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Diversity indices of double classification in the study of *Ichneumoninae (Hymenoptera, Ichneumonidae)* communities[1]

Abstract: Diversity indices of double classification (considering the species' assignment and place of catching) were employed for the analyses of *Ichneumoninae* communities of *Peucedano- and Leucobryo-Pinetum* in three regions of Poland, with four successional stages included. The obtained values of indices allow evaluation of structural changes of *Ichneumoninae* communities of Scots pines crown canopies, in the course of succession and they reveal the regional differences of the process' development. In the climax phase of succession the similar structural pattern of the community for the three regions of Poland was observed. The process of optimal *Ichneumoninae* community formation is connected with the rise-and-fall succession, with diversity and complexity growing in the earlier stages of the succession and then subject to slow decrease in the later stages. An assessment of 9 indices usability for analysing structural changes in the fauna associations has been completed. Out of them, particularly important for the studying the processes of mature community formation proved two indices: the mean niche width and the mean degree of habitats overlap.

Key words: diversity indices of double classification, complexity, community, *Ichneumoninae*, *Peucedano- and Leucobryo-Pinetum*, succession

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INTRODUCTION

The most frequently used measure of diversity in the faunistic study, has been the Shannon-Wiener index, coming down from the information theory.

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In faunistics, the index expresses the degree of uncertainty, considering the species assignment of an individual randomly chosen from the community. Its numeric value depends on the number of species and the eveness with which the individuals are apportioned among them. In the comparative study, the index cannot be accepted as satisfactory characteristic of the community diversity. This is because any comparison of the actual diversity of communities from two different habitats that have differentiated potential for 'reception' given number of species, does not reflects the conditions under which the communities of interest have developed (TROJAN 1994). One can, however, consider the effect of species capacity on diversity, by using the index of eveness, the latter being a measure of a particular community's maximum diversity accomplishment.

Assuming, the study is aimed at understanding the mechanisms of the community formation, more complex methods of diversity description are needed like, e.g., the measurement of range of resource diversity *per* species of a community that is, the average width of niche for the community's species as well as its mean degree of overlap (MAGURRAN 1988). These indices of diversity are, also, based on the Shannon equation but they are linked with the double classification of objects that is – the community's specimens are classified in two respect: their species and their habitat are identified. The theoretical background and methods of measurements are given by PIELOU (1969, 1972, 1975) and ROUTLEDGE (1979).

Based on the diversity indices of double classification of a faunal community members, the measure of ecosystem's complexity was also proposed (CANCELA DA FONSECA 1993) under the assumption that complexity can be defined as a function of the number of interrelations among the ecosystem's particular elements (KIKKAWA 1986) and it grows with growing diversity. Considering the above, it is assumed that complexity is such a characteristic that results from the diversity of particular components of the ecosystem, i.e., the species and so called coenotic levels; the latter are assumed to be different habitats or microhabitats occupied by species of the same or similar behaviour type.

The faunistic study nowadays needs, except gathering of elementary data on fauna structure, also a more dynamics oriented attitude, in order to get closer look at the processes of fauna temporal and spatial transformations (TROJAN 1980; TROJAN, WYTWER 1997, TROJAN 1998). To develop the methods of study, a profound analysis of diversity of possibly largest number of well documented reliable data on taxocens, considering the communities' variability, may contribute significantly. So far, no communities diversity analyses based on the double classification are available in the study of faunistics. Such analyses are aimed at building a synthetic picture of a community's structural changes, in order to investigate either temporal or spatial changes.

The purpose of this paper was to verify the usability of diversity indices of double classification for the faunistic study and particularly so – for the needs of structural description of communities.

The object of present study were *Ichneumoninae* living in the crowns of Scots pines in the *Peucedano-* and *Leucobryo-Pinetum* associations. We attempted at defining the structural changes as they occur in the communities of the parasitoids of *Lepidoptera*:

- in the temporal aspect, represented in the study by the successional series of moderately humid coniferous forest type;
- in the spatial (geographic) aspect that is, in different regions of Poland: Bory Tucholskie Forest, Puszcza Biała Forest and Białowieża Primeval Forest. These three forest complexes represent the three zones of forest health in Poland.

METHODS OF INVESTIGATIONS

Material

The empirical faunistic data were collected in the canopies of Scots pines of moderately humid coniferous forest type, using the yellow plates (Moerick traps). The successional series has been represented by the following age stages of Scots pine stand: culture, thicket, pole-stage (premature stand) and mature stand. Each successional stadium was represented by three experimental plots, explored during two consecutive catching seasons (April–October) in years 1986–1987. A total of nearly 5 thousand specimens were caught, belonging to *Ichneumoninae* subfamily: out of them, 1838 specimens were collected in Bory Tucholskie, 1557 – in Puszcza Biała, and 1583 – in Białowieża Forest. The material had been collected within the framework of research problem CPBP 04.10.07, which purpose, assumptions and methods are given in the paper by BAŃKOWSKA (1993), and a detailed description of the study plots can be found in MATUSZKIEWICZ, DEGÓRSKI and KOZŁOWSKA (1993).

The data analysed in this work were, partly, presented and described for the Białowieża Forest (TROJAN et al. 1994, SAWONIEWICZ 1995). Qualitative and more detailed data characterising the communities from all of the three regions of Poland as described in this paper can be found in the monograph of the entire *Ichneumonidae* family, in the context of fauna succession (SAWONIEWICZ, in print).

Analyses

The analysis of diversity of *Ichneumoninae* communities was based upon the double classification of specimens collected (PIELOU 1969, 1975): in respect of their species assignment and their occurrence in the research plot of interest. Thus, as a result, except the index of **species diversity *H(x)*:**

$$H(x) = -\sum_{i=1}^{S} P_i \log P_i \ ,$$

where P_i is the portion of specimens belonging to species *i* in the community having S specimens and the **index of eveness *J***:

$$J(x) = H(x)/H(x)_{max}, \text{ where } H(x)_{max} = log_2 S$$

we also obtain the **index of habitat diversity *H(y)***, which is (similarly as the index of species diversity) a measure of probability that the randomly selected member of the community (here: all the specimens collected) was caught in given plot (regardless the specimen's species assignment). According to the Shannon equation:

$$H(y) = -\sum_{j=1}^{R} Q_j \log Q_j$$

where Q_j is the portion of specimens of plot j in the total number of specimens of plot R. The numeric value of $H(y)$ depends on the eveness of specimens distribution between particular plots and on the number of plots considered, and, similarly, $H(x)$ depends on distribution eveness of specimens between particular species and the number of species.

Assuming: π_{ij} is the portion of specimens of species i in plot j of total number of specimens collected, and p_{ij} and q_{ij} are the portions of species i in plot j in: the number of specimens of species i or – in number of specimens of plot j- respectively, then the remaining characteristics of diversity that may be derived from the double classification are:

- **mean niche width or mean habitat span *$H_x(y)$***, that is the mean habitat diversity of occurrences of one species averaged over all species:

$$H_x(y) = -\sum_{i=1}^{S}\sum_{j=1}^{R} \pi_{ij} \log p_{ij} \quad = -\sum_{i=1}^{S} P_i \sum_{j=1}^{R} p_{ij} \log p_{ij} \,;$$

- **mean habitat overlap or mean habitat span *$H_y(x)$***, that is the mean species diversity of occurrences within one habitat averaged over all habitats:

$$H_y(x) = -\sum_{i=1}^{S}\sum_{j=1}^{R} \pi_{ij} \log q_{ij} = -\sum_{j=1}^{R} Q_j \sum_{i=1}^{S} q_{ij} \log q_{ij}$$

According to the conceptual assumptions, the measurements of the indices of mean niche width and mean habitat overlap are exclusively aimed at finding differences in the scope of habitat utilisation and thus the Hutchinson's definition of niche may be ignored with this respect (PIELOU 1972). The niche is here "a success measure of the species on an environmental hyperspace" (PIELOU 1975) and the method of its measure "may be applicable when the animals' habitat is divisible into a number of separate, clearly distinct, subhabitats" (PIELOU 1972). Depending on the way of classification the places of species occurrence (different habitats, microhabitats, hosts) different aspects of the niche can be discussed (MAGURRAN 1988). In this paper, the places of occurrence of *Ichneumoninae* species were limited exclusively to those specimens caught in the yellow plates in the site of moderately humid coniferous forest, in particular research plots representing different age stages of forest stands in three regions of Poland. Following this formulation, the term 'niche' of *Ichneumoninae* is meant to be understood as the range of occurrence in the Scots pines crowns layer of a phytosociologically defined forest community of moderately humid coniferous forest (represented by two vicarian vegetation associations: *Leucobryo-Pinetum* in Bory Tucholskie and *Peucedano-Pinetum* in Puszcza Biała and Białowieża Forest) – and, such defined 'niche' was subjected to comparisons in order to state the differences in its utilisation by taxa studied of the habitat.

The double classification of specimens of the community allowed, also, the assessment of **global diversity of the system *H(x,y)*.** This last index reflects both the species differentiation as well as the habitat differentiation (in the case reported: differentiation of plots, of forest stand age stadium or region differentiation):

$$H(x,y) = -\sum_{i=1}^{S}\sum_{j=1}^{R}\pi_{ij}\log\pi_{ij}$$

There are functional interconnections between the indices. In case of situation when all specimens of given plot belong to one species only, and a different species is found in every plot (the species classification and the plot classification are completely dependent: from the fact that given specimen belongs to given species it results that the specimen was caught in specified plot and *vice versa*), the following equation holds: $H(x,y) = H(x) = H(y)$, while $H_x(y) = H_y(x) = 0$. However, if all the species are equally distributed among all the plots (the species classification and the plot classification are completely independent – the identification of the specimen's species gives no hints as to the plot of catching), then the niche width is equal the habitat diversity: $H_x(y) = H(y)$, while the mean niche overlap is equal the species diversity: $H_y(x) = H(x)$; and then $H(x,y) = H(x) + H(y)$. Except of the two particular cases, the two classifications are neither completely dependent on each other nor completely independent, therefore the general formula holds: $H(x,y) = H(x) + H_x(y) = H(y) + H_y(x)$.

Following the proposal of CANCELA DA FONSECA (1993) of measurements of complexity, the analysis of the parameter was carried out based on the three indices:

- **the index of global diversity *H(x,y)*;**
- **the index of complexity *C(H)*** defined in terms of the sum of both habitat and species diversity (the species-coenotic diversity):

$$C(H) = H(x) + H(y);$$

- **the index of complexity C** as equal the sum of species diversity of particular coenotic levels (compound species diversity):

$$C = \sum_{j=1}^{R} H(x)_j ;$$

Following the idea of Cancela da Fonseca, the coenotic level is defined as "the ecological level where a set of species having the same or similar biological and ecological behaviour can be placed". In the present work, the term was understood as a unit (class) of the explored habitat or, simply, a defined place of occurrence of *Ichneumoninae*. Depending on the needs for comparison this unit – coentic level – is:

- elementary research plot, when indices are computed for each successional stage of the forest in given region; if so, the index numeric value concerns the three coenotic levels (3 research plots in every successional stage of each region);
- successional stage of the forest type in given region, when general comparisons were accomplished; if so, 3 coenotic levels were considered (containing empirical data from 9 plots altogether); the general values of indices for the coniferous forest type in given region were computed, however, for the four coenotic levels (data collected from a total of 12 research plots).

As a consequence of using the term "coenotic level" (CANCELA DA FONSECA 1993) habitat diversity ***H(y)*** was called coenotic diversity, this last term was also accepted as a generalized term for classification of the habitat under study.

RESULTS

The changes of parameters of *Ichneumoninae* community diversity in the course of secondary succession of pine forest type of three regions of Poland

In the course of secondary succession of pine forest type, the structure of *Ichneumoninae* communities is subjected to substantial alterations. The parameters studied are characteristic of very consistent, nearly parallel course for the communities of Puszcza Biała Forest and Białowieża Forest (Figs 1a, b – 9a, b).

The observed changes in **species richness index (S)** for the two regions represent the rise-and-fall type of succession (TROJAN et al. 1994), showing nearly two fold increase between the stage of culture-thicket, and then a smooth decrease in the subsequent stages of forest stand development and the value of the index becomes in the mature stand even smaller that that in the culture (Fig. 1a, b). A very much similar has been the course of numeric values of **species diversity index *H(x)*** dynamics: an increase till the phase of thicket and a subsequent fall in the next stages, down the level below the starting value (Fig. 2a, b).

On the other hand, the changes of **Pielou index *J(x)*** represent the model of regressive succession (TROJAN et al. 1994): a continuously decreasing tendency is observed and the index reaches its minimum in the mature stand (Fig. 3a, b). Thus, as the stand is getting more mature the *Ichneumoninae* community accomplishes its potential species diversity *H(x)max* in still lesser degree. In the case of interest, the decrease in *J(x)* continues despite the decreasing *H(x)max*, or, in other words, shortening the 'tail' of accessory species (the latter resulting in increase in value of *J(x)*). The observed decrease in *J(x)* has been, therefore, first of all the effect of *H(x)* decrease, or in other words 'sharpening the dominance structure'.

The **index of habitat diversity** – *H(y)* is dependent on frequency distribution of individuals but not – species, among particular plots. Given the fixed number of plots considered, its value brings information exclusively of specimens distribution eveness between particular plots. The actually very similar values of the index as observed for particular successional stages of each region (Fig. 4a, b) suggest that regardless the stage, the selected plots represented a similar pattern of differences in specimens frequency.

The effect of the diversity level, both species- and coenotic diversity, are the further diversity parameters of double classification. These last mentioned parameters' changes in the course of succession are, therefore, the result of the ecological attributes of the communities and their species.

In case of *Ichneumoninae* communities, in each region under study the same pattern of the index change course was observed: as the succession of pine forest proceeded, at the beginning the growth of the index of **mean width of niche $H_x(y)$** was fast but it became still slower with time (Fig. 5a, b). This parameter is a measure of 'commonness' of occurrence in the studied plots and degree of dominance of average species in the community. Growing value of the index shows that in the course of succession, still more and more species of high fidelity towards the explored habitat and stronger dominants can be found in the community of *Ichneumoninae*.

The index of **mean overlap of habitats $H_y(x)$** showed an inverse trend: in general, its value is on the decrease with the progress of succession. In case of *Ichneumoninae* communities of Puszcza Biała and Białowieża Forest, the following pattern has been observed: at the beginning (till thicket phase) the index was growing and in the further successional stages it was falling down – showing thus the model of rise-and-fall succession (Fig. 6a, b). 'The system ordering', or the growing degree of niches separation has been initiated in the *Ichneumoninae* communities as late as the thicket phase, the latter represents the stadium of maximum 'chaos'.

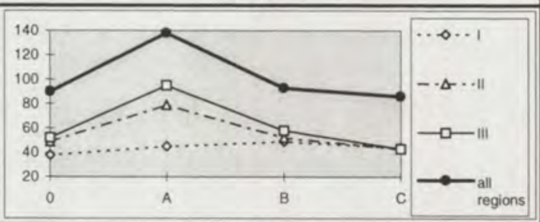
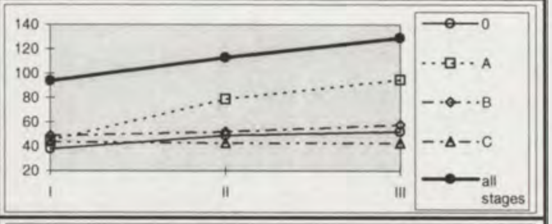
It is the thicket stage where the highest values of global diversity index **$H(x,y)$** as well as all the remaining indices **of system complexity: $C(H)$ and C**, were observed. The course of the indices values represents the model of rise-and-fall succession, with the minimum diversity or complexity arrived at the final stage of succession as represented in this paper by Scots pine stands of age over 100 (Figs 7a, b – 9a, b).

According to the parameters studied, the communities of *Ichneumoninae* of the successional series of pine forest type tend clearly towards the common point which could mean the process of formation of communities of similar structure.

The change of diversity indices of *Ichneumoninae* communities of pine forest type as conditioned by regional peculiarities

The gradient of change of a majority of parameters studied of *Ichneumoninae* communities is the same: from Bory Tucholskie, through Puszcza Biała to

Fig. 1–9. The changes of values of the different measures of diversity for the *Ichneumoninae* communities of pine canopies in three regions of Poland according to the succession series of pine forest; I – Bory Tucholskie Forests, II – Puszcza Biała Forests, III – Białowieża Primeval Forests; 0 – forest culture, A – thicket, B – premature stand (pole-stage), C – mature stand.

<table>
<tr><th>Fig.</th><th colspan="7">a</th><th>b</th><th>c</th></tr>
<tr><td rowspan="5">1</td><td rowspan="5">S</td><td></td><td>0</td><td>A</td><td>B</td><td>C</td><td>all stages</td><td rowspan="5">
</td><td rowspan="5">
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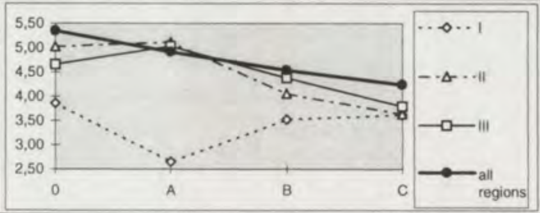
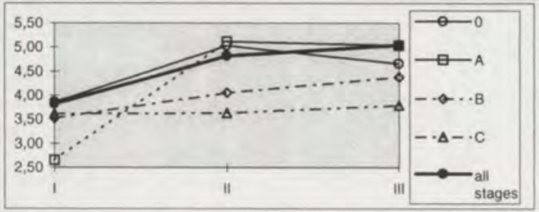
<tr><td>III</td><td>52</td><td>95</td><td>58</td><td>43</td><td>129</td></tr>
<tr><td>all regions</td><td>90</td><td>138</td><td>93</td><td>86</td><td></td></tr>
<tr><td rowspan="5">2</td><td rowspan="5">H(x)</td><td></td><td>0</td><td>A</td><td>B</td><td>C</td><td>all stages</td><td rowspan="5">
</td><td rowspan="5">
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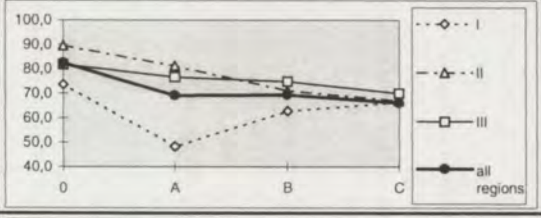
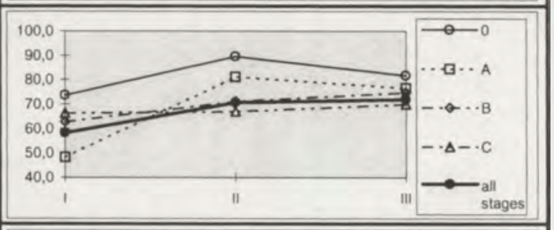
<tr><td rowspan="5">3</td><td rowspan="5">J(x)</td><td></td><td>0</td><td>A</td><td>B</td><td>C</td><td>all stages</td><td rowspan="5">
</td><td rowspan="5">
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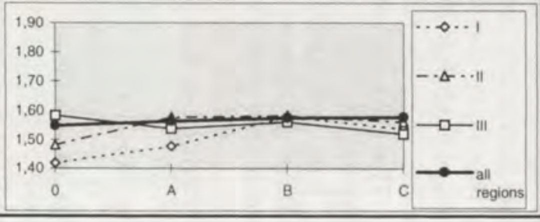
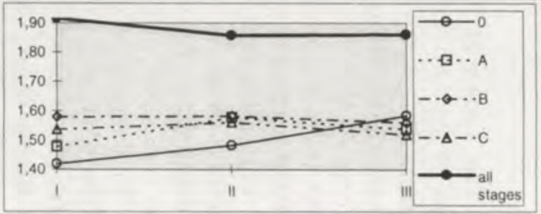
<tr><td rowspan="5">4</td><td rowspan="5">H(y)</td><td></td><td>0</td><td>A</td><td>B</td><td>C</td><td>all stages</td><td rowspan="5">
</td><td rowspan="5">
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<tr><td>all regions</td><td>1,55</td><td>1,56</td><td>1,57</td><td>1,58</td><td></td></tr>
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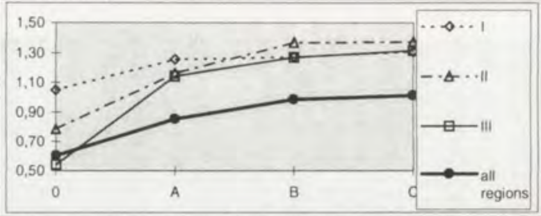
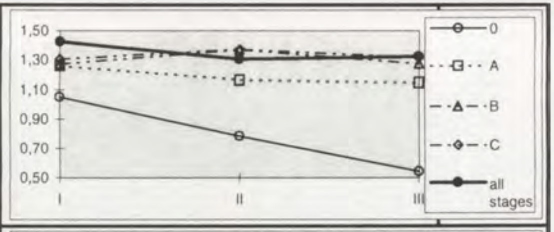
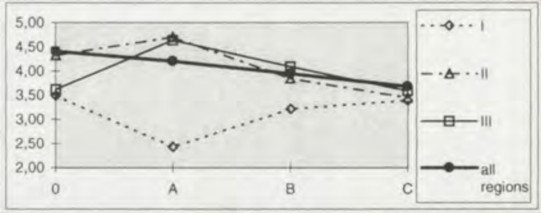
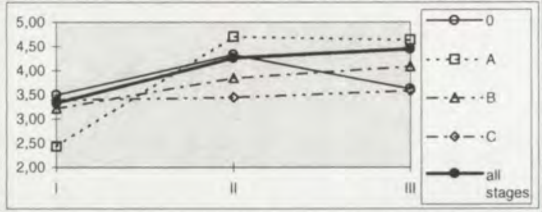
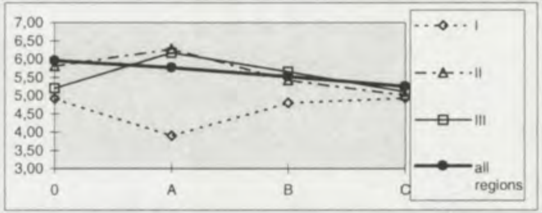
			0	A	B	C	all stages
5	Hx(y)	I	1,05	1,26	1,27	1,30	1,43
		II	0,78	1,16	1,37	1,37	1,30
		III	0,54	1,14	1,27	1,31	1,32
		all regions	0,60	0,85	0,99	1,01	
6	Hy(x)	I	3,49	2,43	3,22	3,39	3,33
		II	4,33	4,70	3,85	3,45	4,26
		III	3,62	4,64	4,09	3,59	4,45
		all regions	4,41	4,20	3,95	3,68	
7	H(x,y)	I	4,91	3,91	4,80	4,93	5,25
		II	5,81	6,28	5,43	5,01	6,12
		III	5,20	6,18	5,65	5,11	6,36
		all regions	5,96	5,77	5,52	5,25	
8	C(H)	I	5,28	4,13	5,11	5,16	5,74
		II	6,51	6,69	5,64	5,20	6,67
		III	6,24	6,57	5,94	5,32	6,90
		all regions	6,90	6,48	6,11	5,82	
9	C	I	10,49	7,99	9,75	10,07	13,67
		II	12,63	14,04	11,54	10,46	17,84
		III	10,73	13,98	12,29	10,78	17,87
		all regions	13,55	12,80	11,97	11,06	

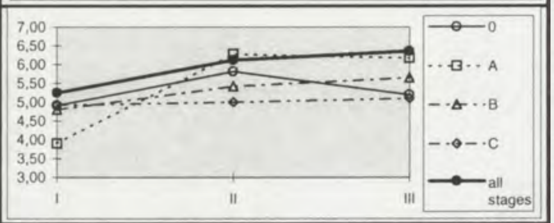


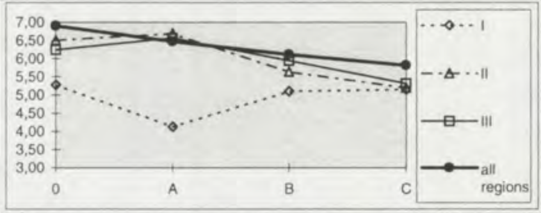


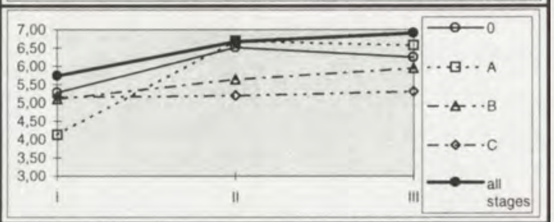


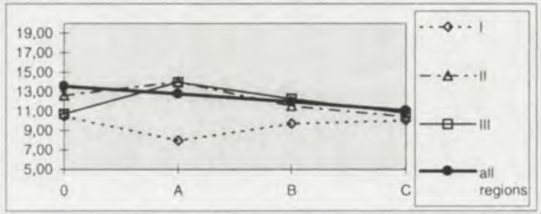


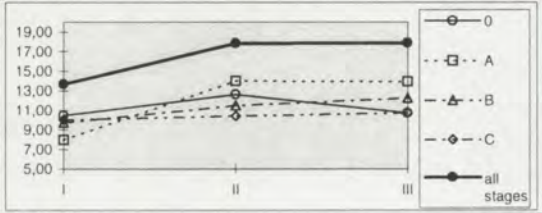












Białowieża Forest, being thus in perfect agreement with the decreasing threat caused by Scots pine primary invaders (Figs 1a, c – 9a, c).

Along this gradient, a clear growth of the index of **species richness (S)** was observed, both for each stage communities separately and for all the communities put together (Fig. 1a, c). Similar has been the trend of the index of **species diversity *H(x)*** in the late successional stages: premature (polewood stage) and mature stand stage (Fig. 2a, c). Only for younger stages, the parameter reached its maximum in Puszcza Biała. A similar pattern is to be observed for the **Pielou index *J(x)***. Following this last index values, *Ichneumoninae* communities of early successional stages of coniferous forest in Puszcza Biała represent a higher degree of species diversity accomplishment than the communities of Białowieża Forest (Fig. 3a, c). Thus, they are characteristic of a more even (less 'sharpened') domination structure as compared with the Białowieża Forest communities, even though the actually smaller number of species in Puszcza Biała.

The values of the index of **coenotic diversity *H(y)*** are, as a matter of fact, nearly identical in particular successional stages of the coniferous forest type in each of the regions (Fig. 4a, c). Some small differentiation can only be found at the stage of forest culture, with H(y) slightly growing, in accordance with the decreasing threat from the side of pests. This parameter, however, when computed for all the successional stages of the coniferous forest type jointly, suggests somewhat higher frequency differentiation of *Ichneumoninae* communities in the region of Bory Tucholskie, comparing with the regions of Puszcza Biała and Białowieża Forest. Generally, however, the values of this index suggest that the Scots pine canopies favour the occurrence of *Ichneumoninae*, regardless the region or the successional stage of forest.

As the pest threat decreases, falling are also the general values of the **index of niche width $H_x(y)$** (Fig. 4a, c). This trend has been particularly clear in the stands of juvenile age stages, while in the older stages of forest stand, the largest values of the index of niche width were recorded in the Puszcza Biała Forest. Thus, the Bory Tucholskie Forest *Ichneumoninae* communities are composed of the species most widely distributed over the habitat of interest.

Reverse has been the direction of change of the **index of habitats overlap $H_y(x)$** (Fig. 5a, c). Its minimum values were found for the *Ichneumoninae* communities from the Bory Tucholskie Forest, while maximum – in the late successional stages of Białowieża Forest and younger successional stages of Puszcza Biała.

The studied *Ichneumoninae* communities of Bory Tucholskie are characteristic of the lowest values of the index of **global diversity *H(x,y)*** as well as the **indices of complexity *C(H)*** and **C** (Figs 7a, c – 9a, c). The highest values of the indices were found for the Puszcza Biała Forest *Ichneumoninae* communities in the early successional stages of pine forest, and for Białowieża Forest communities in the successional stages of premature and mature forest stand.

DISCUSSION

The analysis of *Ichneumoninae* communities living in the coniferous forest type as based upon the indices of double classification, has resulted in a number of new data important for the understanding of structural changes during the succession course. The changes found are far less dependent on the region than on the successional stage of the pine forest type (Figs 1a, b, c – 9a, b, c).

A very high degree of agreement of the run of the indices studied was observed for the communities of Ichn*eumoninae* from Puszcza Biała and Białowieża Forest. The coniferous forest type of the two regions represent the more rich floristically variety of *Peucedano-Pinetum*. Also, the *Ichneumoninae* communities of Scots pines canopies are richer with respect to species number (though not with respect to the number of specimens). This last phenomenon is particularly clearly visible in the stands of younger age classes. The Bory Tucholskie Forest, belonging to zone I – of the highest threat from the side of pest – was subjected at the beginning of the first observation season to chemical treatment against European pine sawfly (*Neodiprion sertifer* (GEOFFR.)) – a damage agent of chiefly younger stands. This chemical control application has been, undoubtedly, the main reason of the observed perturbation in the course of a majority of indices of diversity and complexity. The disturbing effect of the chemical treatment of stands was relatively smallest in case of old-growth stands. Nonetheless, some regional-related trends are visible: those difference between the communities of Puszcza Biała and Białowieża Forest were not the effect of chemical intervention but, at most, the effect of indirect anthropogenic impacts. The Białowieża Primeval Forest Ich*neumoninae* communities living in the canopies of Scots pines in the coniferous forest, subject to the least intensity pest threat zone III, are during the earlier successional stages, the richest in species. At this stage of development they are not, however, the most species diversified and, thus, they do not accomplish fully their potential of diversity. Moreover, they are characteristic of the lowest value of the index of mean niche width, but not – the highest degree of habitats overlap. The three parameters considered in this paper that are related to the system complexity, do not reach their maximum values. Quite different, however, look the values of all these indices in the stages of premature and mature forest stand. When considering these last mentioned stages, the Białowieża *Ichneumoninae* communities have the highest values in every respect, despite the fact that they were characteristic, as compared with the communities of Puszcza Biała Forest, of just slightly higher number of species in the premature stand and the equal number of species in the mature stand. It should be emphasised that the regional differences in the value of double classification indices studied are the smallest for the stage of mature stand. Thus, it is to conclude that the I*chneumoninae* communities living in the canopies of Scots pines on the coniferous forest type create all very much the same structural model.

The application of the diversity indices of double classification for the structural description of *Ichneumoninae* communities has resulted in the following description of the successional changes. Because of the large increase in species richness at the stage of thicket, species diversity represents the rise-and-fall succession type. As the succession proceeds, however, the community accomplishes its potential for maximum species diversity in still decreasing degree. During the early stages of succession, the most rapid growth of the mean niche width is accompanied by a growth of the mean overlap of habitats. Before the stage of thicket is arrived at, the community 'collects' species but 'ecological chaos' is still observed in it – the realised niches of the species overlap with one another to a high degree. One may conclude that not all of the species present are needed, because in the course of the next successional stages: the stages of premature and mature stand, a further widening of the niche width is taking place, together with the process of decreasing the mean overlap of habitats. This is the stage of the community 'ordering'. In this stage the frequency of occurrence of some species is on the increase – they become gradually dominants, while the share of the others is falling down and they are gradually eliminated from the community. As a result, in different regions of the country a similar dominance structure (that is, of similar values of diversity indices of double classification) of the *Ichneumoninae* communities of Scots pines canopies of coniferous forest type is being formed.

In the light of the state-of-the-art knowledge, considering the relationships between diversity and succession, the observed structural changes of *Ichneumoninae* communities studied fully confirm the general ecological theories. The *Ichneumoninae* communities of the termination successional stage of the coniferous forest,type (over 100 years old Scots pine stands) are characteristic of clearly lowered diversity, comparing to the preceding stages. According to considerations of MAY (1973) and other authors (DEANGELIS 1975, LAWLOR 1978, PIMM 1979), an increase in species richness and the number of interrelations within a system, is followed by a decreased dynamics and stability of the system. In the stage of climax which, per definition, is the most stabile one (HORN 1966), both the system diversity and complexity should be the lowest. And this means that one can talk about the climax stage also in the case of *Ichneumoninae* communities of the coniferous forest type canopy layer. According to the climax system hypothesis (KREBS 1997), assuming a continuous sequence of different climaxes exists, differentiated along environmental gradients of soil humidity, biogenic compounds content and other factors, we have also to do with the regional differentiation of the studied climax communities. Their comparison reflects, in turn, the other aspect of relationships between the communities diversity and stability. The more diverse the system's components the more effective are the homeostatic mechanisms thank the possibility of energy flow along alternative routes (MACARTHUR 1955, TROJAN 1984). Also PUTMAN (1994) explained that "the more complex it is the more likely it is to be able to continue functioning in some form following perturbation, because of its capacity to absorb such perturbation, as 'damage' to one part of the system is compensated for by adjustments in other parts of the complex whole". While considering the studied *Ichneumoninae* communities, the absolutely highest values of indices of diversity were found in case of Białowieża Primeval Forest. These communities are, in the context of the above considerations, the most stabile ones, able to compensation of disturbance. The least stabile communities proved to be those of Bory Tucholskie Forest. Having considered the fact that *Ichneumoninae* are parasitoids of forest pest lepidopters, the system is in a perfect agreement with the degree of forests resistance to pests, and this finding confirms the ecological importance of the insect group for the maintenance the health condition of forests.

The implementation of diversity indices of double classification for the analysis of variability of *Ichneumoninae* communities of Scots pine crowns of the coniferous forest type in the context of successional changes and regional alterations, proved without doubt a good working method of assessment the degree of optimality of the structural model of the community. Even more important is the proof that the model cannot be identified with the system highest diversity or complexity. The fully developed natural community of *Ichneumoninae* of lowland Poland coniferous forest type Scots pine canopies has accomplished its potential for species diversity in merely 70% (Pielou index). The habitat and those available elements of the faunal community have produced the ecologically most functional system and not – the most complicated one.

CONCLUSIONS

1. The diversity indices of double classification substantially develope the analysis of structural changes of faunal communities and they are useful for the assessment of the communities formation.

2. The indices commonly used in the faunistic study (they do not imply the need for double classification of data): species richness S, species diversity $H(x)$ and Pielou index of eveness $J(x)$, are substantial parameters in the analysis of structural variability of communities, but they do not supply the possibility for the assessment of ecological processes taking part in the transforming community. Such a possibility can be created, however, by the indices resulting from the double classification: the mean width of niche $H_y(x)$ and the mean degree of habitats overlap $H_x(y)$. The index of coenotic diversity $H(y)$ is helpful in the assessment of habitat's population homogeneity by given taxon (assumed unchanged number of coenotic levels).

3. The indices of complexity as based on species- and coenotic diversity in case of evenly populated habitat do not bear new significant information for the analysis of structural changes of communities (they chiefly reflect the changes in species diversity) and as such, they can be well ignored.

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STRESZCZENIE

[Tytuł: Indeksy różnorodności podwójnej klasyfikacji w badaniach zgrupowań *Ichneumoninae* (*Hymenoptera, Ichneumonidae)* borów świeżych Polski]

W pracy badano zmienność strukturalną zgrupowań *Ichneumoninae* koron sosen w czterech stadiach sukcesji wtórnej boru świeżego: uprawa, młodnik, drągowina, starodrzew, które były rozmieszczone w trzech regionach Polski: Bory Tucholskie, Puszcza Biała i Puszcza Białowieska. Osobniki *Ichneumoninae* odłowione za pomocą pułapek typu Moerick'ego – żółtych misek, zostały sklasyfikowane ze względu na przynależność gatunkową i miejsce złowienia określone do jednostkowej powierzchni badawczej. Dzięki temu możliwe było zastosowanie w badaniach nad zmiennością strukturalną zgrupowań nie tylko standardowych w faunistyce indeksów: bogactwa gatunkowego S, różnorodności gatunkowej H(x), wskaźnika Pielou J(x), ale i współczynników wynikłych podwójnej klasyfikacji jak: różnorodność cenotyczna H(y), szerokość niszy $H_x(y)$, stopień zachodzenia nisz $H_y(x)$ oraz mało znanych miar złożoności: różnorodność globalna H(x,y), różnorodność gatunkowo-cenotyczna C i różnorodność gatunkowa składana C(x). Analiza wartości tych współczynników dała wyczerpujący obraz zmian stukturalnych zgrupowania *Ichneumoninae* koron sosen w trakcie sukcesji boru, ujawniając różnice regionalne przebiegu tego procesu. Niemniej, wykazano dużą zbieżność badanych parametrów dla zgrupowań *Ichnemoninae* w klimaksowym stadium sukcesji borów sosnowych świeżych trzech regionów. Stwierdono również, że proces wykształcania się optymalnego zgrupowania *Ichneumoninae* koron sosen w borze świeżym związana jest z typem sukcesji załamanej, w której różnorodność i złożoność wzrastają do stadium młodnika, a następnie ulegają powolnemu spadkowi, osiągając najniższe wartości w stadium dojrzałego drzewostanu. Przekształcenia te zachodzą przy jednoczesnym wzroście szerokości niszy i spadku stopnia jej zachodzenia.

Uzyskane wyniki pozwoliły na ocenę przydatności uwzględnionych w badaniach 9 indeksów dla analiz zmian strukturalnych zgrupowań faunistycznych. Poza indeksami: *S*, *H(x)* i *J(x)*, które mają podstawowe znaczenie dla analiz strukturalnych, za szczególnie ważne dla poznania procesów kształtowania się dojrzałego zgrupowania uznano: $H_x(y)$ i $H_y(x)$. Indeksy złożoności oparte na różnorodności gatunkowej i cenotycznej: *H(x,y)*, *C* i *C(x)* uznano za mało przydatne w przypadku, gdy badania wykonywane są środowisku jednakowo zasiedlanym przez badany takson – o podobnych wartościach *H(y)* przy tej samej liczbie uwzględnianych poziomów cenotycznych

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