# MUSEUM & INSTITUTE OF ZOOLOGY POLISH ACADEMY OF SCIENCES

# FRAGMENTA FAUNISTICA

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# The meaning and measurement of species diversity

**Abstract**. Studies of species diversity give rise to a number of questions related to theoretical aspects and methodology. The questions deal with 1) estimation of the number of species inhabiting an area, 2) the measurement of species diversity by means of statistical indices, 3) the relation between changes in diversity and the structure of animal communities, 4) estimation of diversity in succession series of biocenoses 5) defining species diversity in a landscape, 6) reduction in species diversity due to anthropogenic pressure. The application of quantitative measurements that afford precise answers to these questions has given contemporary students of fauna tools with which to evaluate habitat quality and produce evidence-based directives for nature conservation.

Key words: species diversity, concepts, measurement, perspectives

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## INTRODUCTION

The present interest in biological diversity can be traced back to a political document: in the introduction to the 1969 UNO report, U'Thant, former Secretary General of the United Nations Organization, wrote about "impending doom for numerous forms of the animal and plant world". That report prompted the International Union for Conservation of Nature to develop the "World Conservation Strategy", published in 1980. In that publication biological diversity was mentioned in the context of two issues: 1) the diminishing genetic pool of breeding animal species and cultivated plant species due to the introduction of new varieties with better production parameters; 2) the extinction of wild animal and plant species following transformation and destruction of their habitats. Work on the latter topic was later resumed by the National Science Foundation Committee in the USA, which published a report

in 1989 entitled "Loss of Biological Diversity: A Global Crisis Requiring International Solutions". In the summary section of this document it is asserted that losses of biological diversity represent a threat to both the scientific understanding of the world and the welfare of humanity. The authors of the report state that this crisis is global in character and that it can only be solved through international co-operation. This issue has been the topic of "Agenda 21" and the "Convention on Biological Diversity" adopted during the Earth Summit organized by UNEP in Rio de Janeiro in June 1992.

The task of specifying the objectives for biological sciences has been undertaken by such organizations as the IUBS, SCOPE, UNESCO, ICSU, IGBP-GCTE and IUMS. The Diversitas programme, the outcome of their work lists major programme elements and cross-cutting programme elements, and actually encompasses all basic issues related to species diversity.

In research practice, as discussed by TROJAN and WYTWER (1996), the basic tasks related to the assessment of species diversity have been addressed for a long time by specialists in faunal and floral research. In the animal world, faunistics investigates species diversity in specific areas and habitat conditions. The results of such studies allow for defining structural patterns in faunal systems, identifying regularities in changes which these systems undergo and the factors that provoke these changes. Faunal data are indispensable in studies of the species diversity of fauna inhabiting all ecosystems found on Earth. The content of faunal papers, and particularly descriptions of theoretical concepts, methodological solutions and generalizations elucidating the genesis, structures and processes occurring in faunal communities at present, including the effect of various forms of anthropogenic activity on fauna, provides indispensable input for evaluation of methods of assessment of biological diversity. The present paper aims to discuss selected issues of contemporary faunal studies and point out possibilities that present-day faunistics offers with respect to solving problems of species diversity.

# SPECIES CAPACITY OF THE HABITAT AS A MEASURE OF SPECIES DIVERSITY

The number of species (S) inhabiting a given area is the basic parameter utilised in all measures of both species richness and species diversity. Determining the value of (S) also answers another important question, namely, what is the species capacity of a given ecosystem, its segment or even an entire landscape. Thus, species diversity and species capacity emerge as closely related notions.

Classical faunistical analysis supplies tentative assessments of the richness of the animal world. The outcome of such studies consists of lists of species inhabiting study areas, often referred to specific localities, ecosystems or their substructures. By merely comparing such lists one can identify localities rich and poor in fauna. The value of (*S*) established empirically, in the course of faunistical exploration is, however, difficult to interpret as there are no statistical methods for evaluating an isolated numerical value. Nor can the

researcher ever be certain that the available list of species is genuinely exhaustive for the study area. It depends on the methods for collecting animals, the size of the study material as well as the time and season when it was collected. Hence, conclusions derived from classical faunistical studies, even if they have been carried out by experienced faunologists, are burdened with error whose magnitude is difficult to estimate – the error of underestimating or, less frequently, overestimating the faunal resources of a given area. There may be more or fewer species inhabiting the area than have been recorded during the investigations. Such objections may be raised with respect to the results of any classical faunistical study.

The fauna, like any other system in nature, is dynamic rather than static. The faunistical background to every area consists of resident species, inhabiting the locality permanently and for a long time. These are usually eurytopic species, associated with the habitat type rather than the ecosystem itself. They occur in different landscape zones and belong to every kind of ecosystem – forest, grassland, cultivated field, swamp, and also in town (TROJAN, 1984). A second group is formed by immigrant species, penetrating into the area, which is new for them, and thus enriching its faunal resources. Yet another group is made up of eliminated species, disappearing from the area as a result of changes to the environment or competition. The fourth group consists of visiting species, migrating across the study area or visiting it periodically but never settling down to live there permanently. The relations between these groups of species provide the basis for evaluating the dynamics of processes occurring within the fauna.

Dynamic phenomena occurring in the fauna are universal and can be observed everywhere and at all times. Their effects are particularly evident in the case of small isolated natural objects such as small islands, urban lawns, solitary clumps of trees or small bodies of water. Two factors which exert a particularly strong influence on the fauna in such cut-off enclaves are immigration and extinction (MACARTHUR and WILSON, 1963), and the actual number of inhabitant species is the resultant of the two processes mentioned above.

One notable consequence of adopting the dynamic concept of fauna is a change in the approach to evaluating the number of species inhabiting a given area. If one assumes, after SIMBERLOFF (1978), that immigration rate declines exponentially with species capacity of the area under study, whereas extinction decreases with its size, then larger areas that show greater environmental diversity should also be home to a more diverse and stable fauna. Such an approach attaches crucial importance to the identification of changes in species capacity in space and time. Any assessment of the state of the fauna should be anchored in a definite period of time and a locality; data so obtained may be compared, but compilations are risky.

Assessment of immigration, extinction and visiting rates is difficult and can rarely be addressed by faunistical studies. As a result, other methods are usually employed to estimate the number of species inhabiting a given area at

a time. Such methods make use of statistical functions based on species-area curves and species frequency distribution.

**Species number estimation by species area curves.** In faunistical estimations, the practice of relating samples to area size is chiefly used in studies of vertebrates. The number of individuals caught is generally considered much more important in studies of animals with a small body size. After a good fit is established between the empirical curve and one of the three known species-area curves (Arrhenius', Kylin's or Romell's, see TROJAN, 1992) the value of estimated number of species (S\*), sometimes different from empirical (S) can be tentatively defined. When the empirical data are compatible with the Arrhenius curve, as transformed by CONNOR and MCCOY (1979)

$$S^* = cN^2$$

where c and z are parameters of modified Arrhenius' equation, N = number of individuals in sample, there are no limits to their being extrapolated by increasing the number of individuals. The main benefit from this procedure is that it helps to establish the number of individuals that must be collected so that a previously unknown species can be found. Thus, in order to provide a more realistic estimate of the number of species inhabiting an area, the sample must be related to the size of the area. Samples then have to be collated to determine the area subjected to the scientific exploration. To this end, an arbitrary coefficient is used to convert sample size into area units and then the upper limit of the extrapolation procedure, i.e. the size of the study area, is established. The point where the curve approximates the limit is the estimated number of species ( $S^*$ ) inhabiting the area. The conversion of sample size to the area and the application of the extrapolation procedure are burdened with a cumulative error that is difficult to estimate and weighs on the results.

**Species number estimation by the species frequency distribution** is used when the empirical distribution fits one of the following two statistical distributions. The first one, PRESTON'S (1962) log-normal distribution is particularly useful when the number of species exceeds 100. When the empirical curve fits this statistical distribution, the number of species is estimated using a formula

$$S^* = S_0 \frac{\sqrt{\pi}}{\varepsilon}$$

where  $S_0$  is empirical number of species,  $\pi = 3.1416$ ,  $\epsilon$  is obtained from variance ( $\sigma$ ) of distribution from the formula:  $\epsilon = (2\sigma^2)^{-0.5}$ .

This number S\*, according to PRESTON (1962), "exposes" the missing part of the log-normal distribution curve. The other distribution, the negative binomial distribution, is usually employed to systems numbering several to several dozen species. In case of fit between the empirical and statistical distributions, the number of species is defined using the formula

$$S^* = \frac{S_0}{1 - q^v}$$

where q and v are the parameters of the negative binominal equation. Faunistical material contains no empty samples, which is sometimes the case with ecological sampling. Thus, analyses of faunistical material should use the truncated negative binomial distribution, without the zero (TROJAN 1992).

Species numbers estimated (S\*) by means of statistical functions and distributions are the essential parameter for mathematically correct analyses of faunal species diversity and they also help establish the species capacity of a habitat.

# STATISTICAL MEASURES OF SPECIES DIVERSITY

Two measures of species diversity, the Shannon-Weaver and Simpson indices, enjoy wide use in faunistical research. Their mathematics does not need to be discussed here. Other measures of diversity, usually referred to as species richness, relate the number of species to the size of the sampled material, being thus dependent on the latter parameter and not satisfying the statistical criteria. They are rarely applied to faunistical research.

Both the species diversity indices actually only provide information on the likelihood of capturing an individual representing a given species. This likelihood is highest in communities made up of only one species, and lowest when the community comprises several species of equal abundance. This relationship has been best figured by MAGURRAN (1988). This feature of the species diversity indices demonstrates their independence from the number of species forming a community. This proposition is corroborated by results of studies on weevils (CHOLEWICKA 1994). Communities rich and poor in species alike may show similar species diversity values. Similar information may be found in the work by HAGVAR (1968), where the results of calculations using two measures of species diversity of soil fauna have been grouped along the gradient of increasing soil fertility. Species capacity was the only index whose value rose with increasing soil fertility, while species diversity in the forest with the most fertile soil was similar to that in Pineto-Cladonietum forests, whose soil ranks among the least fertile ones. In comparison to species diversity as shown by HAGVAR (1968), the percentage-of-rare-species index follows the opposite pattern, with the highest values registered in the forests with the most and the least fertile soils. The example data quoted above show that despite the simplicity of these indices, the interpretation of faunistical data provided by them presents much difficulty.

The maximum  $(H'_{men})$  and minimum  $(H'_{min})$  values of the indices that a community may reach in a given area can serve as reference values for the interpretation of these diversity measures. An example of the use of this possibility is the PIELOU evenness index (1969), which describes the range of vari-

ability in species diversity indices in a given locality. By placing an empirical result on this range scale (TROJAN, 1994), one can see by how much actual diversity differs from potential diversity for a given habitat and observe differences between the two measures. The variability range of Shannon-Weaver index (H') is much wider than that of Simpson (I) and the differences in interpretation of the same set of results using these measures do not correspond. The above indicates that when interpreting the results of analyses the nature of the measure must be taken into consideration alongside the magnitude of the difference.

# SPECIES DIVERSITY VERSUS SPECIES FREQUENCY DISTRIBUTION

The independence of the measures of species diversity from the number of species parameter and the fact that the results are only related to the contributions of individual species to the community suggest that both the Shannon-Weaver and Simpson indices are chiefly to be regarded as approximate measures of the skewness of species frequency distributions. The values of both indices in animal communities characterised by sharp domination of one species approximate H' = 0 and I = 1 respectively, while in skew distributions they approximate  $H'_{max}$  and  $I = 1/S^*$  respectively.

A good estimate of a community's diversity can be obtained by directly analysing species frequency distribution with the help of descriptive characteristics that allow for assessment of such features of distributions as their evenness, skewness and oblateness and how well they fit the statistical distribution. By using these distributions as models of community structure it is possible to program and test the empirical data. Such analyses can be particularly useful in studies of species diversity of communities aiming at 1) identification of structural patterns in a community in natural conditions; 2) evaluation of the wellbeing of a community; 3) assessment of the degree of transformation of a community due to external factors; 4) identification of endangered species.

Work on methods of statistical description of community structure is far from being completed. However, it is known that most of the statistical distributions available do not reflect the structure of animal communities. In natural communities, with few signs of anthropogenic transformation the abundance of certain few species, called dominants in descriptive ecology, is high and there are a number, sometimes quite large, of species of low abundance, which are described as the tail of the distribution or accessory species. Such a distribution reflects the structure of numerous types of natural ecosystems. In practice, deviations from this pattern occur quite frequently, allowing for application of structural data to comparative studies.

In our further considerations, the three measures of species diversity named above: species number, species diversity indices and species frequency distribution will be treated on equal terms.

# FACTORS INFLUENCING THE SPECIES DIVERSITY OF FAUNA

The experience of zoogeographical and faunistical research suggests that the diversity of the fauna of an area is contingent upon a variety of factors: 1) the geological history of the area, 2) its size, 3) its habitat differentiation, 4) ecological succession and 5) anthropogenic impact. They will be analysed below individually.

**The geological history of the area**. It is assumed that continuous development of the flora and fauna of an area, undisturbed by ecological disasters, results in increased species diversity of the biota found there. This regularity manifests itself when species diversity is compared between areas where the fauna has developed continuously and those which have suffered destruction of some biota. Such comparisons also make it possible to evaluate the usefulness of the three measures of species diversity discussed above. The following example comparisons involve the horse-flies family (*Diptera: Tabanidae*) and soil mesofauna.

Horse-flies are part of the guild of haematophages. The two areas under comparison are the Puszcza Białowieska primeval forest, whose area of about 10,000 ybp used to be covered by an ice sheet, and the tropical rain forest of Panama, situated in a region that did not suffer glaciation in the Quaternary. A comparison of data on the species diversity of horse-flies reveals that the species diversity indices (H') and (J) show little difference between the two areas and species frequency distributions of the guild are similarly dominative whereas the number of species in the Panamanian forest is much higher than that in Puszcza Białowieska.

The other example comparison involves soil mesofauna of deciduous forests of former Yugoslavia and Poland. The former area was free of glaciation in the Quaternary, with the exception of mountain areas, while the northern part of the latter was completely covered with the ice and other lowland areas there had no forests. The values of the three measures are again similar in both areas. The differences between the respective species diversity indices are small, dominance patterns being similar as well. However, the number of species indicates a much higher richness of the mesofauna in Yugoslavian deciduous forests, where the fauna has developed unperturbed, in comparison with central Europe, where reconstruction of the fauna has been going on for a relatively short time.

The differences observed are also partly due to a warmer climate of the areas unaffected by glaciation. However, it is difficult to speak in definite terms about its effect on structural measures, such as species diversity and evenness or species frequency distribution.

The size of the area occupied by a specific type of ecosystem decides a number of species found there. This relationship has been well documented in studies on island fauna. In studies on continental biota, the relationship between the size of the study area and the number of species was first formulated by ARRHENIUS (1923) in the form of a function described earlier in this

paper. Some good examples to illustrate this issue are provided by data on the horse-flies of the forest ecosystems of the Palaearctic Region (Table I).

Table I. Species diversity of horse-flies (Diptera: Tabanidae) of the forest ecosystems of the Palaearctic Region; N – number of individuals in a sample, S – empirical number of species; H' – Shannon-Weaver index.

Ecosystem	Region/Country	Subregion	N	S	H
Deciduous forests	Switzerland	Lausanne	596	17	2.2120
	Poland	Nida Valley	265	21	2.5788
		Kampinos Forest	1947	24	2.5268
	Slovakia	East Slovakia	9348	36	2.3983
Coniferous forests	Belarus	Grodno	9315	29	2.4161
	Russia	St. Petersburg	1788	16	2.1826
	Central	Northern taiga	9925	22	2.8275
	Siberian	Middle taiga	3450	28	2.9662
	Plateau	Southern taiga	4227	30	2.9473

Horse-flies communities in individual forest regions can have similar species diversity indices and also dominative patterns of species frequency distribution. The main difference is in the total number of species inhabiting several forest ecosystem. Similar species diversity is found in Nida Valley counting some tens square kilometers as in taiga of Central Siberian Plateau with the area of approximately 4 millions square kilometers.

Habitat differentiation. The issue of changes in species diversity seen with increasing habitat diversity has been dealt with by a number of authors (WHITTAKER, 1972; BLONDEL, 1979; CANCELA DA FONSECA, 1993). The most significant development in this field has been WHITTAKER's (1972) concept of the coenokline, which states that the populations of individual species overlap and that their abundance centres are distributed along habitat gradients. As a result, the niches of individual species become progressively narrower while changes in the composition of the community get bigger in time. Whittaker defines three categories of species diversity: intrabiotopic  $\alpha$ -diversity, interbiotopic β-diversity and landscape-scale y-diversity. Measurements of these three types of diversity are usually based on the Shannon-Weaver index. Special importance under this concept is attached to the  $\alpha$ -diversity measure (HALFFTER, 1998) insofar as it is the one best reflecting actual species diversity in a landscape with a high degree of patchiness resulting from its being restructured by human activity. An analysis of 9 measures of diversity using data on parasitic Ichneumonidae (Hymenoptera) communities of canopies of pines in Polish pine forests (WYTWER, SAWONIEWICZ 1998) revealed that apart from the S, H' and J indices, also useful are the mean width of niche  $(H_{(y)})$ and the mean overlap of habitats  $(H_y(x))$  indices. The global diversity index  $(H_{(x,y)})$  and system diversity indices (C(H)) and (C) are of little use when a series of habitats is occupied by the taxon under study in equal numbers.

The variability of the species diversity indices within a diversified landscape with a preponderance of arable land has been studied on bees by BANASZAK

(1983). It was shown that anthropogenic habitats were characterized by similar values of these indices in comparison with natural habitats, while in agricultural land, characterized by a similar species capacity to that in natural forests, much lower values of the species diversity indices were registered.

The above examples point out to the importance of and possibilities for developing cumulative assessments of species diversity in landscape scale.

**Ecological succession**. Secondary succession has been studied over a period of 150 years in *Peucedano-Pinetum* pine forests in the Białowieża Biosphere Reserve (TROJAN et al., 1994). 28 faunal groups with a total of 1200 species were included. In contrast to the development of flora, the succession of fauna is a multidirectional process that can follow either of five patterns referred to as a) creative, b) stabilising, c) rise-and-fall, d) regressive and e) restorative succession. Some groups of animals did not exhibit any discernible changes throughout the succession series. Using the number of species, abundance, species frequency distribution and species diversity indices as measures of succession processes, the following findings were obtained:

1. Number of species: 6 patterns of changes were seen in the animal groups studied. The restorative pattern was the most popular, where an initially high number of species decreases until the pole wood stage to be restored in older forests. The regressive and rise-and-fall succession patterns both lead to a decrease of the number of species in the climax-phase forest. Five groups of animals did not show any changes in the number of species during the 150 years. Increases in the number of species in the course of the succession were seen as frequently as the opposite trend.

2. Changes in the abundance of animal communities follow a similar diversity of patterns. Regression and restoration were the dominant trends, and about a third of the communities were more abundant early in the series than at the end of the study period. On the opposite end are communities in which a fall in abundance was stopped in the intermediate phase of the succession series and followed by an increase continuing as long as the climax phase. Only four of the taxa registered constantly increasing abundance throughout the series. A frequent finding was that of divergent trends in abundance changes during the succession of ecologically related groups of animals.

3. The species diversity indices are the most evenly distributed among the various patterns of succession. Regression of species diversity in the course of succession of the pine forest was the dominant pattern, but increases in species diversity were observed as frequently. In the case of potential diversity  $(H_{max})$ , regression was by far the most frequent pattern, seen in 60% of the animal groups. This means that, in a structurally developed ecosystem, species that are not necessary for its functioning are eliminated. In the pine forests the stability of the climax phase was achieved through simplification of the ecological structures of the communities forming the biocenosis, i.e. at the cost of reduced species diversity.

**Anthropogenic pressure**. The development of agriculture and forestry, industry, transport, the urbanisation of large areas and more intensive exploitation of natural resources combine to form a complex system of anthropo-

genic pressure exerted on ecosystems. Its simplest form is trampling on the soil surface, which causes significant changes to the vegetation cover, and the most extreme form is intoxication of the environment with industrial immissions leading to eradication of life from sometimes large areas. The issues connected with the effect of anthropogenic pressure on fauna have been described in a large number of publications. In this paper, I shall concentrate on only a few aspects of this broad subject.

Degradation of the environment in terms of the effect of anthropogenic pressure on animals results in several types of change depending on the nature of the impact. The most notable types are:

1. Unification of the environment, presenting itself as the existence of uniform environmental conditions in large areas. This factor is chiefly associated with the growth of plant production and leads to the disappearance of habitat patchiness typical of naturally developing ecosystems.

2. Homogenisation of the environment for animals manifests itself as destruction of the vertical structure of ecosystems, which is particularly deleterious to fauna in agroecosystems without plant litter or trees. In artificial forest ecosystems, the dominant process is the destruction of age structure due to the practice of simultaneous tree felling and tree planting in large areas.

3. Simplification of biocoenoses owing to the introduction of monocultures.

4. Aridification of agricultural habitats through drainage practices and the destruction of litter in the curse of agrotechnical procedures. In urbicoenoses, water drainage is accomplished through underground plumbing systems. The drying of soils is also related to a higher temperature of the air and the soil in towns and cities.

5. Intoxication of the environment by various chemical immissions. This factor has been listed as the last one even though it has received most attention in the literature of the subject to date. However, the first 4 factors seem to influence fauna to a larger extent than chemical pollution alone.

In contrast to the observed diversity of changes to the environment due to human activity, the picture of responses of animal communities is rather uniform. Supporting this assertion is a body of results of long-term studies of the Institute of Zoology PAS concerned with the effect of anthropogenic pressure on animals in forest and urban habitats. The rationale behind selecting these two types of habitat was that the habitat types of deciduous forests and Polish towns are comparable to each other as most commonly they correspond to the linden-oak-hornbeam forest plant association. As a result, Polish cities, and especially Warsaw – the most thoroughly studied town in the world in this respect, are mostly settled by species migrating there from nearby deciduous forests. The urban environment is not equally suitable for every group of fauna. Its "attractiveness" diminishes towards the centre, with less and less green areas and more and more ground covered with concrete and asphalt, expressed as the so-called urbanization gradient, is convenient for analysing individual groups of animals (TROJAN, 1993). The greatest reductions in numbers are seen in the case of parasitic species, whose occurrence is limited to suburban areas and city outskirts.

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Predators can still be found in larger parks. A similarly profound reduction is also observed in communities of phytophages, which, nevertheless, may still be found in city centres. Saprophages suffer the smallest losses as towns and cities are abundant in organic matter from refuse and faeces of domesticated mammals. Similar trends can be observed with regard to the trophic habits of species settling down in an urban environment. Herbivorous weevils are represented by more than 400 species in the Mazovia region in central Poland that includes Warsaw (CHOLEWICKA, 1981), while in the centre of the city the number of species is reduced to a fourth of the original figure, and the narrower the food specialisation, the greater the reduction. A similar study of spiders (KRZYŻANOWSKA et al. 1981) revealed that the number of species was reduced by 81-91% in downtown areas. Anthropogenic pressure is best tolerated by eurytopic species, while oligotopes suffer the most. Sharp changes also affect species frequency distribution. In a near-natural forest habitat a species frequency graph showed that the proportions of successive species declined gradually while in a markedly transformed park there was a pronounced dominance of one species, Nebria brevicollis, which occupied a minor position in community structure in the semi-natural habitat. The discovery of similar responses of animal communities to diverse changes to their habitats has led to the determination of a pattern of structural change in animal communities based on differences in species frequency distribution (TROJAN, GÓRSKA and WEGNER, 1982). If a dominative species frequency distribution with gradually decreasing proportions of successive species is considered the basic structural pattern, degradation of the environment changes this structure so that there is an increase in the proportions first of a small group of species and later of one species only. A concomitant process is the shortening of the "tail", i.e. lowabundance species with narrow trophic and environmental ranges are eliminated. Since this process affects all groups of animals, it means that biocoenoses in transformed habitats lack specialised species and are thus based on eurytopic and euryphagous species. As such, they represent "skeleton" communities and may be viewed as unsaturated biocoenoses, with a limited scope of internal regulation, vulnerable against invasions of alien forms.

### FINAL CONCLUSION

The above outline of measures of the species diversity of fauna and factors affecting this parameter indicates that with the support of quantitative measures contemporary faunistics is able to accurately examine and assess phenomena that are seen in faunal communities and affect changes occurring therein. Thus, faunistics has at its disposal tools which enable evaluations of habitat quality to be carried out based on statistical indices and evidencebased directives for nature protection to be prepared.

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STRESZCZENIE

[Tytul: Znaczenie i pomiar różnorodności gatunkowej]

Badanie różnorodności gatunkowej rodzi szereg pytań teoretycznych i metodycznych. Dotyczą one 1) liczby gatunków zasiedlających badany obszar. 2) określania różnorodności gatunkowej za pomocą wskaźników statystycznych, 3) związku zmian różnorodności ze strukturą zgrupowań zwierząt, 4) oceny różnorodności w szeregach rozwojowych biocenoz, 5) określania różnorodno-

ści gatunkowej w obrębie krajobrazu, 6) redukcji różnorodności pod wpływem działalności człowieka. Zastosowanie miar ilościowych pozwalających na precyzyjne odpowiedzi na te pytania daje współczesnej faunistyce narzędzia oceny jakości środowiska oraz udokumentowane wskazania dla ochrony przyrody.