non-randomness in the distribution of tree species have been made. These have involved measures of point-to-plant and plant-to-plant distances. Basically all the methods employing distance measures between individuals or between random points and individuals depend on the relationship between these measures in a random population. Thus when individuals are distributed at random, the ratio of mean distance from a random point to the nearest individual, to the mean distance between randomly selected individuals to its nearest neighbour, should be unity. This ratio will be greater than one when individuals are contagiously distributed and less than one when they are evenly distributed (corrected for the relative density of individuals). The significance of departure from expectation can be tested in a variety of ways.

Contagious distributions

Following the demonstration that the observed distribution of individuals in a plant community did not fit a Poisson series, a considerable effort was made to find some mathematical series to which field data of this nature could be satisfactorily fitted. The type of function used in all cases involves parameters relating the distribution of

individuals to random central points, around each of which a number of 'offspring' is scattered. Thus contagious distribution of individuals is related to the most obvious and likely causal factor – that of vegetative spread or heavy seeds from a parent individual, the parents being distributed at random. Archibald (1948; 1950) found a satisfactory fit for many (though not all) species, to Neyman's contagious distribution and also to a similar distribution, Thomas's Double Poisson. Similarly, Barnes and Stanbury (1951) found a satisfactory fit to Neyman's and Thomas's distributions using data taken from uniform deposits of china clay residues in the process of being colonized. On the other hand, Thomson (1952) found only one species out of three tested that fitted these distributions at all satisfactorily. Several other distributions have been suggested, based on the premise that contagion in vegetation is largely due to the morphology of the individual or the efficiency of seed dispersal mechanisms, and operates at one (small) scale only. Unfortunately the value of this approach is minimized by two considerations: (i) later work has shown that contagion in vegetation is due to a multitude of factors and is present on numerous scales in any one site; (ii) the mathematical parameters employed to define the distribution and generate the series have no meaning ecologically, or at least it is impossible to relate known ecological factors to these parameters. Thus whilst the approach is of considerable academic interest to the mathematician it is of little use to the ecologist and it would appear that the complexity and variation in the distribution of individuals is of such an order that the formulation of a mathematical model is virtually impossible and it is necessary to fall back on rather simpler empirical approaches.

The effect of quadrat size on the detection of non-randomness

One of the criticisms made of the variance:mean ratio and goodness of fit as tests of non-randomness in vegetation, has been the dependence of its detection on quadrat size (Skellam, 1952). On theoretical grounds it can be readily shown that in any contagious population the use of a Poisson series and tests of departure from it will show both random, contagious and regular distribution as the size of quadrat is steadily increased. This is illustrated below (Fig. 7.3) where sampling with quadrats A

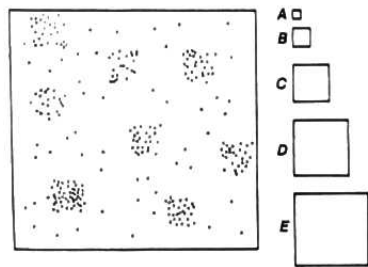


Fig. 7.3 The relationship between quadrat size and variance (see text).

or B the population would probably show slight contagion, sampling with quadrat C very marked contagion (each quadrat would contain very many or very few). With quadrats D and E the distribution would appear to tend towards a regular distribution with all quadrats containing approximately the same number of individuals. Thus the most marked demonstration of contagion would be with the quadrat with an area approximately equal to the area of the clump.

Table 7.4 Density data from Experiment 5 (Mosaic of irregularly shaped areas), showing the change of contagion detected with increase of quadrat size. (From Greig-Smith 1952a; courtesy of *Ann. Bot., Lond.*)

Quadrat size (cm)	Mean	Mean per 100 cm ²	Variance: mean ratio	t	p	χ^2	n	P
10	0.07	0.07	0.9394	0.43	0.6–0.7	–	–	–
15	0.18	0.08	1.0527	0.37	0.7–0.8	–	–	–
20	0.29	0.07	0.9958	0.03	0.9	–	–	–
25	0.39	0.06	1.1342	0.94	0.3–0.4	1.56	1	0.2–0.3
30	0.68	0.08	1.3928	2.76	0.001–0.01	4.00	1	0.02–0.05
35	0.79	0.06	1.5674	3.99	0.001	2.29	1	0.1–0.2
40	0.97	0.06	1.6340	4.48	0.001	26.14	2	0.001

Greig-Smith (1952a) gives data obtained from a series of artificial layouts of coloured discs, and some of the data are presented above (Table 7.4), which illustrate the apparent change of distribution of individuals in a population with increase in size of the sampling unit. For quadrat sizes 10, 15, 20 and 25 cm there is marked indication of randomness; at 30 cm the relative variance (variance:mean ratio) increases sharply to a significant level which is maintained in the 35 and 40 cm quadrats, indicating the contagious nature of the artificial population. (The relationship between quadrat size and variance can be readily appreciated from the hypothetical scheme above (Fig. 7.3). With the small quadrat A roughly equal proportions of the quadrats will contain high, intermediate and low densities of individuals. With quadrat C on the average high or low values will predominate and the variance accordingly will be high. Finally, a very large quadrat (E) will contain roughly equal numbers of individuals and the variance of the data will be very low.) The χ^2 goodness of fit gives a closely comparable picture but it does not reach a significant level of departure from expectation until the 40 cm sampling quadrat. The approximate area of the 'mosaic' employed of high and low densities in this particular layout corresponds more or less with the 35–45 cm quadrat.

The importance of the relationship between quadrat size and detection of contagion lies in the fact that the actual scale at which clumping occurs can be detected merely by resampling the population several times with different sizes of quadrats. Since non-randomness may thus be demonstrated in vegetation where a close visual inspection does not reveal any obvious sign of clumping, this is an important step forward. The mere demonstration of non-randomness in vegetation is of very limited interest but once information is available as to the scale or scales at which this non-randomness occurs, it becomes possible to relate some environmental factor or factors to scales of the detected non-randomness.

The analysis of a contiguous grid of quadrats and the detection of pattern

The development of the analysis of a grid of quadrats is a logical step following the demonstration of the dependence of the detection of non-randomness on quadrat size. Instead of throwing a range of quadrat sizes over an area, a grid of contiguous quadrats is laid out and enumerated, the increasing 'quadrat' sizes then being built up by blocking adjacent quadrats in pairs, fours, eights, etc. An analysis of variance of the data is then carried out, the variance being partitioned between the different block sizes (see Appendix 6). In the graph relating the mean square (variance) to block size the different scales of pattern appear as peaks at a block size corresponding to the mean area of 'clump'. As was pointed out above, this approach is normally used where no