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Statistical analysis of the phytocoenose homogeneity. I. Distribution of the total species diversity and evenness indices as a homogeneity measure

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Abstract

Homogeneity of the *Leucobryo-Pinetum* phytocoenose was assessed on the grounds of distributions of the total species diversity ($\bar{H}$) and evenness *e* indices. In spite of the uniform physiognomy of the patch, caused by pure, even-aged, one-layered forest stand and apparent dominance of dwarf-shrubs in the ground layer, phytocoenose under study was heterogeneous. It resulted in the discrepancy between empirical distributions of $\bar{H}$ and *e*, and the normal distribution, as well as in the contagious spatial distributions of both indices.

Key words: phytocoenose homogenity, Shannon's index, evenness index

INTRODUCTION

Term "homogeneity" has been used by two oppose geobotanical schools: Anglo-American, associated with the concept of continuum of vegetation cover (Whittaker 1970a), and Middle-European, representing a discontinuum concept (Braun-Blanquet 1951). True enough, both schools postulate homogeneity of the area under study, but both criteria and indices of homogeneity have been based on different assumptions.

In the contemporary phytosociological papers term "homogeneity" has been considered from the statistical point of view, covering Kylin's (1926) criterion of homogeneity. Vegetation patch can be treated as homogenous when individuals of all species are dispersed at random, according to the appropriate model of theoretical distribution: Poisson's or binominal (Greig-

-Smith 1952, Moore 1953, David and Moore 1954, Kwiatkowska and Symonides 1980).

Kylin's criterion is related to spatial ecological arrangements, so it concerns type of the spatial distribution of the analysed measures. In practice, such distribution has not been studied due to random sampling or mischoise of homogeneity indices. The type of species dispersal depends on the sample area (quadrat) size which makes all the conclusions more difficult. The problem has been first mentioned by Skellam (1952) and further discussed in detail by Greig-Smith (1964) and Pielou (1969). Therefore, systematic sampling has become more common. It has enabled to use different size quadrats in the spatial analysis of one population.

In most papers phytocoenose homogeneity has been assessed on the grounds of the type of density distributions of one, or at most a few selected species characteristic of this phytocoenose type (Dahl and Hadač 1949). There are no works where a judgement on the patch homogeneity is based upon all its components, both qualitative and quantitative. Also papers are lacking which compare results of the homogeneity analysis of one patch based upon one index but taking into account various qualitative and quantitative measures. At last, only a few studies concern different indices, such as series of papers of French authors who have compared the results where different indices, with respect to qualitative measures, have been used (Calléja 1962, Dagnelie 1962, Gounot 1962, Gounot and Calléja 1962).

Series of papers presented here aim at: 1) comparison of results of the homogeneity studies for one model phytocoenose, with respect to quantitative and qualitative measures, and 2) comparison of results of the homogeneity studies when different indices are used. Presence of species and their standing biomass have been analysed at various quadrat size.

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 species spatial distribution with respect to quantitative and qualitative measures, 4) species number and mean standing biomass as a function of the quadrat size, 5) the type of distributions of the similarity and distance coefficients at various quadrat size, 6) distributions of the total species diversity and evenness indices as a function of the quadrat size.

All the results are to be presented in six successive papers in the order mentioned above. The last paper will also include summing-up discussion.

MATERIAL AND METHODS

Due to complexity of the homogeneity analysis investigations were carried-out in floristicly poor, 30-years-old pine monoculture in the *Leucobryo-*

-*Pinetum* Mat. (1962) 1973 habitat, the Kampinos Forest. Pure, even-aged and one-layered forest stand was composed of *Pinus sylvestris* L. Tree-layer coverage equaled 70%, that of the ground layer — 80%. In the latter dwarf-shrubs: *Vaccinium myrtillus* L., *V. vitis-idaea* L. *Calluna vulgaris* (L.) Salisb. dominated. The moss-lichen layer was composed mainly of *Entodon schreberi* (Willd.) Mnkm., but also *Dicranum undulatum* Ehrh., *D. scoparium* (L.) Hedw., *Pohlia nutans* (Schrebn) Lindb., *Polytrichum attenuatum* Menz., *Hylocomium splendens* (Hedw.) Br. eur., and *Cladonia* sp. div. occurred.

The study object was chosen on following premises: 1) pure, even-aged and one-layered forest stand due to which homogeneity analysis could be restricted only to the ground layer; 2) small number of elements (plant populations) and simple spatial relationships between them; 3) strong limitation of one of the source of ground-layer variability — changes in insolation which occur otherwise when forest stand is more complex; 4) age of the forest stand and concordance of tree planting with the habitat.

In the 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) in each quadrat all species were recorded. Next, above-ground parts of all vascular plants were clipped, clippings were segregated into species and their air-dry biomass was assessed to an accuracy of 0.01 g. The data were arranged in plans of species occurrence and cartogramms of their biomass in the successive quadrats. They served as basic data in the statistical analysis of the phytocoenose homogeneity. The same homogeneity criterion — model of the random distribution of each measure showing the good fit with Kylin's (1926) random distribution was used both in the analysis of qualitative and quantitative characters.

In this paper, data were elaborated as: 1) to design empirical frequency distributions of both total ground-layer biomass and those of individual species, 2) to make charts of the total ground-layer biomass diversification and those of individual species, 3) to calculate coefficients of importance of individual species in the whole phytocoenose and in the successive quadrats, i.e. ratio of their biomass to the total biomass, respectively for the whole study area and for successive quadrats. Coefficients of importance formed the grounds for a calculation of the total species diversity — $\bar{H}$ (Whittaker 1977) and evenness — e (Pielou 1966a) indices, in a scale of the whole study area and of individual quadrat, according to the formulae:

$$\bar{H} = -\sum\left(\frac{n_i}{N}\right)\ln\left(\frac{n_i}{N}\right) \quad \text{and} \quad e = \frac{\bar{H}}{\ln S},$$

where: n_i — coefficient of importance of individual species, N — total of all importance coefficients, S — number of species.

Spatial variability of the values of total species diversity and evenness indices was ilustrated in the charts. The fact, whether frequency distributions of $\bar{H}$ and e fitted normal distribution was taken as the homogeneity criterion. It was verified with Chi^2 test of goodness of fit, $\alpha = 0.05$.

In calculations of the total species diversity and evenness indices natural logarithms were used (cf. Odum 1982).

RESULTS

SPECIES OCCURRENCE, THEIR STANDING BIOMASS AND ITS SPATIAL DIVERSIFICATION

In the study area ground layer was composed of 21 species of plants: 3 dwarf-shrubs, 10 perennials and 8 shrubs and trees represented by seedlings and individuals of the early juvenile phases (Table 1).

Ground-layer physiognomy was governed by dwarf-shrubs: *Vaccinium myrtillus*, *V. vitis-idaea* and *Calluna vulgaris*. Their frequency, coverage and, above all, biomass were higher than those of remaining species; e.g. they contributed to the total biomass of ground layer 92.5%. Both red whortleberry and bilberry played the important role due to their high and almost identical (88-89%) frequency. However, bilberry was an

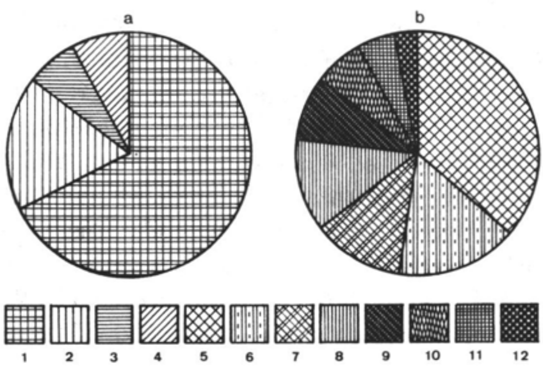

Fig. 1. Quantitative structure of the ground-layer dominants in the study area (512 m^2). a — total biomass of the ground layer, b — biomass of the ground layer with the exception of dwarf-shrubs. 1 — *Vaccinium myrtillus*, 2 — *V. vitis-idaea*, 3 — *Calluna vulgaris*, 4 — herbs and seedlings of shrubs and trees together, 5 — *Molinia coerulea*, 6 — *Sorbus aucuparia*, 7 — *Quercus robur*, 8 — *Melampyrum pratense*, 9 — *Pinus sylvestris*, 10 — *Luzula pilosa*, 11 — *Frangula alnus*, 12 — perennials and seedlings of the remaining tree and shrub species

Table 1

Description of the ground layer in the study area (512 m^2)

Species	Frequency, %	Abundance and grouping	Biomass, g	Coefficient of importance
Vaccinium myrtillus L.	88	4.4	13 168.6	0.67
Vaccinium vitis-idaea L.	89	2.1	3 531.5	0.18
Calluna vulgaris (L.) Salisb.	39	2.2	1 404.1	0.07
Molinia coerulea (L.) Moench	20	1.3	561.0	0.03
Sorbus aucuparia L.	3	+	228.9	0.01
Quercus robur L.	18	1.1	179.3	0.009
Melampyrum pratense L.	48	2.3	176.7	0.009
Pinus sylvestris L.	53	1.1	116.4	0.006
Luzula pilosa (L.) Willd.	4	+.2	104.6	0.005
Frangula alnus Mill.	7	+	69.9	0.004
Rubus saxatilis L.	1	+	13.1	0.0007
Festuca ovina L.	0.8	+.2	11.1	0.0006
Populus tremula L.	0.8	+	5.8	0.0003
Betula pubescens Ehrh.	1	r	2.8	0.0002
Potentilla erecta (L.) Hampe	0.2	r	1.8	0.0001
Betula pendula Roth.	0.4	+	0.4	0.00002
Corylus avellana L.	0.2	r	0.3	0.00002
Calamagrostis arundinacea (L.) Roth	0.2	r	0.2	0.00001
Rumex acetosella L.	0.6	r	0.2	0.00001
Deschampsia caespitosa (L.) P.B.	0.2	r	0.1	0.000005
Monotropa hypopitys L.	0.2	r	0.1	0.000005

* according to Braun-Blanquet's (1951) scale

absolute dominant as it covered more than a half of the area and contributed 67.3% to the total biomass of ground layer (Fig. 1).

In the phytocoenose under study most species (67%) had got low frequency, cover and biomass. Occasional species with frequency n.e. 1% and minimum contribution to the total biomass of ground layer, represented by a few individuals, were numerous (Table 1).

Among the last four species *Pinus sylvestris* was the only one which attained high frequency, *Melampyrum pratense* — high cover and *Molinia coerulea* — high biomass (Table 1).

Standing biomass of individual species and that of the whole ground layer were very variable within the area under study. At the quadrat of 1 m^2 frequency distributions of biomass were positively skewed (asymmetric), independent of a species (Fig. 2). It indicates that: 1) under the whole area scale the highest probability of biomass occurrence is characteristic of the lowest values class, and 2) quadrats with the relatively high

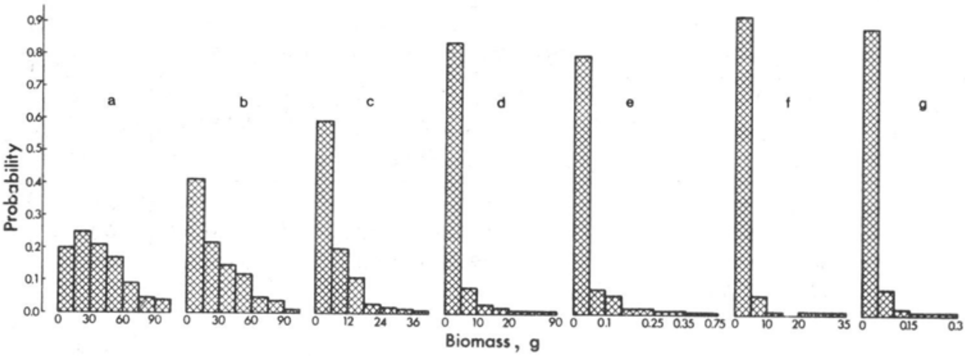

Fig. 2. Frequency distribution of the total ground-layer biomass and biomasses of individual species on the study area (512 m^2). a — total biomass of the ground layer, b — *Vaccinium myrtillus*, c — *V. vitis-idaea*, d — *Calluna vulgaris*, e — *Melampyrum pratense*, f — *Molinia coerulea*, g — *Pinus sylvestris*

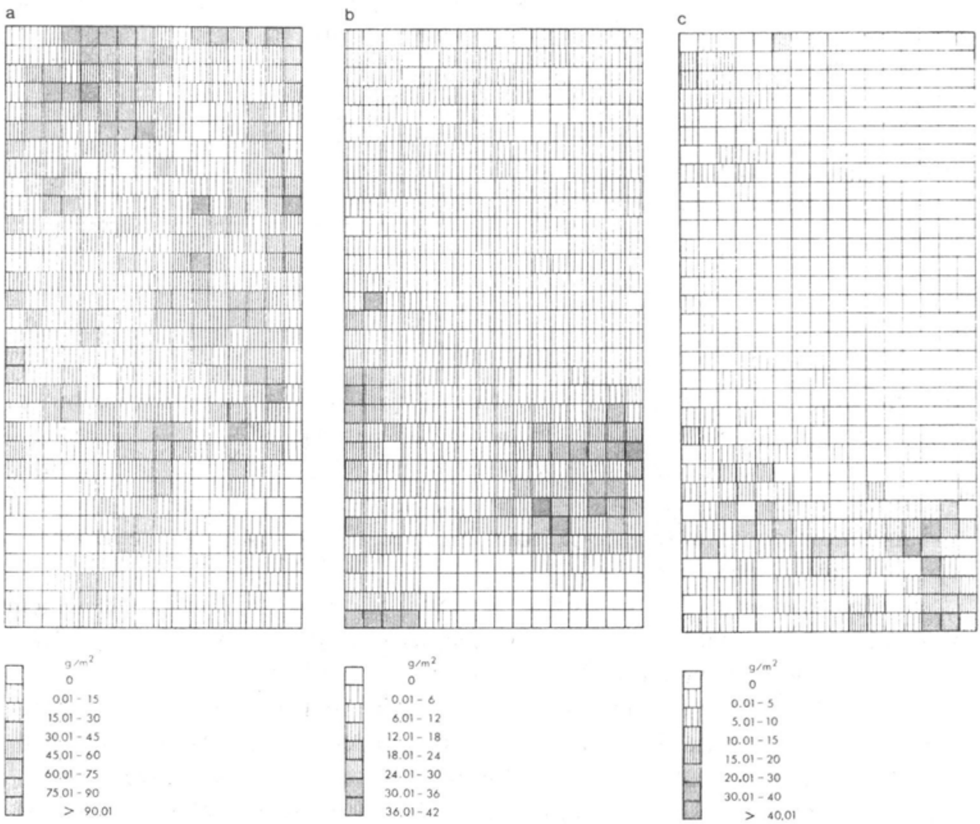

Fig. 3. Spatial variability of the dwarf-shrub biomass. a — *Vaccinium myrtillus*, b — *V. vitis-idaea*, c — *Calluna vulgaris*

standing biomass are very few; their total area does not exceed 5% of the whole grid.

Asymmetric (positively-skewed) was also frequency distribution of the whole ground-layer biomass. It differed significantly from the normal distribution. However, in this case differences in probability of falling of biomass values in the extreme frequency classes were not so high (Fig. 2).

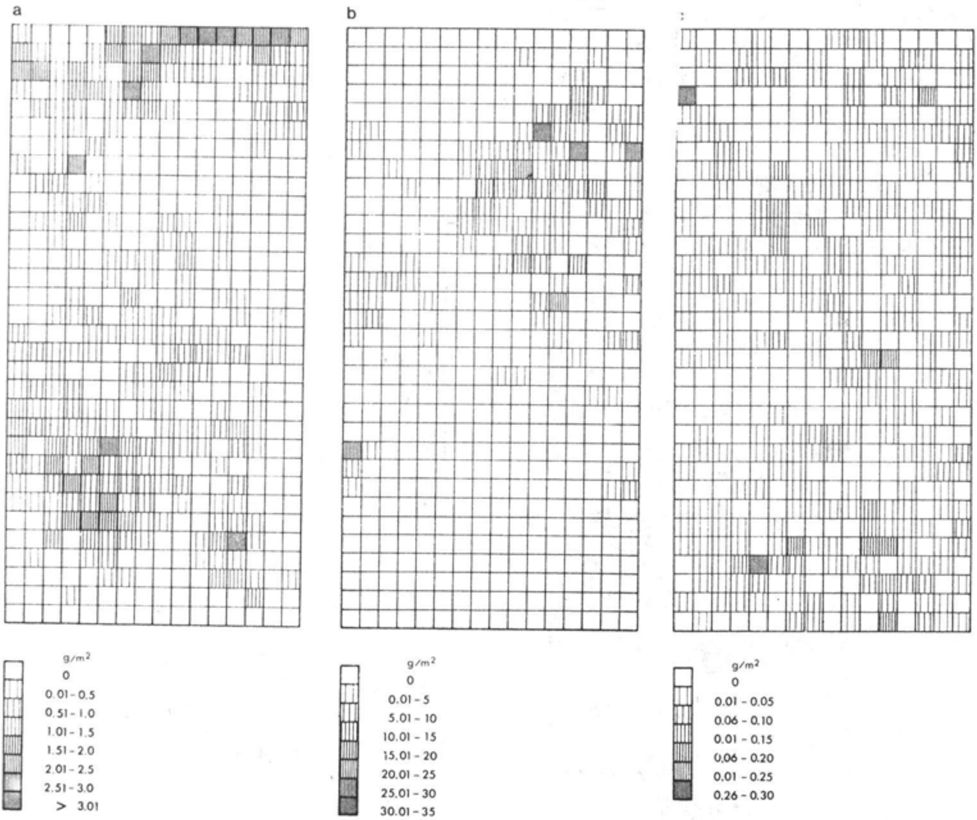

Fig. 4. Spatial variability of the biomass of *Melampyrum pratense* (a), *Molinia coerulea* (b) and *Pinus sylvestris* (c)

Probability of falling of standing biomass values in a particular class differed within the grid. It depended on the spatial arrangement of quadrats with different values of the analysed measure. Exemplary charts of the spatial dispersal of standing biomass of few dominants have indicated that this dispersal is of the mosaic type. Patches with high values neighboured on those with low, or nearly null values. Size, number and the arrangement of these patches were different and depended on a species (Figs. 3 and 4).

Chart comparison has indicated that aggregations with the high standing biomass of each analysed species, as a rule, did not overlap in space. This was the most clear in dwarf-shrubs, *Vaccinium myrtillus* and *Calluna vulgaris* (Figs. 3a, b).

In *V. myrtillus*, although patches with high biomass were of different size (2 m^2-20 m^2) and located in different parts of the grid, their biggest aggregation was in its top part. Whereas aggregations of other two dwarf-shrubs, less intensive and surface-smaller, were located at the grid bottom. Moreover, the "densest" *Calluna vulgaris* patches did not overlap similar *V. vitis-idaea* patches (Figs. 3b, c).

In other species aggregations with high and mean biomass values

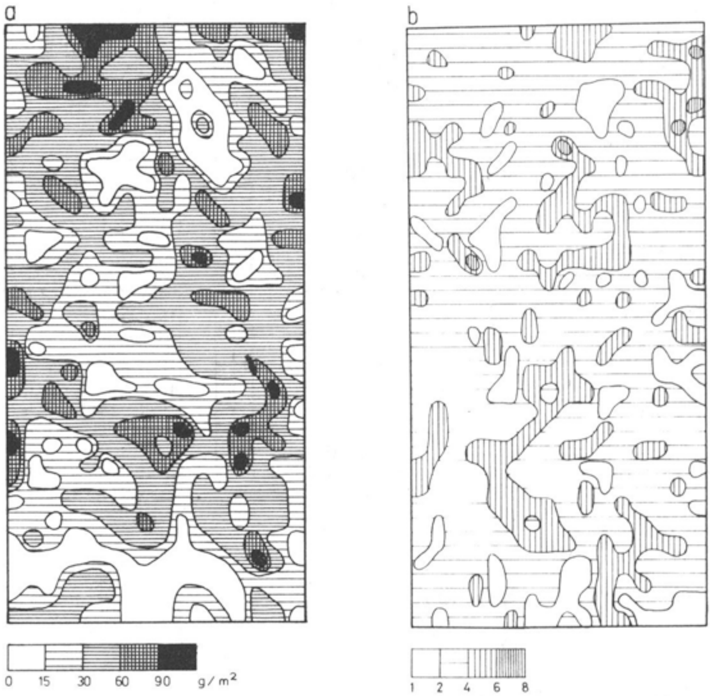

Fig. 5. Spatial variability of the ground-layer biomass (a) and species number (b)

were rare, small and highly scattered within biochore. They excluded each other in space, e.g. *Molinia coerulea, Melampyrum pratense* and *Pinus sylvestris* (Figs. 4a, b, c).

Characteristic, typically mosaic dispersal of the total biomass of ground layer is the effect of spatial dispersal of biomass of its components, especially dominants (Fig. 5). Quadrats with the similar, higher value were arranged in patches (10-20 m^2) dispersed unregularly all over the grid. Lack of spatial correlation between the standing biomass of ground layer and the species number is also worth noting (Fig. 5). The latter is relatively stable as it ranges from 1 to $7 \cdot 1m^{-2}$. Usually only 4 species of vascular plants occurred in one quadrat.

FREQUENCY DISTRIBUTION AND SPATIAL VARIABILITY OF THE TOTAL SPECIES DIVERSITY AND EVENNESS INDICES

From Table 1 it may be inferred that the phytocoenose under study is characterized by dominance structure, typical of the most of natural plant communities. Hence, it consists of small, clear group of dominants and of many species which contribute to the total biomass of ground layer only to small extent.

Both, low value of the total species diversity index ($\bar{H} = 1.09$) and low value of the evenness index ($e = 0.36$) indicate uneven division of the biomass among species of the analysed phytocoenose.

Detailed analysis of $\bar{H}$ and e values in the successive quadrats shows big differences in different parts of biochore. Shannon's index highly varies within the investigation area (standard deviation — S.D. = 0.3, coefficient of variation — V = 0.55) and ranges from 0 to 1.6. Mean value of the $\bar{H}$ index is 0.55, but probability of the occurrence of values higher than 0.85 ($\bar{x}$ + S.D.) and lower than 0.25 ($\bar{x}$ − S.D.) is higher than it can be expected from the normal distribution (Fig. 6a).

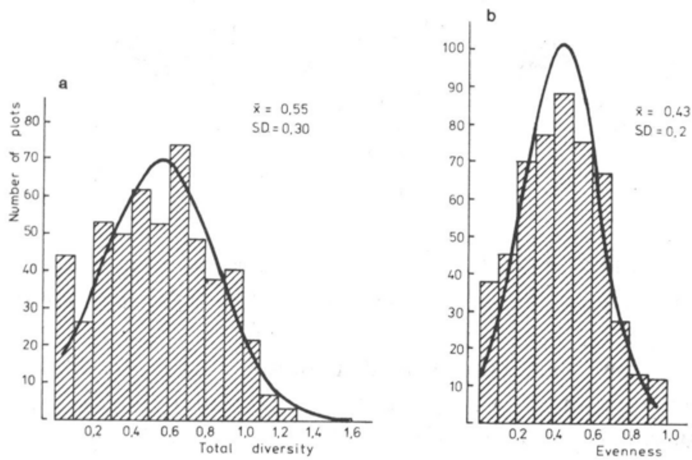

Fig. 6. Frequency distribution of the total species diversity (a) and evenness (b) indices

The evenness index e covers the whole range of its values, but is less variable (S.D. = 0.2, V = 0.47). Similarly to the Shannon's index probability of the occurrence of e values higher than 0.63 ($\bar{x}$ + S.D.) and lower

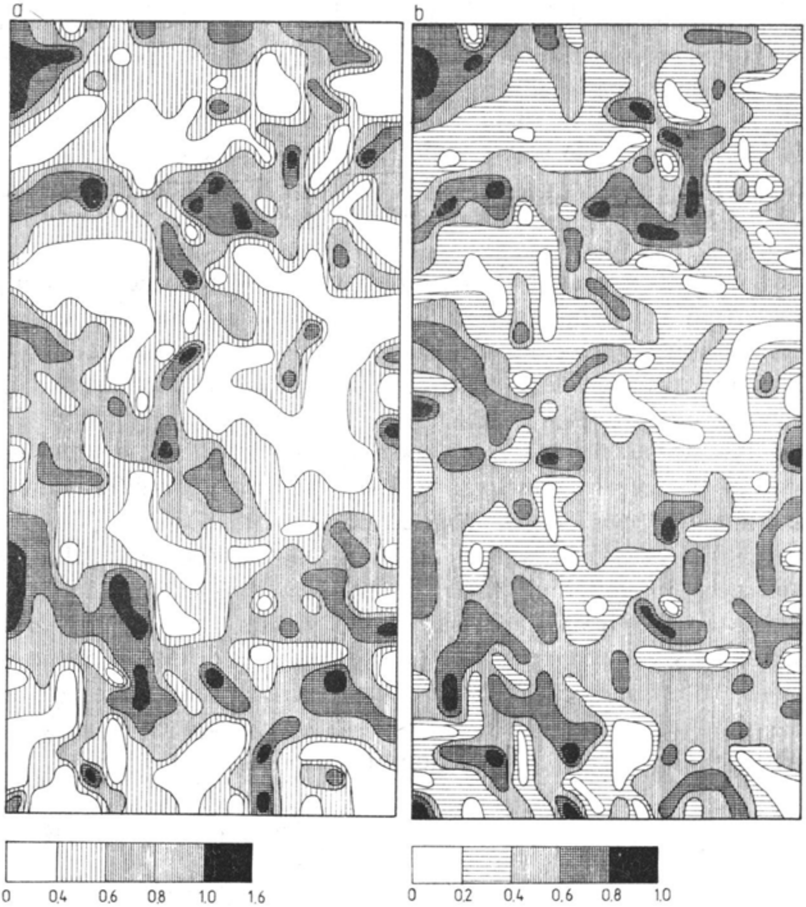

Fig. 7. Spatial variability of the values of the total species diversity (a) and evenness (b) indices

than 0.23 ($\bar{x}-$S.D.) is high due to the more numerous quadrats with high and low values than it can be derived from the normal distribution (Fig. 6b).

The data show that empirical distributions of both indices do not fit the normal distribution. Probability of the null hypothesis of goodness of fit is smaller than 0.001. Chi^2 values, for the $\bar{H}$ index — 55.3 and for the e index — 41.4, indicate nonrandom distribution of both indices.

Picture of the spatial diversification of the total diversity and evenness indices confirms results of the statistical analysis. It illustrates clearly contagious distribution of the values of both indices. In charts patches with high $\bar{H}$ and e values are visible against the background where species diversity and evenness are low (Figs. 7a, b). Relatively good correlation between patches with high and low $\bar{H}$ values and those with high and low e values results, above all, from small variation of the species number in the investigation area (cf. Fig. 5b).

DISCUSSION

Choice of the patch of *Leucobryo-Pinetum* phytocoenose has been governed by the uniform physiognomy of ground layer. Regular dispersal (due to the tree planting) of even-aged forest stand has guaranteed even better unification of microclimatic and edaphic conditions. High physiognomic uniformity of the patch is caused mainly by the high frequency of dominant dwarf--shrubs. However detailed analysis of the spatial standing biomass diversification has showed that positively skewed frequency biomass distributions, which do not fit the normal distribution, are characteristic of all species.

According to the assumed criterion of goodness of fit of empirical and theoretical distributions, all analysed species are dispersed non-randomly. Therefore, the phytocoenose under study is heterogenous with respect to analysed measures of its structure. Also frequency distribution of the total biomass of ground layer differs significantly from the normal distribution. Relatively weak asymmetry is caused by the spatial exclusion of the patches with high biomass values of different species. Therefore, aggregations with high biomass values are scattered all over the grid.

From the analysis of the occurrence of individual species and dispersal of their biomass it may be inferred that quadrats which are similar in their standing biomass and species composition may essentially differ in their dominance structure. The type of distributions of the total species diversity and evenness indices has been considered a measure of the diversification of inter-species relationships, namely, a measure of the phytocoenose homogeneity. In both cases assessment of the species importance in the patch and in successive quadrats has served as grounds for further calculations. It has been conducted with respect to the contribution of each species in the total biomass of ground layer in the grid and in 1 m^2 plots, respectively.

Diversity of the different ecological patterns, its measurement and criteria for assessment of the "importance" of individual populations have been often discussed (Pielou 1966a, b, c, Whittaker 1972, 1977, Peet 1974, 1975, Tepedino and Stanton 1981 and others). Shannon's index has been commonly considered as the best, as it takes into account species richness, as well as even division of environmental resources between populations of individual species (Whittaker 1970b). Its value depends on the importance of species located in the middle of the runs ordered with respect to values of importance coefficients (Whittaker 1965, 1977). However, it is worth to use also the evenness index (e) as it depends, contrary to $\bar{H}$, on the total number of species which compose analysed community (Whittaker 1977, Symonides 1985).

Diversity analysis, independent of the index used (Shannon's, evenness, species richness, dominance), can be based on various measures such as frequency, density, cover, standing biomass, or biomass production (cf. Whittaker 1965, 1977, Tepedino and Stanton 1981, Lindholm and Nummelin 1983, Vasander 1984). According to Whittaker (1965) the best measure of species importance in phytocoenose (also in biocoenose) is its production. However, due to the labour-consuming methods of the production assessment, standing biomass — an alternative measure — is more often used. It reflects species position in phytocoenose better than e.g. species number (Dickman 1968, Wihlm 1968, Tramer 1975, Symonides 1985). Whittaker (1965) has shown that shapes of curves of species importance coefficients based on the production and standing biomass are similar. It proves that standing biomass is an appropriate measure in the comparative studies on diversity of various ecological patterns.

The total diversity and evenness indices have not, so far, been used in the analysis of phytocoenose homogeneity, although their mathematical characteristics fully that justify. According to Bowman et al. (1970) and Hutcheson (1970) Shannon's index has the normal distribution. That enables to use common methods of the parametrical statistical analysis.

In the course of present studies it has been shown that for 1 m^2 empirical distributions of $\bar{H}$ and e values differ significantly from the normal distribution. Values of both indices also vary in space. There exist in the patch fragments with high diversity ($\bar{H} > 1.0$) and evenness ($e > 0.6$) values separated by fragments with low values ($\bar{H} < 0.2$, $e < 0.2$). Contagious dispersal and empirical distributions of $\bar{H}$ and e values differing from the normal distribution indicate phytocoenose heterogeneity.

The results have shown that both indices are very sensitive even to small changes in the phytocoenose structure. The wide range of both $\bar{H}$ and e values within one patch with highly uniform physiognomy is startling. Moreover, this range is comparable with the range of temporal changes in their values in the course of 20-years secondary succession in the *Peucedano-Pinetum* Mat. (1962) 1973 habitat (Symonides 1985). It may be concluded that both indices can be used in the analysis of changes in diversity of one phytocoenose in time and space, as well as, to the same extent, in the comparison of wholly different phytocoenoses (biocoenoses).

High difference between $\bar{H}$ values for 512 m^2 and 1 m^2, respectively 1.09 and 0.55, is worth noting. It suggests dependence of $\bar{H}$ values on the quadrat size and is contradictory to Odum's (1982) opinion. It will be discussed later in the series.

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Statystyczna analiza jednorodności fitocenozy. I. Rozkład wartości wskaźnika ogólnej różnorodności gatunkowej i równomierności jako miara homogeniczności

Streszczenie

Praca jest pierwszą z cyklu publikacji prezentującycych wyniki badań jednorodności modelowej fitocenozy boru świeżego w Puszczy Kampinoskiej. Celem badań było porównanie wyników analizy homogeniczności przeprowadzonej dla cech jakościowych i ilościowych z zastosowaniem różnych wskaźników. W każdym przypadku przyjęto to samo kryterium jednorodności — model losowego rozkładu badanej cechy, zgodny z kryterium losowego typu rozkładu Kylina (1926). W zbiorze materiału posłużono się tzw. kratą Greig-Smitha (1952) o powierzchni 512 m^2, podzieloną na jednometrowe poletka. Materiał wyjściowy w analizie stanowiły plany rozmieszczenia poszczególnych gatunków roślin naczyniowych runa na kolejnych poletkach oraz stan biomasy ich części nadziemnych. Przedmiotem rozważań niniejszej pracy jest ocena homogeniczności badanej fitocenozy, przeprowadzona na podstawie rozkładu wskaźników ogólnej różnorodności gatunkowej (Shannona) $\bar{H}$ i równomierności e (Pielou 1966a, Whittaker 1977). Jako miarę znaczenia populacji poszczególnych gatunków przyjęto udział ich biomasy w całkowitej biomasie runa (Whittaker 1965). Stwierdzono, że mimo fizjonomicznej jednorodności płatu spowodowanej jednowiekowym, jednowarstwowym i jednogatunkowym drzewostanem oraz wyraźną dominacją borówki czernicy w runie (tabela 1, rys. 1) badana fitocenoza jest niejednorodna. Świadczą o tym: 1) niezgodność empirycznego rozkładu wartości biomasy poszczególnych gatunków z rozkładem normalnym i skupiskowa struktura przestrzenna wartości biomasy (rys. 2-4) oraz 2) niezgodność empirycznego rozkładu wartości

wskaźnika ogólnej różnorodności gatunkowej i równomierności z rozkładem normalnym, a także skupiskowy rozkład przestrzenny obu wskaźników (rys. 6-7). Uzyskane wyniki dowiodły, że zarówno wskaźnik $\bar{H}$, jak też wskaźnik e mogą służyć do analizy różnorodności jednej fitocenozy w czasie i w przestrzeni w tym samym stopniu, co do porównania całkowicie różnych fitocenoz.