

**Statistical analysis of the phytocoenose homogeneity.  
VI. Frequency distribution of the total species diversity  
and evenness indices as a function of the area size.  
Summing-up discussion**

ANNA JUSTYNA KWIATKOWSKA, EWA SYMONIDES

Department of Phytosociology and Plant Ecology, Institute of Botany, Warsaw University,  
Al. Ujazdowskie 4, 00-478 Warszawa, Poland

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Abstract

Homogeneity of the *Leucobryo-Pinetum* phytocoenose was assessed on the grounds of the agreement of frequency distributions of the total species diversity ( $H$ ) and evenness ( $e$ ) indices with the normal distribution. It was confirmed that: 1) empirical frequency distributions of  $H$  and  $e$  fitted the normal distribution only at some quadrat sizes; 2) values of mean, standard deviation and coefficient of variation were non-linear functions of the area size; 3) mean  $H$  and  $e$  values calculated for small quadrats (1 and 2 m<sup>2</sup>) differed from those calculated for average (4 and 8 m<sup>2</sup>) and large (16 and 32 m<sup>2</sup>) quadrats; 4) the area size at which frequency distributions of both indices were symmetrical determined the scale of spatial differentiation of the phytocoenose, under which it was homogeneous.

*Key words:* phytocoenose homogeneity, Shannon's index, evenness index

INTRODUCTION

The type of frequency distributions of the total species diversity index and its derivative — evenness index as a function of the area size so far has not been included in the analysis of the phytocoenose homogeneity, though it is theoretically possible due to the mathematical characteristics of Shannon's index. According to Bowman et al. (1970) and Hutcheson (1970)  $H$  has the normal distribution which enables to use routine methods of parametric analysis in a statistical inference.

In the first paper of the series the type of frequency distributions of both indices was used in the analysis of the phytocoenose homogeneity

(Kwiatkowska and Symonides 1985a). The agreement of empirical frequency distributions of  $H$  and  $e$  with the normal distribution was taken as a homogeneity criterion.  $H$  and  $e$  values were calculated for 512 quadrats of 1 m<sup>2</sup> each, which composed Greig-Smith's (1952) grid. Indeed, the phytocoenose has been shown to be non-homogeneous according to this criterion, but contagious spatial distributions of both indices and considerable discrepancy between their values and those calculated for the whole grid suggest that, contrariwise to the common knowledge, both  $H$  and  $e$  values and the type of their distributions depend on the area size.

The paper aims at the analysis of homogeneity of the model phytocoenose, on the grounds of frequency distributions of the total species diversity and evenness indices as functions of the area size. The fact whether empirical frequency distributions of  $H$  and  $e$  fit the normal distribution has been assumed as a homogeneity criterion. This has been verified with Chi-square test. The phytocoenose has been considered homogeneous when a probability of finding high and low  $H$  and  $e$  values is statistically the same within biochore, and not higher than it can be expected from the normal distribution.

The paper is the last in the series of works which compare results of studies with respect to qualitative and quantitative measures, as well as different homogeneity indices. Following indices have been treated as homogeneity indices: 1) the type of distributions of the total species diversity and evenness indices, 2) the type of species frequency and their standing biomass distributions, 3) the type of spatial distributions of species and their biomass, 4) species number and mean standing biomass, 5) the type of distributions of the similarity and Euclidean distance coefficients—always treated as functions of the area size (Kwiatkowska and Symonides 1985-e).

The studies were carried-out in the *Leucobryo-Pinetum* phytocoenose Mat. (1962) 1973, with the uniform physiognomy. It was composed of pure, even-aged, one-layered forest stand and floristically poor ground layer (21 species of vascular and 7 species of sporogenous plants) dominated by dwarf-shrubs. The full floristic composition of the phytocoenose, and interpopulational quantitative relationships in the ground layer have been presented in the first paper of the series (Kwiatkowska and Symonides 1985a).

#### MATERIAL AND METHODS

In sampling Greig-Smith (1952) grid was used. It was composed of 512 square quadrats (sample areas) of side 1 m each. In the period of maximum standing biomass (July) above-ground parts of all vascular plants

in the ground layer in each quadrat were clipped and their air-dry biomass were assessed with accuracy of 0.01 g. For each quadrat values of the total species diversity and evenness indices were calculated.

In the further result elaboration 5 new "grids" were formed. Each one composed of quadrats with sizes ascended with geometric progression from 2 to 32 m<sup>2</sup> (cf. Kwiatkowska and Symonides 1985b). Next, 20 quadrats for each of four smaller grids were sampled. The fifth grid consisted of 16 quadrats so they all were taken into account with addition of 4 quadrats of 2 × 16 m each, which were also sampled within the grid.

Values of  $H$  and  $e$  for each quadrat size were segregated into classes. Then, basic distribution characteristics such as mean ( $\bar{x}$ ), standard deviation (S.D.) and coefficient of variation (V) were calculated. Empirical distributions of both indices were compared to the normal distribution at the significance level  $\alpha = 0.10$ .

The significance of differences in mean  $H$  values between different quadrat sizes was verified with a nonparametric test of the sum of ranks. Chi-square value was calculated according to the formula:

$$\chi^2 = \frac{12}{n(n+1)} \sum_{i=1}^k \frac{T_i^2}{n_i} - 3(n+1),$$

where  $T_i$  — sum of ranks determined separately for each sample,  $n$  — sum of all results,  $k$  — number of samples compared,  $n_i$  — sizes of samples compared.

Hypotheses were tested at two stages. At the first, the significance of differences in  $H$  values between different quadrat sizes was verified. At the second, results for small (1 and 2 m<sup>2</sup>), average (4 and 8 m<sup>2</sup>) and large (16 and 32 m<sup>2</sup>) quadrats were grouped and then the significance of differences between them was tested.

## RESULTS AND DISCUSSION

Analysis of frequency distributions of the total species diversity ( $H$ ) and evenness ( $e$ ) indices as functions of the area size has shown that the type of both distributions depends upon it.

Probability of hypothesis of goodness of fit between empirical frequency distribution of  $H$  and the normal distribution is higher than 0.90 only for 2, 8 and 32 m<sup>2</sup> (Fig. 1). In other cases high and low  $H$  values are more frequent in empirical than in the normal distribution. It indicates contagious distribution of  $H$  values. It is particularly evident for 4 and 16 m<sup>2</sup>. Both distributions are bimodal and consist, in a way, of two parts: high and low values. Differences between empirical ( $H$ ) and theoretical

(the normal) distributions result also from an increase in the skewness. As a fraction of the lowest  $H$  values (0-0.2) decreases or disappears, distributions become positively skewed (Fig. 1).

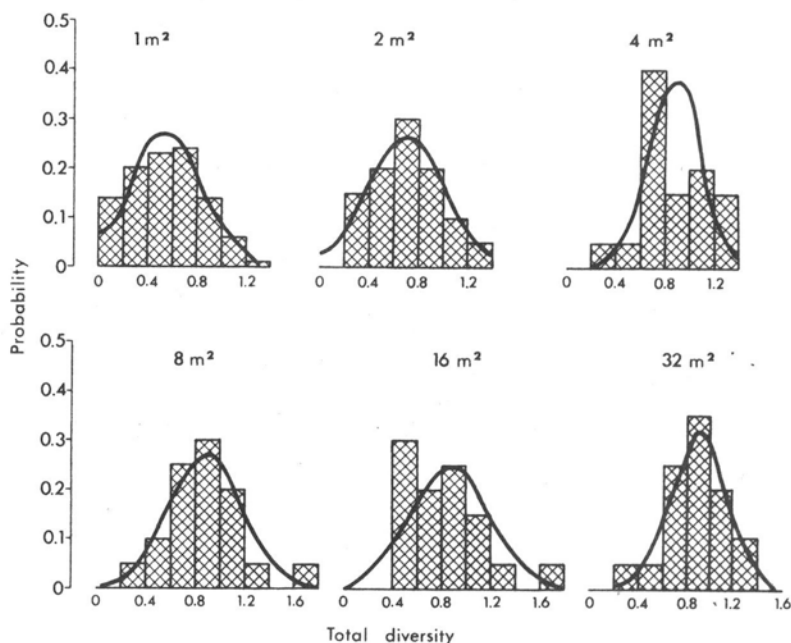


Fig. 1. Effect of the area size on the frequency distribution of total species diversity index

Obtained results suggest that the bigger quadrat size the higher mean value of the total species diversity index. It has been shown by the results both of a test of the sum of ranks and of regression analysis.

The mean  $H$  value for 2 m<sup>2</sup> equals 0.71 and is significantly lower than means calculated for 8, 16 and 32 m<sup>2</sup> (Table 1). Test value of Chi-square, calculated for samples between 2 and 32 m<sup>2</sup>, grows proportionally to an increase in the quadrat size.  $H$  values calculated for small (1 and 2 m<sup>2</sup>), average (4 and 8 m<sup>2</sup>) and large (16 and 32 m<sup>2</sup>) quadrats also differ from each other. Then, probability of the null hypothesis of the lack of differences between them is exceptionally low, lower than 0.001.

From the regression analysis it may be inferred that the mean  $H$  value is a logarithmic function of the area size, of  $y = a \lg x + b$  type. In the case studied equation  $y = 0.07 \lg_2 x + 0.63$ , where  $x$  denotes a quadrat size, circumscribes relationship.

Instead, variation of  $H$  value decreases with an increase in the area size (Table 2). Values of standard deviation (S.D.), variance ( $S^2$ ) and coefficient of variation (V) are approximated by hyperbolic functions of

Table 1

Values of Chi-square test function for differences between mean  $H$  value for 2 m<sup>2</sup> quadrat and those for other quadrat sizes

Quadrat size, m <sup>2</sup>	1	4	8	16	32
Chi-square test value	1.3	.3	3.3	3.6	7.4
Chi-square threshold value (for $\alpha = 0.1$ )	2.71				

Table 2

Basic statistical characteristics of frequency distributions of  $H$  index

Statistical characteristic	Quadrat size, m <sup>2</sup>					
	1	2	4	8	16	32
$\bar{x}$	0.55	0.71	0.87	0.88	0.88	0.92
S.D.	0.03	0.29	0.28	0.29	0.32	0.24
S <sup>2</sup>	0.09	0.08	0.08	0.08	0.10	0.05
V	0.55	0.42	0.32	0.33	0.37	0.26

$y = \frac{a}{x} + b$  type. Coefficient of variation assumes values according to  $y = \frac{0.26}{x} + 0.27$  equation, over the studied range of quadrat sizes ( $x$ ).

It has been revealed that the type of frequency distribution of evenness index ( $e$ ) depends on the area size in the same way as that of  $H$  index. Empirical frequency distributions of  $e$  fit the normal distribution only for 2, 8 and 32 m<sup>2</sup>. For other quadrat sizes distributions are characterized by higher frequency of high and low values, than it may be derived from the normal distribution (Fig. 2).

On the other hand, the mean value of evenness index  $e$  depends on the area size otherwise. An increase in the quadrat size is followed by a decrease in  $e$  values. Variation of  $e$  index also changes this way according to a hyperbolic function of  $y = \frac{a}{x} + b$  type. Values of standard deviation (S.D.), variance (S<sup>2</sup>) and coefficient of variation (V) indicate it (Table 3).

Summing-up, investigations have showed that: 1) the mean  $H$  value increases and the mean  $e$  value decreases with a growth of the area size; 2) as regards the analyzed measures large and average quadrats are less variable than small; 3) empirical distributions of both indices fit the normal distribution only for some quadrat size; 4) the area size at which frequency

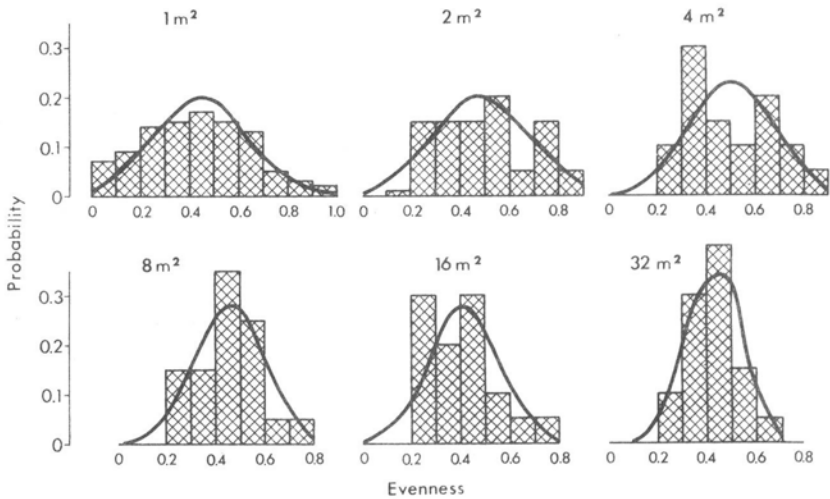


Fig. 2. Effect of the area size on the frequency distribution of evenness index

distributions of  $H$  and  $e$  are symmetrical determines the scale of spatial differentiation of the phytocoenose under which it is homogeneous.

As has been already mentioned the total species diversity index has not been used in the homogeneity analysis yet. Therefore, obtained results cannot be widely discussed. However, they doubt opinion, prevalent in literature,

Table 3

Basic statistical characteristics of frequency distributions of  $e$  index

Statistical characteristic	Quadrat size, m <sup>2</sup>					
	1	2	4	8	16	32
$\bar{x}$	0.43	0.48	0.49	0.46	0.41	0.42
S.D.	0.20	0.20	0.17	0.14	0.14	0.11
S <sup>2</sup>	0.04	0.04	0.03	0.02	0.02	0.01
V	0.47	0.42	0.34	0.30	0.34	0.26

that  $H$  index has the normal distribution (Bowman et al. 1970, Hutcheson 1970, Odum 1971). It results in serious methodical consequences: to verify the significance of differences in  $H$  values between analyzed objects with parametric tests, frequency distribution of  $\bar{H}$  has to fit the normal distribution. It is true only for some scale of spatial differentiation of the phytocoenose. Therefore, differences in  $H$  values between small, average and large quadrats have been verified with a nonparametric test of the sum of ranks.

From the results it may be inferred that the size of the representative sample, which enables to estimate reliably mean values of  $\bar{H}$  and  $e$  indices, depends on the quadrat size.

#### SUMMING-UP DISCUSSION

On phytosociology term "homogeneity" plays a role of an axiom, though its meaning and range are neither unequivocal nor precisely defined. No has objective criterion of the phytocoenose uniformity been found yet to enable to solve this problem practically in the specific situation. Indices proposed for and used in an analysis of the patch uniformity have neither been compared. However, it may be noticed from literature that views of phytocologists have changed towards statistical consideration of the problem and formulation of the statistical criterion of uniformity.

Dahl and Hadač (1949) have been among the first who have attempted to state precisely statistical criterion of uniformity. Their judgement on the phytocoenose uniformity consists of judgements on its components (character species). Mostly it has been formed on the grounds of only one chosen floristic measure, e.g. density of a selected plant population or species number for the unit area, and afterwards has served to describe the phytocoenose, what is logically unjustified (Kershaw 1958, 1959a, 1961, 1963, Goodall 1952a, b, 1954a, b, Greig-Smith 1952, 1961).

Dahl (1960) has essentially contributed to the studies on uniformity as he has distinguished two types of floristic uniformity. The first concerns spatial uniformity — homogeneity, the second applies to uniformity of the structural type — homotoneity (Dahl 1960). Vasilevič (1969) has developed Dahl's concept and defined those two types as follows: "homogeneity — the type of uniformity when any, big enough parts of the sample area are practically the same in respect of the analyzed measures. No directional changes in the structure and species composition occur. Homotoneity — the type of uniformity when runs of areas group around specific structural type — around one mean."

Many authors have shown that numerical values of homogeneity indices depend on the quadrat size (Goodall 1954b, 1961, Anderson 1961a, b, 1963, Gounot 1962, Calléja et al. 1962, Greig-Smith et al. 1963 and others). Calléja et al. (1962) have analysed this relationship taking into account following indices: the type of species distribution in the analysed area, the type of frequency distribution of interspecific correlation coefficients, the type of species frequency distribution, value of the coefficients of similarity between quadrats as a function of the distance between them, species-area relationship. This is probably the only work where the judgement

on homogeneity has been formed on the grounds of various, both synthetic and global, indices.

In the homogeneity analysis of a ground layer of the *Leucobryo-Pinetum* phytocoenose the same sampling and, as regards qualitative measures, the same indices have been used. Results of the analysis have confirmed basic relationships, which Calléja, Dagnelie and Gounot (1962) have found. Indeed, it has been proved that homogeneity is a function of the area size. Therefore, it should always concern a specified scale of the spatial differentiation of a phytocoenose determined by the representative area size. Following tendencies, concerning indices used in respect of qualitative measures can be expressed statistically:

1. The type of species frequency distribution and its statistical characteristics, the type of species spatial distributions, portion of species with random spatial distributions, as well as the type of frequency distributions of similarity coefficients and its statistical characteristics are functions of the area size.

2. In a phytocoenose there can be determined the quadrat size at which species frequency distribution is symmetrical (U type) and that at which number of species with random distributions is significantly higher than at other quadrat sizes.

3. The size of area at which portion of species with contagious spatial distributions and that of "contagious tests" decrease significantly, as well as that at which frequency distribution of similarity coefficients fits the normal distribution agrees with the minimal area size, calculated according to the method of differential quotient.

From the comparison of results concerning various homogeneity indices it may be inferred that nearly all methods result in the same scale of spatial differentiation of the phytocoenose at which it is homogeneous; that agrees with the results obtained by French authors. However, indices used are not of the same value as regards statistical criterion of homogeneity. Although their shortcomings and advantages have been discussed in successive works of the series, it is worth stressing that their relations to Dahl's (1960) and Vasilevič's (1969) concepts vary.

Analysis of the type of spatial species distribution with a nonparametric runs test is undoubtedly the most correct method in studies on spatial uniformity — homogeneity. Analysis of the type of similarity coefficient distribution concerns rather homogeneity of a patch. If frequency distribution of similarity coefficients fits the normal distribution then areas studied have relatively stable floristic composition and their majority groups around the mean value characteristic of that area size. Analysis of the agreement of the type of coefficient distribution with the normal distribution with Chi-square test enables only to determine whether frequencies of low, average and high values of coefficient are such as in the normal distribution. Indeed, this



method does not give information on the spatial relationship between quadrats characterized by different coefficient values and so enables to analyse only the structural type of a patch, not its homogeneity.

Results of the homogeneity analysis as regards quantitative measures enable to reveal similar tendencies as in respect of qualitative measures. It has been shown that homogeneity is always a function of the area size, independent of the index used. Therefore, only the specific scale of spatial differentiation of the ground-layer biomass, related to the specific quadrat size, is homogeneous from the statistical point of view. It has also been proved that, at least for distance coefficients and diversity indices, the scale of spatial differentiation of the phytocoenose at which it is homogeneous as regards the index used can be determined. At the same scale the phytocoenose can be homogeneous and homotoneous in respect of some measures and non-homogeneous and non-homotoneous in respect of others.

Tendencies as regards uniformity indices used are expressed by following statistical relationships:

1. The type of frequency distribution of the ground-layer biomass and its statistical characteristics, as well as the type of distributions of individual species biomass are functions of the area size.

2. Phytocoenose homotoneity, determined by the random type of frequency distributions of distance coefficients and diversity indices, depends on the quadrat size.

The contagious type of biomass distributions, typical of the ground layer and majority of species explains the fact that homogeneity indices depend on the area size. For small quadrats it is positively skewed with "surplus" of low and high values, compared to the normal distribution. Spatial distribution of those values is also nonrandom. Therefore, probability of finding biomass values from each interval varies within biochore. Such a spatial organization of biomass values results in a nonlinear relation of biomass to the area size.

It has been determined that the type of spatial distribution of the total ground-layer biomass and those of individual species is contagious for small (1, 2 and 4 m<sup>2</sup>) and random for large (32 m<sup>2</sup>) quadrats. Under a big scale of its spatial differentiation the *Leucobryo-Pinetum* phytocoenose is homotoneous, as the type of frequency distributions fits the normal (for 8 and 16 m<sup>2</sup>) or the uniform (for 32 and 64 m<sup>2</sup>) distribution, as well as homogeneous, as the type of spatial distribution is random (for 32 m<sup>2</sup>).

The similarity between different biochore fragments also depends on the quadrat size. As a rule, it decreases with a growth of the quadrat size, indicated by changes in the mean value of distance coefficient. Therefore, only small quadrats (2 m<sup>2</sup>), at which frequency distribution of coefficients

fits the normal distribution, are statistically similar. Frequency distributions of diversity and evenness indices fit the theoretical distribution also for small quadrats ( $2 \text{ m}^2$ ).

Therefore, it may be inferred that the phytocoenose under study is homotoneous in respect of individual species biomass and dominance structure under the small scale of its spatial differentiation (the quadrat size equals  $2 \text{ m}^2$ ). Only then different biochore parts are equisimilar from the statistical point of view and represent one structural type in respect of species composition and biomass of individual populations.

As regards quantitative measures statistical criterion of homogeneity is directly associated with: 1) nonparametric runs test — homogeneity index as it verifies the type of spatial distribution of analysed measures, 2) Chi-square test of goodness of fit of empirical biomass distribution with the normal distribution — global homotoneity index, and 3) Chi-square test of goodness of fit of empirical distributions of Euclidean coefficients and diversity (the total species diversity and evenness) indices with the normal distribution — synthetic homotoneity index.

From the result comparison in respect of quantitative and qualitative measures it may be concluded that the scale of spatial phytocoenose differentiation at which it is uniform (homogeneous and homotoneous) depends on a kind of the analysed measure.

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*Statystyczna analiza jednorodności fitocenozy. VI. Typ rozkładu wartości wskaźnika ogólnej różnorodności gatunkowej i wskaźnika równomierności jako funkcja wielkości powierzchni. Dyskusja podsumowująca*

Streszczenie

Praca jest ostatnią częścią studiów problemu homogeniczności fitocenozy, mających na celu porównanie wyników uzyskanych dla cech jakościowych i ilościowych, z zastosowaniem różnych wskaźników homogeniczności. Do badań wytypowano fizjonomicznie jednorodną fitocenozę *Leucobryo-Pinetum* Mat. (1962) 1973, szczegółowo opisaną w pierwszej pracy cyklu (Kwiatkowska i Symonides 1985a). W kolejnych opracowaniach miarą jednorodności był: typ rozkładu wskaźników ogólnej różnorodności gatunkowej i równomierności, rozkład frekwencji i rozkład wartości stanu biomasy jako funkcja wielkości powierzchni, typ rozkładu przestrzennego gatunków i ich biomasy jako funkcja wielkości powierzchni, liczba gatunków i średnia wartość stanu biomasy jako funkcja wielkości powierzchni oraz typ rozkładu wartości współczynników: podobieństwa i odległości jako funkcja wielkości powierzchni (Kwiatkowska i Symonides 1985a-e).

W niniejszej pracy analizę homogeniczności badanej fitocenozy przeprowadzono na podstawie rozkładu wartości wskaźników ogólnej różnorodności gatunkowej ( $H$ ) i równomierności ( $e$ ) jako funkcji wielkości powierzchni. Za kryterium jednorodności przyjęto zgodność empirycznych rozkładów wartości  $H$  i  $e$  (obliczonych dla wzrastającej w postępie geometrycznym wielkości powierzchni podstawowej) z rozkładem normalnym, zweryfikowaną testem  $\chi^2$ . W wyniku przeprowadzonej analizy stwierdzono, że: 1) rozkład empirycznych wartości wskaźników  $H$  i  $e$  jest zgodny z rozkładem normalnym tylko dla niektórych rozmiarów powierzchni podstawowej (rys. 1 i 2). Wielkość powierzchni, której odpowiada symetryczny rozkład wartości obu wskaźników określa równocześnie tę skalę zróżnicowania przestrzennego, w której fitocenoza jest jednorodna; 2) średnia wartość wskaźnika  $H$  jest logarytmiczną funkcją wielkości powierzchni, typu  $y = a \lg x + b$ .  $H$  wyznaczone dla powierzchni 2 m<sup>2</sup> różni się istotnie od wartości wskaźnika obliczonych dla powierzchni 8, 16 i 32 m<sup>2</sup> (tabela 1); 3) wraz ze wzrostem wielkości powierzchni maleje zmienność wartości wskaźnika  $H$  (tabela 2). Wartości odchylenia standardowego (S.D.), wariacji ( $S^2$ ) i współczynnika zmienności ( $V$ ) aproksymuje funkcja hiperboliczna, typu  $y = \frac{a}{x} + b$ ; 4) średnia wartość wskaźnika równomierności  $e$  ma tendencję malejącą w miarę wzrostu wielkości powierzchni. W tym samym kierunku maleje zmienność wskaźnika  $e$ , zgodnie z funkcją hiperboliczną typu  $y = \frac{a}{x} + b$  (tabela 3). Uzyskane wyniki sugerują, że wielkość próby reprezentatywnej służącej do wiarygodnego oszacowania średniej wartości wskaźnika  $H$  i wskaźnika  $e$  jest mniejsza w przypadku dużych powierzchni podstawowych niż małych. Reasumując, wyniki analizy jednorodności przeprowadzonej za pomocą różnych wskaźników są w zasadzie zbieżne dla określonego typu cech: jakościowych lub ilościowych. Niezależnie od przyjętego wskaźnika i cechy — jednorodność jest zawsze funkcją wielkości powierzchni.