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STUDIES ON THE VEGETATION DYNAMICS OF NANOCYPERION COMMUNITIES IV. DIVERSITY AND SUCCESSION

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Abstract

The paper deals with studies on the temporal and spatial changes in the diversity and evenness of the vegetation of the Nanocyperion zone found on the river-bed. A relatively lower diversity is characteristic of the more or less typical associations developing during the course of the succession, while the stands representing transitional cenoses between the associations are characterized by a higher diversity. The increase in diversity of the vegetation on the lower reliefs developing in the direction of the Agropyro-Rumicion is accompanied by an increase in the value of evenness.

Introduction

Depending on relief, two kinds of courses are distinguishable for the succession of the lower, Nanocyperion zones of the river-bed. This is supported by a comparison between the ordination and classification of the stands and the characteristic indicator values (BAGI 1985), as well as by a cenosystematic evaluation of the ordination and classification of the species (BAGI—KÖRMÖCZI 1986). This notion is verified by the results obtained with the "degree of succession" index of Numata, which have also provided the possibility for the more precise cenosystematic categorization of this part of the river-bed (BAGI 1987).

The spatial segregation of the succession types is determined by the localization of the relief and the differences developing on account of this: in the development of the vegetation at a higher relief compared to the lower relief, decisive factors are the longer vegetation period, the drying out of the soil to a greater extent, the accumulation of organic debris, the direct connection with the higher reliefs of the flood-plain. The lower reliefs adjacent to the river-water are characterized by an extremely short vegetation period and constant favourable soil humidity. Owing to these differing abiotic circumstances, the processes of succession take up divergent courses. The vegetation in the lower zone develops in the direction of the Agrorpyo-Rumicion, that in the upper zone towards the Bidentetea (Bidention tripartitae). (Further details are contained in Parts I—III of this study.) The divergent development is indicated by differences in the changes of the degree of succession. The relationship between degree of succession and diversity is one of the most studied fields of succession research.

The connection between succession and diversity in the succession series is well-known (McNAUGHTON 1968, MORRISON—YARRANTON 1973, PRÉCSÉNYI 1981). There are also sufficient published data on the diversity changes accompanying secondary succession. There are significant studies pertaining to plough lands no longer under cultivation (NICHOLSON—MONK 1974, BAZZAZ 1975) or to other strongly perturbed systems (SHAFI—YARRANTON 1973, LEHTONEN—YLI—RECOLA 1979, PAPP 1984). However, only a few publications report on studies regarding the diversity changes of objects where the life-span of the components (individuals) and the duration of environmental fluctuations are of an almost similar length. The paper of PRÉCSÉNYI—DÖMÖTÖR—CZIMBER (1984) can rather be regarded as an exceptional example. From this point of view, the analysis of the diversity changes in the case of the succession types initiating from the Nanocyperion associations bridges the gap. It is also worthwhile dealing with the changes in diversity of these associations because the diversity may be connected with several other (structural) properties of the system. A large number of data are available, pro and con, regarding propositions on the different parameters (e.g. stability) and the relationship of diversity (MCNAUGHTON 1968, HAIRSTON et *al.* 1968).

The relatively (seemingly) easy practicability of the diversity indices is the reason why these are given preference over traditional statistical methods (EBERHARDT 1969), for instance, or the topological models (POSTON—STEWART 1978, SHAFFER 1985).

Materials and Methods

For estimating diversity, three diversity indices differing from each other in approach and possibility of demonstration, as well as their corresponding evenness values were used:

1. SIMPSON (1949) index

This expresses the probability by means of which an individual can be chosen from one and the same species of the studied specimen by two independent samplings.

For the specimen of a finite element-number we have:

$$H^*_{SI} = \frac{\sum_{i=1}^{s} n_i(n_i-1)}{N(N-1)}$$

where S is the number of species, n_i is the number of individuals belonging to the i species, N is the total number of individuals (designations are the same in the rest of the indices, too). A more frequently used variant is (PIELOU 1969):

$$H_{SI} = 1 - H^*_{SI}.$$

However, this must be compared with the publication of HILL (1973).

2. SHANNON—WEAVER (1949) index

There is a degree of uncertainty whereby an individual of a pre-determined species may be chosen at random from the studied specimen (PIELOU 1966). Its cybernetic interpretation and deduction can be found in the work of BRILLOUIN (1951) p. 341. The Shannon—Weaver index may be written down in the following way:

$$H_S = k \sum_{i=1}^{S} p_i \log p_i$$

where k is an optional constant, in expedience, and hereinafter $k=-1$, $p_i=n_i/N$. Based on the general equation of FAGER (1972): $E = H - H_{min}/H_{max} - H_{min}$, the evenness of the SHANNON—WEAVER index is:

$$E_S = \frac{-\sum_{i=1}^{S} p_i \log p_i - \log N - \frac{N-(S+1)}{N} \log [N-(S+1)]}{\log S - \log N - \frac{N-(S+1)}{N} \log [N-(S+1)]}$$

which, in practice, correspond to the $J=H_s/\log S$ formula (PIELOU 1969), where $\log S=H_{max}$. The evenness calculated in such a manner is independent of the species number (SHELDON 1969). The table of PRÉCSÉNYI (1981), usable for calculating the evenness of cenological tables comprising relative abundance-dominance data, was used in the calculations. The result of this ('E' in Table 1) almost agrees with the value of J and E_S. The decimal logarithm was used.

3. MCINTOSH (1967) index

$$H_M^* = \sqrt{\sum_{i=1}^{S} n_i^2}$$

This formula expresses the interpretation of the diversity as such an Euclidian-distance, which "can be regarded as the distance value of the sample from an area of bare ground with zero individuals" (MCINTOSH 1967). The generally used form of the index is:

$$H_M = \frac{N-\sqrt{\sum_{i=1}^{S} n_i^2}}{N-\sqrt{N}}$$

In this form its value falls between 0 and 1. Since, in the given case, the SIMPSON and MCINTOSH indices led to results identical with the SHANNON—WEAVER index, from the viewpoin of interpretability, the evenness values of these are not given in the paper.*

* According to DEJONG (1975), the evenness of the SIMPSON index based on the general equation of FAGER (1972) is:

$$E_{SI} = \frac{1-\frac{\sum_{i=1}^{S}(n_i(n_i-1))}{N(N-1)}-\frac{(S-1)(2N-S)}{N(N-1)}}{\frac{N(S-1)}{S(N-1)}-\frac{(S-1)(2N-S)}{N(N-1)}}$$

The evenness of the MCINTOSH index is:

$$E_M = \frac{\frac{N-\sqrt{\sum_{i=1}^{S} n_i^2}}{N-\sqrt{N}}-\frac{N-\sqrt{(S-1)+[N-(S-1)]^2}}{N-\sqrt{N}}}{\frac{N-\sqrt{\left(\frac{N}{S}\right)^2}}{N-\sqrt{N}}-\frac{N-\sqrt{(S-1)+[N-(S-1)]^2}}{N-\sqrt{N}}}$$

Among the diversity-indices, these three belong to the ones most frequently used. Their properties are analysed in several theoretical essays (WHITTAKER 1965, PIELOU 1969, HILL 1973, PEET 1974, DEJONG 1975, NOSEK 1976).

The dominance-diversity curves were applied in accordance with WHITTAKER (1965): the ordinates illustrate the logarithm of the relative dominance of species.

The description of the study area and the cenological table are found in the previous parts of the paper.

Results

Table 1 comprises the dominance-diversity values characteristic of the different relevés. From the viewpoint of interpretability, the three diversity-indices used led to similar results. This is also true with respect to their evenness. Therefore, only the results of the most frequently used SHANNON—WEAVER index are reported (Fig. 1).

The lower zones of the river-bed are generally characterized by high diversity (cf. the data of PRÉCSÉNYI (1981) concerning the sandy succession series). A particu-

Table 1. *Diversity-data of the relevés*

Serial no.	I*	I	H_S	J	E	H_{SI}	H_M
1.	17	14	0.8377	0.7309	0.7223	0.7735	0.5734
2.	30	17	1.0059	0.8175	0.8112	0.8786	0.7102
3.	14	13	0.8887	0.7978	0.7912	0.8135	0.6210
4.	27	19	1.0912	0.8533	0.8489	0.9046	0.7521
5.	18	14	0.8728	0.7615	0.7539	0.8018	0.6066
6.	20	13	0.9180	0.8241	0.8184	0.8347	0.6482
7.	21	18	1.1112	0.8853	0.8818	0.9189	0.7752
8.	28	16	1.0535	0.8749	0.8711	0.8889	0.7262
9.	24	19	1.1504	0.8996	0.8966	0.9220	0.7830
10.	31	20	1.1817	0.9083	0.9056	0.9349	0.8082
11.	16	10	0.6280	0.6280	0.6149	0.6305	0.4302
12.	21	17	1.0751	0.8738	0.8699	0.9067	0.7556

I* — The number of species in the relevé
I — The number of species in the relevé with an estimate coverage of 1 % or more.

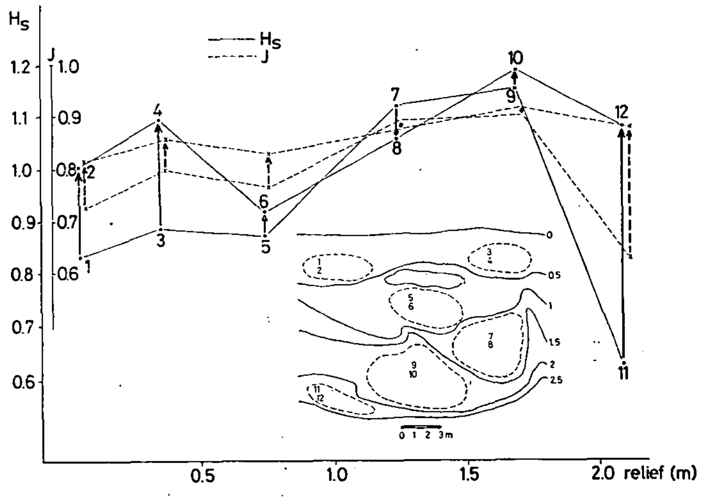

Fig. 1. Temporal and spatial changes of diversity (H_S) and evenness (J) in the studied area. The numbers indicate the serial number of the relevé, in accordance with the cenological table found in Part III of this study series. The earlier and later relevés are interlinked by arrows. The boundary of the stands is indicated by a dotted line on the complementary contour map.

larly high diversity is manifest in the case of the relevés cenologically belonging to a transitional group, while the lowest is detectable in the case of the typical *Cypero-Juncetum* association (11). (The serial number of the relevé, according to Part III of this study, is found in parentheses.) Higher diversity is manifest in the relevés containing a transition between the *Cypero-Juncetum* and the *Dichostylidi-Gnaphalietum* Nanocyperion associations (1, 3, 5). A relatively low diversity can be found in the relevé mentioned as *Rorippo-Agrostietum stoloniferae cyperetosum fusci*, characterized by a high degree of succession value (6). A rather high diversity value is characteristic of the relevés representing transitions between association-groups, Thus, from the earlier relevés, we have the Nanocyperion — Chenopodion fluviatile (7, 9) and, from the later relevés, the Nanocyperion — Agropyro-Rumicion (2, 4), the Chenopodion fluviatile — Bidention (8), Chenopodion fluviatile — Agropyro-Rumicion (10), and Bidention — Agropyro-Rumicion (12).

The diversity values generally show an increase with the advance of the vegetation period. The circumstances of this are connected with the increase in sepcies number only to a slight degree. The main cause of the increase in the relevés is that the species coverage becomes more even. This is shown by the rise in evenness values. The increase in evenness is an evident consequence of the fact that the species of slower growth catch up with the species which have reached an outstanding dominance at the beginning of the vegetation period, owing to their faster growth-rate and stronger colonization capability. In relevés 7 and 8 the decrease of the high diversity value indicates the degradation of the community. The Nanocyperion species die out from beside the *Polygonum lapathifolium*. At the same time, the rest of the Chenopodion fluviatile and Agropyro-Rumicion species do not appear. The process can be traced back to pedological reasons, as well as to the economy of water supply.

As regards relief, the diversity values of the higher and lower areas are well distinguishable from the diversity values of the higher reliefs at the time of the earlier recording. The average diversity of the lower relief (1, 3, 5) is 0.8664, while that of the relevés at higher reliefs (with the exception of relevé 11) is 1.1308. (The low diversity found in the relevé 11 is caused by the high covering quota of the *Cyperus fuscus*, the reasons for which are discussed in Part III of this study.) The lower diversity of the lower reliefs can be explained by the remarkable covering quota of the Nanocyperion species. At the higher reliefs the vegetation had enough time for the dispersal of the appearing Bidentetea species to ensure a "more even" vegetation. By the later point in time this difference between the two reliefs decreases, the primary cause of which is the greater increase in the evenness of the vegetation in the lower zones. An 8.2% increase is manifest in the evenness in the lower zones, while practically no changes are visible in the upper zones (except in relevé 11). The comparatively great evenness increase in case of relevés 5 and 6 was not followed by an essential increase in diversity. Meanwhile, a decrease was observable in the number of the reckoned species (the coverage of which reached 1%).

Succession end diversity

Despite the facts that diversity depends on the size (Fekete—Kovács 1978), and shape of stand (Nosek 1976), the diversity calculations were carried out on the basis of single samples — also characteristic of zone and cenosis, according to the experiences of the author —, certain general conclusions serving as a starting-point for further studies could be drawn. (The area and shape of the stands can be defined by Fig. 1.)

Making use of the parallelism within identical zones of the temporal and spatial processes, the relationship between the diversity values and the succession stages of the relevés can be demonstrated in the following manner. The Nanocyperion associations of the lower zone (1, 3, 5) ($\overline{H}_S$=0.8664) form transitional cenoses (2, 4) ($\overline{H}_S$= =1.0486) with the character species of the Chenopodion fluviatile *(Chenopodietum rubri)*, and then the Agropyro-Rumicion association groups. At the end of the process, the developing association is the Agropyro-Rumicion (6) (H_S=0.9180). During the course of the outlined process there is first an increase and then a decrease in the diversity.

In the upper zone the convergence of the processes is more perceivable. Here the appearence of the species belonging to the Nanocyperion associations is followed by the Chenopodium fluviatile — in the beginning, the *Chenopodietum rubri* (7) ($H_S=1.1112$), and later the *Echinochloo-Polygonetum* species (9) ($H_S=1.1504$). In certain areas a typical Chenopodion fluviatile association, the *Echinochloo-Polygonetum* is formed (8) ($H_S=1.0535$), and a slight decrease in diversity is observable. In other areas Bidention tripartitae and Plantaginetea species appear, and a further increase in diversity is manifest (10,12) ($\bar{H}_S=1.1284$).

In the course of a vegetation period, the rapid vegetation-transformation characteristic of the vegetation of lower zones of the river-bed results in the development of several members of the succession series. Meanwhile, the diversity, in the case of the relevés standing closer to the typical associations, is lower, being higher in the case of the transitions.

The changes in diversity of the river-bed vegetation necessitate further studies. This demand is supported by the illustrated dominance-diversity curves (WHITTAKER 1965) (Fig. 2). The curves assume various courses, and the most important types are

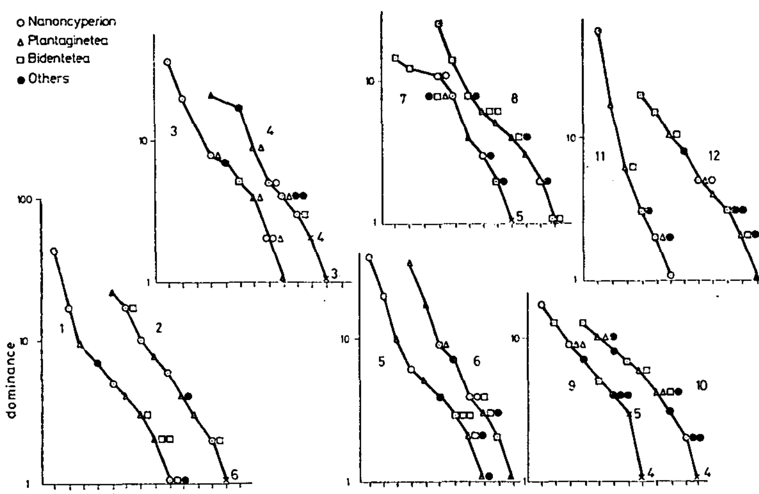

Fig. 2. The dominance-diversity curves of the relevés. The rank-order of the species according to dominance is illustrated on the abscissa, the logarithm of relative dominance on the ordinate. An asterisk indicates the dominance value to which 4 or more species belong in the relevés (the number of species is shown besides the asterisk). The numbers found near the curves, referring to the relevé, can be identified in the same manner as in Fig. 1.

also represented, as mentioned by WHITTAKER. The curves of the earlier and later relevés show a complete rearrangement, as regards species. The changes taking place during the rearrangement require further investigations, as does the demonstration of the differences between the species of the curve with higher serial numbers.

Closing remarks

The main purpose of this study series — apart from a description of the concrete recent results — was to call attention to the possibilities revealed in studying the lower zones of the river-bed. Undoubtedly, these studies may have prime significance in succession research. Though the principle object of succession research is the forest (mainly owing to the reliable estimation of the age of the individuals), through the rapid changes taking place in its vegetation, studies in the lower zone of the river-bed may provide an addition of useful information to our knowledge of the initial stages of succession and of the studies of the transitions from one association to another. The age of the individuals can be determined with exactness following a localization with fixed quadrates. The studies may lead to appreciable results within a few months, while investigations of a forest, with similar aims (if we disregard the possibilities deriving from the principle of timeliness) may require decades.

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Vegetációdinamikai vizsgálatok Nanocyperion jellegű növénytársulásokban IV. Diverzitás és szukcesszió

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Kivonat

A dolgozat a diverzitás és az evenness térbeli és időbeli változását vizsgálja a folyómeder Nanocyperion zónájának növényzetén. A szukcesszió során kialakuló többé-kevésbé tipikus társulásokat relatíve alacsonyabb, a társulások közötti átmeneti cönózisokat reprezentáló felvételeket magasabb diverzitás jellemzi. Az alacsonyabb, Agropyro-Rumicion irányba fejlődő térszínek növényzetének diverzitásnövekedését az evenness érték növekedése kíséri.

Ispitivanje dinamike vegetacije sa karakteristikama Nanocyperion zajednice IV. Diverzitet i sukcesija

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Abstrakt

Ovo delo istražuje prostorne i vremenske promene diverziteta i evenness kod vegetacione zone Nanocyperion u rečnom koritu. Prilikom sukcesije, visě ili manje, razvijaju se tipične zajednice sa relativno nižim diverzitetom, prelazni cenosis između zajednice je karakterisano sa višim diverzitetom. Razvitak prema nižem nivou prostora kao što je Agropyro-Rumicion, povećava se vrednost diverziteta sa evennessom.

Вегетационно-динамические исследования над сообществами растений типа Nanocyperion. Дивергенция и сукцессия

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Резюме

В работе исследованы изменения дивергенции и равномерности (evenness) в пространстве и во времени у растений зоны Nanocyperion русла реки. Типичные сообщества, возникшие в результате сукцессии, характеризуются относительно низкой, а переходные биоценозы — более высокой дивергенцией. Увеличение дивергенции растительности более низких уровней, приближающихся к Agropyro-Rumicion сопровождается ростом показателя равномерности (evenness).