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A method of describing the development and state of a plant community

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Abstract

The Shannon-Wiener formula was modified in such a way as to include, apart from total diversity, also the total volume of the biotical resources of a plant community, i.e. the amount of accumulated biomass or total production. This was used to describe forest regeneration after clear-cutting. The state of each successional stage was evaluated by comparing its structure with the model of mature community belonging to plant association *sensu* Braun-Blanquet, which is a system with a structure corresponding to the equifinal state.

Key words: *diversity index, plant association, secondary succession, woodland clearings*

INTRODUCTION

The problem of describing how ecological systems develop is one of the most intriguing issues in ecology. In vegetation science, Shannon-Wiener's formula is commonly employed for describing the development of a community. This makes it possible to express the main characteristics of the structure, namely total diversity, comprising species richness and equitability. So far this formula was used most often to express communities' structure variability depending on successional time and on habitat conditions.

Odum (1969) generally accepted the growth of an ecological system's diversity as the criterion of its development. However, studies on succession by Shafi and Yarranton (1973), Bazzaz (1975), Whittaker (1977), Bormann and Likens (1979) and Wilkoń-Michalska et al. (1980) indicated that quite often in the process of community development there is either no permanent growth of diversity as calculated by Shannon-Wiener's formula, or, as proven by Morrison and Yarranton (1973), in the system of permanent growth of total diversity, the differences in this parameter for individual stages are negligible. This results from the fact that the Shannon -Wiener formula takes into account only the number of species and quantitative relations between species without regard of the real volume of an entire system and each of its individual elements, expressed by an objective measure, whether as accumulated or produced biomass.

This leads to the same diversity index being obtained for communities which have the same number of species and similar structure although being diametrically different in biomass or production. For this reason a more advanced community of higher biomass or production can get a lower grade than a younger community. For the same reasons the values of total diversity cannot be used in the comparison of communities belonging to different associations.

It seems sensible in this situation to supplement the Shannon-Wiener formula to take into account the size of total biomass or production, which is called the biotical resources of plant community in this paper. Hannon (1976) counts biomass growth as one of the main indicators of the development of ecological systems. Biomass is also an idicator of the congruence of plant community structure with its habitat.

This paper presents modifications of the Shannon-Wiener formula including the biotical resources of community in the calculations. The aim of the work is to prove that this formula with suggested modifications better express structural changes of community during its development than species diversity calculated according to standard method. This was displayed by comparison structural differentiation of communities being consecutive stages of secondary succession at the same habitats described with the use of both methods.

METHOD

The growth or loss of the biotical resources of a plant community in its development can expressed by comparison of the resources of the examined community B_j at consecutive development phases $j = 1, 2, \ldots, m$ with constant value B_m characteristic of the mature community from the examined successional series. The value B_j can be established by direct measurements of the biomass or the production of particular components of the community or be only roughly estimated by means of quantitative data, the cover-abundance value according to the formula:

$$B_j = \sum_{i=1}^{s} b_i = \sum_{i=1}^{s} C_i D_i, \tag{1}$$

where b_i stands for biotical resources of i-th species ($i = 1, 2, \ldots, s$), s is the number of species, C_i is the cover-abundance value, and D_i is the factor expressing the role of i-th species in the examined community on the basis of the group to which the species belongs: trees, shrubs, herbs, bryophytes or lichens.

The standard value of B_m which can be obtained for mature communities belonging to a definite association can be established by means of analysis of an arbitrarily assorted collection of phytosociological releves ($l = 1, 2, \ldots, n$), applying the formula:

$$B_m = \frac{\sum_{l=1}^{n} \sum_{i=1}^{s} C_i D_i}{n}, \tag{2}$$

where n is the number of releves.

After the application of Shannon-Wiener's formula for system diversity,

$$H = -\sum_{i=1}^{s} p_i \log p_i, \tag{3}$$

where $p_i = b_i/B_j$ denotes the proportion of i-th species in the total biomass or production, the real values of the biotical resources of the community are deduced when the formula includes an additional component, the quotient:

$$p_k = \frac{2B_m - B_j}{2B_m} \tag{4}$$

and the value p_i calculated according to

$$p_i = \frac{b_i}{2B_m}. \tag{5}$$

After application of equations (4) and (5), equation (3) assumes the form:

$$H = -\sum_{i=1}^{s} p_i \log p_i + p_k \log p_k. \tag{6}$$

The doubling of the B_m value results from the dependence of product $-p_i \log p_i$ on p_i and from the fact that for two components the sum $-\sum_{i=1}^{2} p_i \log p_i$ is greatest when $p_1 = p_2 = 0.5$. As a result of the processing growth of the biotical resources in the process of development of the community $p_k \rightarrow 0.5$ and $H \rightarrow \max$.

For comparisons of communities of different associations it is possible to use varying calculations according to formula (6), with value B_m for the association achieving the highest values of this parameter. The obtained values of H_M express structural differences concerning richness, equitability and biotical resources resulting from both the succession time and the habitat.

APPLICATION

THE STUDY AREA AND CONVERSION FACTORS USED FOR CALCULATIONS

The usefulness of the discussed method was practically proved in the Bory Tucholskie Forest, a region in North Poland, by the evaluation of the developmental phases of the forest after clear-cutting, on the habitats of the associations *Cladonio-Pinetum* and *Leucobryo-Pinetum*. There were plantations of *Pinus silvestris* with small participation of *Betula verrucosa*.

The structure of the examined communities was determined by the phytosociological releves method according to Braun-Blanquet and expressed by two numerical values calculated according to formulas (3) and (6), which were denoted as H_T and H_M, respectively. In the calculations, according to suggestions by van der Maarel (1979), the following numerical counterparts were used for the cover-abundance factors: r – 1, + – 2, 1 – 3, 2 – 5, 3 – 7, 4 – 8, 5 – 9. As D_i values were used the factors put forward by Kostrowicki (1972), who on the basis of many calculations and comparisons of production volumes of model species *Pinus silvestris*, *Juniperus communis* and *Deschampsia flexuosa* on the habitat of *Cladonio-Pinetum*, as described in works on forestry and ecology, suggested the following values of factors: 1000, 700, 500 for trees from layer a_1, a_2 and a_3, respectively, 100 for shrubs, 1 for herbs and seedlings, 0.1 for bryophytes and lichens. Those factors indicate the relative difference in the productivity of particular layers calculated for one species.

Values B_m for both associations were calculated from sets of phytosociological releves used by Matuszkiewicz and Matuszkiewicz (1973) for the classification of pine forest in Poland. In the case of the *Cladonio-Pinetum* association the set contained 365 releves from 21 phytosociological works. The number of releves and publications used for the calculation of B_m value for the *Leucobryo-Pinetum* association were 201 and 19, respectively. All releves were published between 1952 and 1970. The higher value B_m of the *Leucobryo-Pinetum* association was used in calculations of the H_M index and in comparison of the communities from various habitats. Logarithms to base 2 were used in calculations of H_T, H_m and H_M values.

RESULTS

The results of the calculations confirmed the fact that total diversity as calculated in the commonly applied way does not characterize the development of a plant community during secondary succession. It was found at the habitats of *Cladonio-Pinetum* and *Leucobryo-Pinetum*, in communities arranged in order of advancing age, that the diversity calculated for all species of community (H_T) is highest in the first year after cutting (Fig. 1). High total diversity of initial stages results from the occurrence of many species of the first succession phase in similar amounts. In older cultivations the predominance of some species, especially the pine trees, increases, while as a result of competition a number of early successional species disappear and so diversity decreases. Total diversity archieves the lowest values in the phase of the most intensive growth of the pine tree, i.e. in 30-40 year old stands. In the consecutive stages of development, a less closed canopy, the appearence of understory and the appearance of more numerous species in the herb layer, leads to higher total diversity.

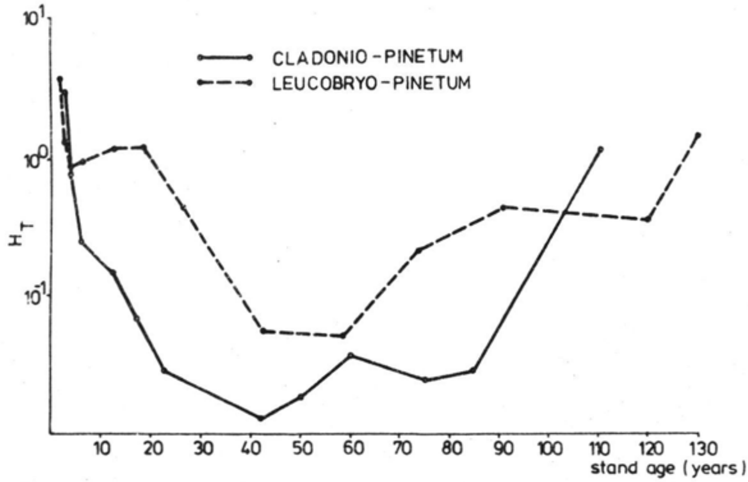

Fig. 1. Total diversity of a plant community (H_T) in consecutive years after clear-cutting

The suggested modifications well characterize the development of a plant community. An increase of the H_m index was observed for the above-described successional sequences (Fig. 2). Moreover, at consecutive successional stages the value of differences of this parameter are more distinct than the differences of total diversity.

Comparison of the structure and the biotical resources of communities in

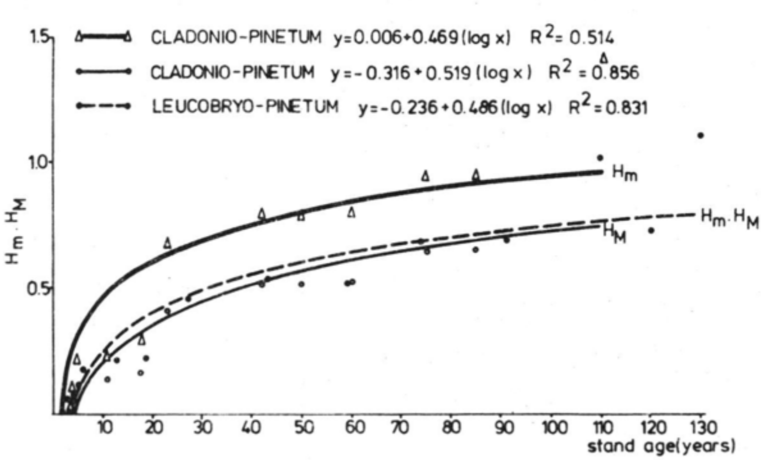

Fig. 2. Comparison of H_m and H_M indexes in two successive series

relation to the same value B_m makes it possible to make a better comparison of the observed objects. Communities of the *Leucobryo-Pinetum* habitat achieved higher H_M index values than communities of the *Cladonio-Pinetum* habitat, which is characterized by lower species diversity and lower biomass and production at a similar age (Fig. 2).

DISCUSSION

The discussed method permits quick comparison of the structure of forest communities in respect to age and habitat conditions. The rough-estimate way of evaluation of species abundance with the use of D_i factors makes the changes of values H_m and H_M stepwise in the analyzed successional series. It is yet to be proven whether the application of more exacting methods of evaluation of species abundance in smaller samples will cause their course to be softer.

The H_m and H_M values of a discrete community may be compared with the standard value for association distinguished according to the method of Braun-Blanquet. So standard values – reference points for comparison may be constructed on the basis of sets of phytosociological releves made by uniform method. For associations of *Cladonio-Pinetum* and *Leucobryo-Pinetum* in Poland such standard values of the index, calculated on the basis of releves with a species composition characteristic for these syntaxa and rich in species in each layer (i.e. overstory, understory, shrub and herb, and bryophytes and lichens), are 1.65 and 2.15, respectively. Comparison to the model of association makes it possible to evaluate the state of the examined community. It is assumed *a priori* that association of mature plant communities is a system in the equifinal state.

Numerical presentation of structures makes it also possible to show the state of communities occurring in an examined area in the form of maps and to express their state to non-professionals in phytosociology.

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Metoda opisywania rozwoju i określania stanu zbiorowiska roślinnego

Streszczenie

W badaniach ekologicznych prowadzonych w latach 60. i 70. dla określania struktury zbiorowisk roślinnych powszechnie używano wzoru Shannona-Wienera. Analiza przedstawionych w literaturze zastosowań tego wzoru do opisu zmian struktury zbiorowisk w sukcesji pierwotnej i wtórnej wskazuje, że w dotychczasowej postaci nie może być on wykorzystany do wyrażania stopnia rozwoju zbiorowiska. Przyczyną jest brak korelacji między wartościami wskaźnika różnorodności gatunkowej i czasem rozwoju zbiorowiska. Dokonano modyfikacji wzoru, polegającej na uwzględnianiu w obliczeniach, oprócz liczby gatunków i relacji ilościowych między gatunkami, biomasy roślinnej zakumulowanej w zbiorowisku lub jego całkowitej produkcji, czyli zasobów biotycznych fitocenozy. Matematycznie uzyskano to głównie poprzez wprowadzenie do wzoru $H = -\sum_{i=1}^{s} p_i \log p_i$, dodatkowego składnika, podwojonej różnicy między aktualnymi zasobami biotycznymi fitocenozy, a wielkością tego parametru w stadium końcowym, dzielonej przez zasoby biotyczne zbiorowiska dojrzałego. Wykorzystano tu przebieg zależności $p_i \log p_i$ od p_i.

Zmodyfikowany sposób obliczeń zastosowano do opisu i porównań przebiegu regeneracji lasu po zrębie zupełnym na siedlisku boru suchego *Cladonio-Pinetum* i boru świeżego *Leucobryo-Pinetum* w Borach Tucholskich. Dla obu serii sukcesyjnych uzyskano ciągły wzrost wartości wskaźników różnorodności gatunkowej i zasobności biotycznej.

Przedstawiona metoda pozwala określić stan badanych zbiorowisk na podstawie porównania ich struktury, wyrażonej za pomocą zmodyfikowanego wskaźnika *H*, ze strukturą fitocenoz modelowych, należących do odpowiedniego zespołu roślinnego. Zakłada się tu *a priori*, że trwały zespół roślinny jest systemem, który osiągnął stan ekwifinalny. Jego strukturze odpowiada optymalne funkcjonowanie.

Strukturę zbiorowisk roślinnych badanego terenu wyrażoną w postaci liczb można przedstawić metodą kartograficzną. Ułatwia to prezentowanie stanu fitocenoz osobom nie związanym profesjonalnie z fitosocjologią.