

Species-area relationships of plant communities and the possibility of predicting plant species diversity – a case study in South-Western Poland

Modele „species-area relationship” w zbiorowiskach roślinnych i możliwości ich zastosowania dla przewidywania różnorodności gatunkowej na przykładzie Polski południowo-zachodniej

„So, I believe that the linearity of the species-area curve remains a fascinating mystery”

Rosenzweig, 1995, p. 268

“Remember that all models are wrong; the practical question is how wrong do they have to be to not be useful.”

George E.P. Box & Norman R. Draper, 1987, p. 74

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Abstract: The main aim of this study was to consider the possibility of predicting the number of plant species in areas occupied by many different habitat types. A very simple mathematical model was proposed for this purpose. It is based on two fundamental assumptions: first – every single type of community has its own species-area model relationship, second – the number of species common to various types of habitats allometrically depends on the number of habitats and on their quality. In order to test the proposed model, first the species-area relationships for single community types should be counted. Basic data were obtained from phytosociological tables published for SW Poland in 1960–2002. Each set of patches of a plant community, represented in one phytosociological table, was treated as one, compact habitat island of a size comparable to the joint acreage of the patches. The research covered all literature-documented plant communities from SW Poland – in all 750 phytosociological tables including 223 associations and plant communities. The data on 173 syntaxa compiled in 667 tables were used in the analysis – the remaining tables were represented by insufficient numbers of syntaxa (fewer than five), or by insufficient number of phytosociological releves (three or fewer). The species-area relationship models for 58 types of communities were counted this way.

The next step involved substituting the results of the single SPAR models in the previously proposed γ -diversity allometric model. The model was tested on 13 different-sized and 18 equal-sized areas in SW. Poland using GIS tools. In both cases the differences between the actual and predicted number of plant species does not exceed 12%.

The consequences of the obtained results were discussed in the light of the main problems implied in the issue of species-area relationship.

Abstrakt: Głównym celem niniejszej pracy było rozważenie możliwości przewidywania liczby gatunków roślin naczyniowych na obszarach zajętych przez różne typy zbiorowisk roślinnych. W tym celu zaproponowano prosty model matematyczny, oparty na dwóch podstawowych założeniach: po pierwsze – każdy typ zbiorowiska roślinnego posiada swój własny model species-area relationship, po drugie – liczba gatunków wspólnych dla różnych typów zbiorowisk ma charakter zależności allometrycznej, zależnej od liczby zbiorowisk oraz ich jakości (immanentnego bogactwa gatunkowego).

W pierwszym etapie, dla potrzeb testu proponowanego modelu γ -różnorodności konieczne było obliczenie indywidualnych modeli species-area relationship dla największej możliwej liczby typów zbiorowisk. Podstawowe dane uzyskałem z tabel fitosocjologicznych opublikowanych z terenu Polski Pd.-Zach. w latach 1960–2002. Każdy zestaw danych pozyskanych z jednej tabeli fitosocjologicznej, z określonego, ściśle zdefiniowanego terenu traktowany był jak reprezentatywny płat zbiorowiska o powierzchni porównywalnej do jednolitego obszaru o powierzchni równej sumie powierzchni zdjęć fitosocjologicznych w tabeli. Badania objęły wszystkie udokumentowane w literaturze zbiorowiska roślinne z terenu Polski Pd.-Zach. – łącznie 750 tabel fitosocjologicznych reprezentujących 223 zespoły i zbiorowiska roślinne. Do analiz użyto 667 tabel reprezentujących 173 syntaksony – dla pozostałych dane były niewystarczające (zbyt mała liczba tabel – poniżej 5, lub zbyt mała liczba zdjęć w tabeli – trzy lub mniej). Na podstawie analizy uzyskano 58 modeli species-area relation dla poszczególnych zbiorowisk roślinnych (zespołów, związków, rzadziej wyższych jednostek syntaksonomicznych).

Następnie podstawiono uzyskane dane do wcześniej zaproponowanego modelu allometrycznego. Model testowany był przy użyciu technik GIS na 13 obszarach o zróżnicowanych powierzchniach (rezerваты dolnośląskie) oraz na 18 obszarach o powierzchniach zbliżonych do 100 ha (Góry Stołowe). Uzyskane rezultaty są zadowalające – różnica pomiędzy liczbą gatunków przewidywaną przez model oraz z badań terenowych nie przekracza 12%.

W dalszym ciągu pracy konsekwencje uzyskanych wyników zostały przedyskutowane w aspekcie głównych problemów związanych z problematyką species-area relationship obecnych w literaturze przedmiotu.

Key words: species-area relationship, α -biodiversity, γ -biodiversity, plant species, biodiversity prediction, ecological modelling

Słowa kluczowe: α -różnorodność, γ -różnorodność, przewidywanie bioróżnorodności, modele ekologiczne

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Contents

Introduction	9
1. Objectives of this study	11
2. Modelling the α - and γ -diversity	11
2.1. Step one – is direct application of the model possible	11
2.2. Step two – each plant community has its own species-area relationship	14
2.3. Step three – predicting γ -biodiversity – introductory remarks	18
2.4. Step four – from single to multihabitat areas species capacity	19
2.5. Step five – the number of common species is adequate to the number of habitats	20
2.6. The last step – the simplest possible model	23
3. Testing the model	23
3.1. Geographical range	24
3.2. Basic data	25
3.3. Methods of analysis	26
4. Results	28
4.1. Models of α -diversity	28
4.2. Species-area relationships for different habitat types	32
4.2.1. Forest habitats	32
4.2.1.1. Oak-hornbeam forest	32
4.2.1.2. Ash-elm-oak riverine forests (<i>Ficario-Ulmetum</i>)	34
4.2.1.3. Acidophilous beech and beech-fir forest (<i>Luzulo nemorosae-</i> <i>Fagetum</i> , <i>Luzulo pilosae-Fagetum</i> , “ <i>Abietetum</i> <i>polonicum</i> ”)	35
4.2.1.4. Sycamore-beech(-rowan) ravine forest (<i>Lunario-</i> <i>Aceretum</i> & <i>Sorbo-Aceretum</i> group)	36
4.2.1.5. Altitudinal differences – ash-alder and rich beech forest	37
4.2.1.6. Ecological similarity between various kinds of broad-leaf forests	37
4.2.1.7. Alder peat-bog forest	38
4.2.2. Natural non-forest communities	39
4.2.2.1. Rock-dwelling communities (Cl. <i>Asplenieta trichomanis</i> , <i>O. Sedo-Scleranthetalia</i>)	39
4.2.2.2. Aquatic communities	40
4.2.2.3. River and lake shore communities	40
4.2.3. Semi-natural non-forest communities	41
4.2.4. Synanthropic communities	42

4.3. Testing the γ -biodiversity model	43
4.3.1. Equal-sized areas	44
4.3.2. Different-sized areas	45
5. Discussion	48
5.1. Simplification of the model	48
5.2. Comparison of various models of species richness prediction	48
5.3. Habitat information conveyed by the Gleason plot	50
5.3.1. Species-poor and species-rich habitats (from <i>closed</i> to <i>open</i> plant communities)	50
5.3.2. Rate of and reasons for the increase in biological diversity (the role of B and z coefficients)	53
5.4. Discretion versus self-similarity of plant communities?	54
5.5. Applicability of the power function to small patches	55
5.6. Small island effect – does it work within habitats?	56
5.7. Consequences for the SLOSS problem	57
6. Conclusions	58
7. Bibliography	60
8. List of sources	74
Streszczenie	81
Appendix I. Analysis of forest communities	95
Appendix II. Analysis of non-forest communities	130
Appendix III. Distribution and vegetation map of nature reserves included in analysis	167
Appendix IV. Predicted number of species for 13 tested, non-equal -sized areas (nature reserves)	181
Appendix V. Distribution and vegetation maps of the 1km x 1km testing plots within the Stołowe Mts.	183
Appendix VI. Predicted number of species for 18 tested, equal-sized areas (Stołowe Mts.)	185
Appendix VII. List of phytosociological tables of analyzed communities	187

Introduction

Arrhenius's (1921, 1923a, 1923b) and Gleason's (1922, 1925) equations which relate the increase in the number of species to the enlargement of the study plot rank among the oldest mathematical models applied in ecology, their value for the development of this branch of knowledge being unquestionable and invaluable.

The first descriptions of the species-area relationship come from the 19th century and its pioneer observers include Candolle in 1820, Watson – two papers from 1895 and 1859, and Wallace in 1910 (after Rosenzweig 1995 and Lomolino 2001b). The knowledge of this relationship (abbreviated as SARs or SPAR) is indeed so popular that it is sometimes referred to as the main rule of ecology (Rosenzweig 1995; Triantis *et al.* 2003). It is not only used to describe the biodiversity patterns in space and time – for any taxon ever investigated – but is also a paradigm of the equilibrium theory in island biogeography. MacArthur and Wilson in their 1967 paper described the SPAR as the “milestone” of this theory. The model is also useful in metapopulation biology (Rosenzweig 1995; Hanski, Gilpin 1997; Matter *et al.* 2002, Hanski 2004) and conservation biology, as the main tool to predict the probability of extinction for various kinds of organisms as a result of habitat fragmentation (e.g. Simberloff, Levin 1985; Brooks *et al.* 1997; Harte, Kinzig 1997; Ney-Nifle, Mangel 1999; Kizing, Harte 2000; Hanski 2000; Bascompte, Rodriguez 2001; Boulinier *et al.* 2001; Brooks *et al.* 2002; Hanski, Ovaskainen 2002; Collins *et al.* 2002; Green *et al.* 2003; Benitez-Malvido, Martinez-Ramos 2003; Ulrich, Buszko 2003b; Ulrich 2005a; Lewis 2006).

There are three main concepts of the species-area relationship.

The first comes from classical papers on island biogeography (Preston 1960, 1962a; MacArthur, Wilson 1963, 1967), and within that theory the main reason for increasing number of species with contiguous pattern is the area occupied by species *per se*, although Whittaker & Fernandez-Palacios (2007) tried to suggest that this assumption resulted from a simplification used by MacArthur and Wilson's (1967) readers.

The second focuses on habitat diversity as the main reason for the species-area relationship (Triantis *et al.* 2003 and references cited therein). The author of this concept was Forster, a naturalist in one of the famous captain Cook's peregrinations (after Lomolino 2001). Obviously, it is likely that both the area size and the number and diversity of habitats play an important role in shaping of the species richness, however the relationships are still unclear (*cf.* Harner, Harper 1976; Rafe *et al.* 1985; Kohn, Walsh 1994; Ricklefs, Lovette 1999; Brose 2001; Triantis *et al.* 2003; Evans *et al.* 2007). Of course, there are also specialists who found no clear relationships between the habitat di-

versity and the species richness (Boström, Nilsson 1983; Nilsson *et al.* 1988; Haig *et al.* 2000) but in the recent studies (cf. Whittaker, Fernandez-Palacios 2007) this phenomenon is rather unquestionable. The models however which try to combine these variables (e.g. Triantis *et al.* 2003) are still of limited use (cf. Whittaker, Fernandez-Palacios 2007, p. 90).

The third concept, known as the passive sampling hypothesis, was proposed by Connor & McCoy (1979). They argued that, if individuals were distributed at random, larger samples would contain more species. An island can be regarded as a sample of such a random community, without reference to particular patterns of turnover (Whittaker, Fernandez-Palacios 2007).

There is a broad consensus on only two fundamental features (Lomolino 2001b): the species richness increases with area and the rate of this increase is slower for larger areas (from islands or habitat patches to biogeographical provinces). The nature of this relationship and its detailed description (including still new or redefined models) is however subject to continuous, and sometimes very hot, debates (Gilbert 1980; Bramson *et al.* 1996; Brown, Kodric-Brown 1977; Heaney 2000; Scheiner *et al.* 2000; Lomolino 2000a, 2000b, 2001; Whittaker *et al.* 2001; Williamson *et al.* 2001, 2002; Brown *et al.* 2002; Cam *et al.* 2002; Triantis *et al.* 2003; Williamson 2003; Ovaskainen, Hanski 2003; Hanski 2004).

Besides, many other relationships were described based on SPAR, such as:

- Time-species-area relationship which affects (both by increasing and decreasing) the total species diversity (e.g. Preston 1960; Rosenzweig 1995; Jacquemyn *et al.* 2001; Hadly, Maurer 2001; Adler, Lauenroth 2003; Price 2004, Adler 2004; Fridley *et al.* 2006, Helm *et al.* 2006).
- Endemic-area relationship (EAR) – e.g. Harte, Kinzig (1997); Kizing, Harte (2000); Green *et al.* (2003); Hobohm (2003); Ulrich, Buszko (2003b, 2004); Ulrich (2005).

In Poland, investigations into the relationship between the number of species and the area size are relatively rarely undertaken (Dzwonko, Loster 1997, 1998; Solon 1988, 1990, 2000), with exception of Mikołaj Kopernik University in Toruń (Ulrich 1999, 2000, 2001a, 2001b, 2004a, 2004b, 2005a, 2005b; Ulrich, Buszko 2003a, 2003b, 2004, 2005; Ulrich, Ollik 2004, 2005). Foreign literature pertaining to this issue is extremely abundant, for example, the annual increase in the number of papers in which only the term "spatial scale" appeared increased by 29% each year during the 1980–2000 period (Schneider 2001). Most of these publications however deal with animal ecology (vertebrates and terrestrial invertebrates in particular) and island biogeography. Moreover, the methods employed by this research are widely discussed not only by naturalists but also by mathematicians and statisticians, who are engaged in studying and modelling of natural processes.

Rarely are the methods devised in ecology transferred to geobotany, their usefulness being sometimes limited to repetitions of the basic information on the Arrhenius or Gleason equations in popular handbooks of plant ecology.

1. Objectives of this study

The correlation between the size of the study area and its habitat diversity on the one hand, and the number of species it holds on the other is not only a field of research, still largely unexplored, but is also of great practical importance. Models which could reliably predict the number of species within given areas would be useful in planning nature conservation strategy even for territories of insufficiently known vegetation, in creating species diversity models for extensive areas, and also in investigating potential species diversity and the degree of its deformation under human impact.

The goals of this study include:

- discussing the possibility of developing and testing a model which would enable predicting the number of vascular plants for heterogeneous habitat patterns composed of various plant communities of different sizes (Chapters 2, 3).
- describing the SPAR relationship for different habitat types defined as plant communities at the level of associations or higher syntaxonomic units, using south-western Poland as an example (Chapter 4.2);
- verifying the functioning of the proposed model using selected, well studied plots in south-western Poland (Chapter 4.3);
- tracing the consequences of the proposed solutions in the context of solutions to SPAR issues currently discussed in the world's literature (Chapter 5).

2. Modelling the α - and γ -diversity

2.1. Step one – is direct application of the model possible

It is impossible to predict current species diversity without basic data on the area and statistical analysis. All the SPAR relationships described have clearly defined areas of investigations and precisely specified groups of extant (or sometimes extinct) organisms. Thus, the only way to estimate the α -diversity of plant communities or higher syntaxonomic units is to count it directly in uniform sets of data. When the analysis yields a distinct SPAR curve with a high determination coefficient, the model may have a predictive value.

All the areas investigated so far were more or less homogeneous in character with respect to higher plants, and the SPAR curves in all the cases fit the data very well. In the first canonical papers by Arrhenius (1921) and Gleason

(1922), as well as in those on coastal dune plants (Specht 1988 after Rosenzweig 1995), plants of Lake Hjälmaren's islands (Rydin, Borgegard 1988), Great Britain plant communities (Hopkin 1955); South African plants from various habitat types (Cowling *et al.* 1992), such as tropical forests (Condit *et al.* 1996; Plotkin *et al.* 2000; Sagar *et al.* 2003), the results generally fit the canonical SPAR curve.

However, none of the cases studied involved a set of smaller areas with randomly distributed plant communities, in which the distribution of species would be determined by the diversity of environmental conditions.

Fig. 1 presents a diagram based on data from 28 well-explored nature reserves and other areas situated in south-western Poland, in the regions of Lower Silesia and Opole province (Table 1), with the number of higher plant species recorded from the area (S) plotted against the area size (A). In the context of the papers cited above, which often claim that the variability in species number is not determined by the habitat diversity but only by the plot size, the diagram would seem to totally refute the species-area relationship concept. Both in Fig. 1 and Fig. 2 the SPAR relationship between the area size and the number of species of higher plants seems not only non-existent optically, but also (after logarithmizing the area and the number of species, which enables correlation analysis) shows no statistical significance ($p=0.087$, $r^2=0.1$).

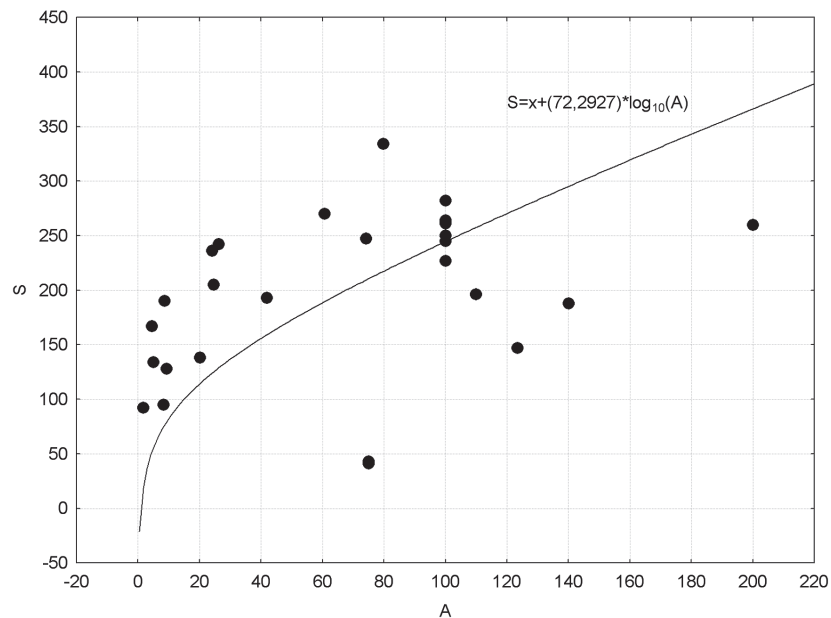


Fig. 1. The SPAR curve for 28 well-investigated areas in Lower Silesia. The SPAR canonical pattern is imperceptible.

Table 1.

List of 28 areas with well-described flora used as the basis for Figs 1 and 2. The areas are sorted by number of species; comparison of columns 2 and 3 shows no simple relationship between the species number and the plot size.

Locality	No of species (S)	Area (A) [in ha]	Data source
Mt. Szczeliniec	43	75	Świerkosz 1998, unpubl.
Grodzisko Ryczyńskie reserve	92	1.8	Anioł-Kwiatkowska 1995
Radziądz reserve	95	8.3	Koła 1995
Jodłowice reserve	128	9.6	Macicka-Pawlik, Wilczyńska 1995
Kanigóra reserve	134	5.6	Kącki, Dajdok 1998, unpubl.; Anioł-Kwiatkowska, Weretelnik 1995a
Leśna Woda reserve	138	20.12	Krawiecowa, Kuczyńska 1968
Puszcza Śnieżnej Białki reserve	147	159.1	Świerkosz 1996, unpubl.
Krokusy w Górzeńcu reserve	167	3.9	Świerkosz 2002
Uroczysko Obiszów reserve	167	6.1	Świerkosz 2004
Góra Ślęza reserve	188	140.3	Kwiatkowski 1995
Zwierzyniec reserve	190	9.1	Anioł-Kwiatkowska, Weretelnik 1995b
Góra Radunia reserve	193	44.7	Berdowski, Panek 1999
Nowe Rochowice – planned reserve	196	110	Berdowski 1993
Las Bukowy w Skarszynie reserve	205	23.4	Pender, Rybałtowska 1995
Łężyckie Skałki in Stołowe NP	227	100.0	Świerkosz 1998, unpubl.
Wzgórze Joanny reserve	236	25.3	Macicka-Pawlik, Wilczyńska 1995
Łąka Sulistrowicka reserve	242	26.4	Berdowski, Panek 1998
Czeska Droga in Stołowe NP	245	100.0	Świerkosz 1998, unpubl.
Olszyny Niezgodzkie reserve	247	74.3	Pender, Anioł-Kwiatkowska 1995
Pasterka village in Stołowe NP	250	100.0	Świerkosz 1998, unpubl.
Góra Miłek reserve	260	137.3	Berdowski 1991
Wodospad Pośny in Stołowe NP	261	100.0	Świerkosz 1998, unpubl.
North Karlów village in Stołowe NP.	261	100.0	Świerkosz 1998, unpubl.
Ostra Góra in Stołowe NP.	264	100.0	Świerkosz 1998, unpubl.
Wawóz Siedmicy reserve	270	60.8	Berdowski, Kwiatkowski 1996
Central Karlów village in Stołowe NP.	282	100.0	Świerkosz 1998, unpubl.
Chojnik Mount (Karkonoski NP.)	334	79.8	Świerkosz 1994a, b

This does not mean that the relationship described for 80 years by hundreds of scientists is nonexistent, but only that the dependence between the area size and the number of higher plant species within it is not a simple derivative coefficient of the area alone.

All the papers mentioned in Chapter 1 (and numerous others) describe the results of investigations which were carried out in more or less uniform habitats. When more diverse data are analysed (as in the case shown in Fig. 1), such a simple explanation is insufficient.

It seems obvious that an ecologically diverse area must have diverse SPAR relationships, and that this habitat diversity is manifest as species richness, which is also affected by the local climate and the anthropopressure level (e.g. Moody 2000, de Bello *et al.* 2007 and many other). Consequently, the SPAR relationship in each case depends on the plant community, which is a direct response to the local combination of various kinds of factors.

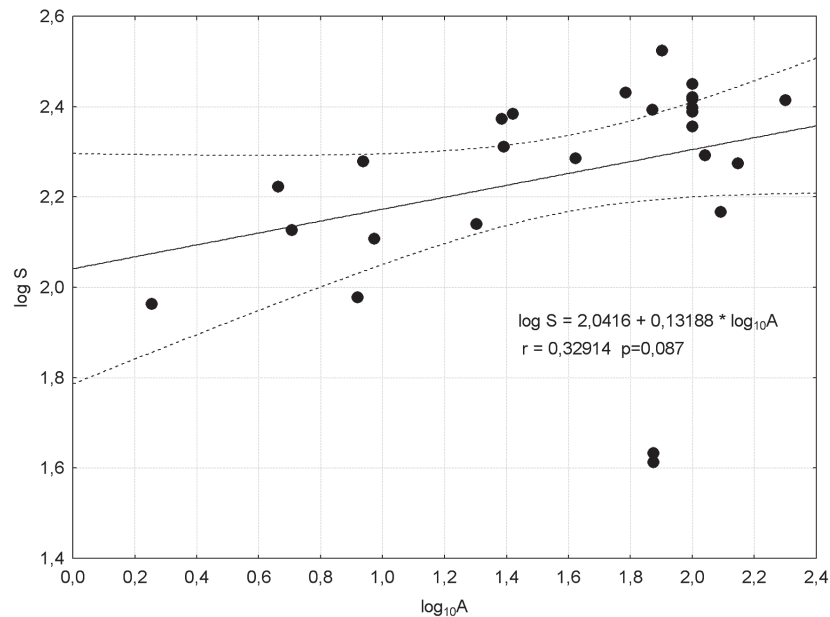


Fig 2. Correlation between $\log S$ and $\log A$ for 28 well-investigated areas in Lower Silesia. The correlation is very weak, and the results are not statistically significant.

2.2. Step two – each plant community has its own species-area relationship

Though the definition of species-area relationship is not problematic (see Whittaker, Fernandez-Palacios 2007 p. 80), a precise description of habitat that would be useful for SPAR study is not as simple. Firstly, habitat can be

defined in different ways, depending on the taxon investigated. The habitat of a big mammal, whose territory can cover more than 1000 square kilometers, is quite different from the habitat of a small mollusc which can spend its life in an area not exceeding a few square metres (Pokryszko 1997) or in one pond (Bronmark 1985). Such definitions are useless for study of plant species distribution. There are also a big differences between various systems of plant habitat classifications (Toby *et al.* 2001).

From the practical point of view, the simplest way to define habitat is to identify it with a single plant community (not always with a single association) or other syntaxonomic unit, more or less uniform in its species composition. The current knowledge of plant communities makes it possible to describe it as a unique “biotic unit” whose species composition is a resultant of abiotic conditions, interactions between co-existing species, history of the region, degree of anthropopressure and many other factors. In this sense, the plant community is a specific, more or less stable manifestation of the response of the natural environment to the unstable and fluctuating conditions (e.g. Franklin 1995; Whittaker, Niering 1975; Saunders *et al.* 1991; Lomolino, Perault 2004). Thus described plant community (association or higher syntaxonomic unit) satisfies the requirements specified by Brown & Lomolino (2000): “[the] *characteristics of islands that affect species diversity and composition include the influence of currents, ice formation, human transport, and other factors which affect the permeability of barriers and habitat heterogeneity, disturbance regimes and the presence of humans and other interacting organisms, which affect both the establishment of colonists and the persistence of natives*”. Moreover, the size of patch of such a community (except very small patches where the *small island effect* occurs) probably does not play any role at all.

The relationship between the area size, the number of habitats available within it and the number of species it holds was investigated by numerous authors. Papers by Harner & Harper (1976), Rafe *et al.* (1985), Kohn & Walsh (1994) or Ricklefs & Lovette (1999) are good examples among hundreds of publications devoted to the issue. All the authors found that the number of species occurring in the site was significantly correlated with both factors, i.e. the area size and the number of habitats.

Investigations of equal-sized samples frequently reveal that areas of higher habitat diversity and longer history of evolution (e.g. *fynbos* south-west of the Breede River as compared to areas south-east of it) hold a considerably greater number of species per unit size. This relationship has been directly shown by e.g. Harner & Harper (1976), who sought a correlation between the species number and soil diversity (meaning the number of microhabitat types) in pine-juniper forests in south-western US, or by Rosenzweig (1995) based

on Haila's data (Haila 1983; Haila *et al.* 1983) on the avifauna of the Åland Islands. The direct correlation between the study area and the number of habitats, and the synergistic relation of these factors and the number of species, have been repeatedly confirmed. The first author who investigated the species-area relation of plant communities *per se* was Hopkins (1955).

Only a few publications suggest that the number of habitats does not play any role at all (e.g. plant diversity on small islands of Lake Hjälmaren (Rydin, Borgegard 1988). Nevertheless, having re-analyzed Rosenzweig's (1995) data, they suppose that "*the diversity of these islands depends mostly on their number of individuals*". Lomolino & Weiser (2001) proposed a new, much better, explanation of this phenomenon, attributing it to a strong and significant SIE (*small island effect*). Also Newmark (1986) found no correlation between the species richness and habitat diversity, and Boström & Nilsson (1983), who increased the area at the same habitat diversity level, did not find a species area curve. Other papers, whose authors did not observe any SPAR relationships, were cited and commented by Dony (1977), who explained their results by a small number of species or individuals within the studied areas (comp. also Whitehead & Jones 1968, who for the first time tried to explain such phenomena).

The situation is different with areas of the same size. Where the area effect is not manifest, it is the habitat diversity that plays the most decisive role in determining the number of species (e.g. Harner, Harper 1976; Rosenzweig 1995). There are also suggestions (Gibson 1986) that a direct area effect is noticeable only in very small patches (up to 0.1 ha). Also, research carried out by Simberloff (1976) on invertebrate species diversity on mangrove islands, which were experimentally gradually reduced in size, revealed the fundamental effect of the area size on species diversity – but within a homogeneous habitat.

The previous studies do not provide a consistent solution to the problem of the relationship between the number of species and that of habitats. Depending on the area and analyzed group, the investigators solve it in different ways, yet numerous papers indicate that such a dependence does exist. However, limiting these considerations solely to the number of habitats is insufficient (e.g. Harner, Harpe 1976; Trantis *et al.* 2003; cf. also Rosenzweig 1995, p. 204–210) when attempting to define their overall biodiversity. It is necessary to take into account also the differences in species composition between particular plant communities (habitat quality), since it is not only the number of habitats that plays an important role in determining plant species richness, but also the habitat '*capacity*' (analogous to *metapopulation capacity* described by Hanski and Ovaskainen 2002), i.e. the number of plant species which every habitat can hold. This capacity is usually called "*saturation*" (e.g. Srivastava 1999; Loreau 2000).

It is assumed that the number of species in a given association or community is correlated with the area size, whether the recorded community patches are adjacent or territorially separated – this assumption is justified by the metacommunity theory (see Leibold *et al.* 2004 for review of earlier studies). The author of this concept was Wilson (1992) who defined the metacommunity as “*A set of local communities that are linked by dispersal of multiple interacting species*”. One of the most important features of metacommunity is that “*the number of species coexisting in the metacommunity can greatly exceed the number of species coexisting in any single patch, despite the fact that the patches are physically identical, the species do not differ in colonization ability, and stochastic effects are absent after the colonization stage*” (Leibold *et al.* 2004). Caswell & Cohen (1993), studying the species area relationship patch-occupancy model, found that “*A simple patch-occupancy model produces quite realistic-looking log-log species-area curve at small sample sizes, eventually becoming asymptotic to the regional species pool as the sample becomes large enough to include all the species*”. Their model considers both non-competitive and competitively saturated communities. The results do not reveal very much. It is all the more strange that the Equilibrium Theory “*is species-neutral i.e. it assumes that all species are independent and equivalent*” (Lomolino 2000a). Considering the species-area relationships without taking into account the species-based features may lead to incorrect conclusions (Lomolino 2000a, b). A similar suggestion comes from Brown & Lomolino (1989, 2000), who point out that special attention should be paid to the difference occurring between islands, including inland islands (isolated habitat patches). Even some adherents of the self-similarity theory suggest that some species are spatially, not fractally distributed (Green *et al.* 2003).

Caswell & Cohen’s (1993) theoretical model was supported by field research, e.g. Partel, Zobel (1999) and Partel *et al.* (2001) who found that the species richness in *alvar* grassland was negatively correlated with the area, in cases when high species richness approached the total species pool (see however Helm *et al.* 2006, who suggest that there are no relationship between current species number and area, although there is *strong relationship between current species number and past habitat area* in this case).

Also other researchers (e.g. Price 2004; see also Rosenzweig 1995), observed that the number of species occurring in an archipelago of isolated islands almost equalled the number of species found within a uniform area of the same size as the joint acreage of these islands¹.

¹ Of course, some researches (e.g. Dzwonko, Loster 1989, 1992; Harrison 1999) do not.

Assuming that this is true, the various sets of data can be used as representation of habitat – both the single patch, and the scattered patches of the same area, which could represent “archipelago of islands” with almost the same number of species as compact habitat patches of the same size.

Such sets of data are available as many phytosociological tables assembled within uniform territories. Each phytosociological table (not single releve) could represent a single habitat “island” and its value for SPAR analyses corresponds to a uniform plot of a defined area occupied by one, compact and homogeneous plant community. Of course the analyzed table must contain relevés originating from the same location or from a clearly defined small geographical area². In this sense the argument of Gray et al. (2004), that SPAR curves are the “*plots of number of species per sample against sample area*” is a very good definition of the assumption. Of course, there is a six convex and eight sigmoid model (Tjørve 2003) and six main types of species area-curves (Scheiner 2003, 2004), differ in their shapes and parameters (comp. also Ulrich 2001b).

In view of all the above, it can be assumed that any plant community has a defined *capacity* (or *saturation*) which is determined by its immanent diversity of biotic and abiotic factors, and the possibility to predict the number of species in this community depends exclusively on the patch area. Each set of patches of a plant community, represented in one phytosociological table, could be in this case treated as one, compact habitat island of a size comparable to the joint acreage of the patches. If this assumption is correct, it should be possible to find individual SPAR relationships for various kinds of habitats treated as single syntaxonomic units, their parts or, on the contrary, higher units such as alliance or order. Then the SPAR relationship for each type of habitat should be the basis for the next step of modelling.

2.3. Step three – predicting γ -biodiversity – introductory remarks

Passing from α - to γ -diversity (as defined by Whittaker 1972) cannot be achieved in a simple way. Obtaining for each habitat type the Gleason equation which fits the saturation of plant communities would be only a partial success. Even being able to predict the number of plant species per community (or higher syntaxa), with strong and statistically significant r^2 -values, means little, when we change the scale from *within-* to *between-*community (Loreau 2000). The γ -diversity is not a simple sum of the α -diversities of each separate habitat (unlike β -diversity) – it has its own specific features, and its measure is not as simple as it may appear (Vellend 2001).

² All the synthetic tables coming from more extensive areas such as "Sudetes" or "Lower Silesia" were excluded from the analyzes for this reason.

The most important problems requiring solution are:

- finding a measure of diversity which would depend on the number of habitats, but could show the species richness of the investigated area as a whole;
- taking into account the huge qualitative differences between plant communities. Possible saturation depends on soil properties, moisture, climatic conditions and many other factors (cf. Solon, Roo-Zielińska 2001);
- the occurrence of species shared by the various habitats, called also *satellite* (Hanski 1982; Collins, Glenn 1991; Perelman *et al.* 2001), *additional* (Bestelmeyer *et al.* 2003) or *common species* (Rosenzweig 1995)³;
- the *small island effect* SIE (Whitehead, Jones 1968; Lomolino 2000c; Lomolino, Weiser 2001; Lomolino, Smith 2003a; Ulrich 2005; Triantis *et al.* 2006), which may be a source of mistakes in predicting the number of species of “small” habitats (Solon 1990, 2000), where stochastic processes could play an important role in shaping the diversity;

Predicting γ -diversity would need different, more sophisticated, tools. Moreover, the model should combine these two levels, so that the species number can be predicted for both single- and multihabitat areas.

2.4. Step four – from single to multihabitat areas species capacity

Let us assume that saturation of a single habitat really occurs (at least on the scale of investigated patches), that it is limited by the patch size, and that the capacity of each habitat can be directly assessed from the data (as described in Chapter 2.2). The number of plant species for each community however conveys no information about the number of plants in a mosaic landscape, which contains more than one habitat patch.

First, it is necessary to find a single value in order to calculate species richness for the whole area. The simplest way is to use the mean number of species per habitat, as shown in Equation 1.

Equation 1

$$\bar{S} = \frac{\sum S_k}{H_n}$$

Where:

\bar{S} – mean number of species;

S_k – total number of species counted in each habitat within the area;

H_n – number of habitats within the area.

³ of course many other terms, such as dominant, matrix and subordinate, redundant, fugitive or scarce species have been used in similar sense (compare Olff, Bakker 1998)

It is important that the proposed equation fits both single-habitat areas ($H_n=1$; which does not change the result of the Gleason single equation) and multi-habitat areas ($H_n=n$), so that it can be used in all cases.

The above equation is a simplification. It is easy to imagine adjacent habitat patches, such as an extremely poor high peat-bog and a very species-rich xerothermic sward, where the mean number of species tells little about the actual biodiversity of the area. Yet from the biological point of view such circumstances exist very rarely, at least within smaller patches (up to 2 km²) which are of particular importance here.

Treating a set of habitat patches as single islands within a wider area it should be possible to count the number of species for each, and the resulting mean number of species per habitat for the area would be a good representation of the “*mean species number*” of that area per unit area.

2.5. Step five – the number of common species is adequate to the number of habitats

Like with inland islands (Rosenzweig 1995), an essential problem in constructing the model is the occurrence of core and satellite species. Studies by Keddy (1981) on *Cakile edentula* or those by Kadmon & Shmida (1990a, 1990b) on *Stipa capensis* are among the abundant papers concerned with species occurring in double role: “*core/satellite*” and “*common*”, depending on the ecosystem.

The regional species pool is more or less constant (Dupre 2000). However, species immigration and extinction within a single habitat can have a very strong dynamics (e.g. Świerkosz 2003). The regional species pool in various communities is determined by the local conditions, through the existence of adequate microhabitats, soil properties and other factors, and the slope of the area-species function can change, depending on those factors (Dupre 2000). For example, Redei *et al.* (2003) found larger species pools in calcareous compared to acid habitats. In fact, the distribution both within and among the habitats is uniform only for a limited number of species. Most of them, due to their being rare or to their habitat requirements, are restricted to specific areas (Ney-Nifle, Mangel 1999; Redei *et al.* 2003), and their distribution is rather stochastic, or depends on their dispersal ability, which is reflected in a defined spatial aggregation pattern (Jacquemyn *et al.* 2001)⁴.

Assuming that each plant community has a constant species composition, which is different from those of other communities, the species from beyond the local species pool of the community are ones which come from the adja-

⁴ The total species pool can approach the asymptote only in very large areas (*cf.* Lomolino 2000c, 2002; Williamson *et al.* 2001), so in this paper the problem can be disregarded.

cent communities. These species are shared by the communities: the satellite species of one community are a part of the species pool (or even core species) of the neighbouring one; in some cases single or a few species will occur in all the communities within the area ("*species communality*"). Identification of this relationship is very important: Partel *et al.* (2001) have shown that β -diversity is correlated with the number of satellite species, while Cagnolo *et al.* (2006) have demonstrated the same kind of importance for rare species in forest patches. Perelman *et al.* (2001) found 70% of investigated plant species of Pampa grassland as satellite.

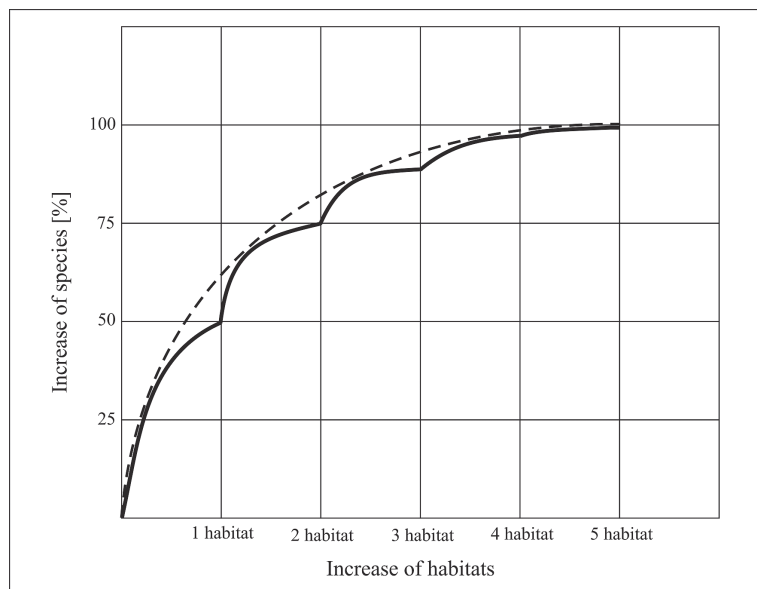


Fig. 3. The first habitat taken into consideration should yield the majority of plant species of the investigated area. Each further habitat should increase the biodiversity by a gradually declining number of species. In this context the canonical SPAR curve is a simplification of a more sophisticated dependence.

Solon (2000) has shown beyond any doubt that a considerable part of floristic biodiversity of a given area is represented by small habitat patches, not marked on geobotanical maps, often without any defined phytosociological affiliation. Thus its occurrence must be interpolated from various sources accompanying the geobotanical map, such as phytosociological relevés and description of local floras.

Assuming that the number of species shared by different communities is proportional to the number of these communities (even very small, such as solitary rocks, springs, forest-edge communities etc.), the increase in the number

of species (β -diversity) from one habitat to another (see Fig. 3) is not a simple derivative of the Gleason equation.

Consequently, it should be possible to find a coefficient which is responsible for this “*species communalit*” $S_c - \omega$ coefficient.

Coefficient ω must meet the following requirements:

- It must assume values from 1 (for $H_n=1$) to infinity (for $H_n=n$), since its bottom limit is determined by the number of species of a single plant community whereas the upper limit, at least theoretically, approaches the asymptote.
- The number of shared species decreases with the increasing number of communities, and thus the correlation is neither linear nor logarithmic in character (logarithm of any base for $1 = 0$).

It follows from these assumptions that the relationship defined by ω shows clearly allometric properties (Equation 2)⁵.

Equation 2

$$S_c = H_n^{\omega}$$

In all likelihood, coefficient ω assumes values corresponding with the SPAR curve slope (parallel to it in the log-log space), which should be contained within the range defined for the canonical z value predicted by Preston (1962a, b) – $z \sim 0.26$ (cf. also Rosenzweig 1995; Lomolino 2001a). The majority of the SPAR curve slopes published range from 0.15 to 0.4, and the median is between 0.25 and 0.3 (Williamson 2003).

In fact, the power function coefficient of this value is nothing else but the number of common species of the overlapping area of sequenced islands.

Assuming that the value of coefficient ω is close to the z coefficient median, the expected common value should be between ω equalling 0.24 and 0.32.

Equation 3

$$S_c = H_n^{0,28 \pm 0,04}$$

The number of shared species will vary from 0% (in a theoretical sample of independent ecosystems such as a xerothermic sward bordering with peat-

⁵ There are probably many other equations which meet the same requirements, but the allometric dependence has its own and long history in ecology (starting with Arrhenius 1921), and is useful to explain many various occurrences also in geobotany and SPAR research (e.g. Gould 1979; Solon 2002; Ulrich, Buszko 2003b; Ulrich 2005a)

bog, or a calcareous rock surrounded by a heath) up to more than 90% (between an ash-elm forest and a riparian oak-horbeam forest). A precise calculation of this value would require a detailed field analysis.

The number of shared species within the area can be excluded from the ultimate number of species, and the equation adopts the form:

Equation 4

$$S = \bar{S} * H_n^{0,28 \pm 0,04}$$

The coefficient z (0.28) can be regarded as a good assumption in the inland-island theory model, but the values of 0.24–0.32 should also be tested.

It should give a good prediction of the species number in both mono- and multihabitat patches, at least in areas not exceeding 1 square kilometer. In this case the mean number of species (\bar{S}) plays the role of z coefficient in the typical Arrhenius equation, but it has a strong empirical basis.

2.6. The last step – the simplest possible model

For the reasons stated above, the equation which a maximum predictive power for γ -diversity should look as follows:

Equation 5

$$S = \frac{\sum S_n}{H_n} * H_n^{0,28 \pm 0,04}$$

Where:

S =predicted number of species;

$S_1 \dots S_n$ =sum of the number of species in all habitats (calculated from Gleason's equation, as a function of habitat area);

H_n =number of habitats;

$H_n^{0,28 \pm 0,04}$ =expected number of common species.

3. Testing the model

Testing the model involves the following:

1. testing if the various patterns of plant species diversity really exist in various habitat types;
2. obtaining Gleason's equation for each habitat type, and checking its predictive value and statistical significance;

3. choosing a well-investigated area with the known number of species and the vegetation map;
4. checking the ultimate model by substituting these real values (point 3) to the theoretical construct (point 2).

3.1. Geographical range

I investigated the relationship between the habitat area and the number of plant species it holds for the regions of Lower Silesia and Opole province (SW. Poland). The area covers a total of 33.000 km², which constitutes ca 10% of the Polish territory.

I decided to limit my research to one specific geographical region and only to higher plant species for the following reasons:

- a. the relative homogeneity of available data for this region;
- b. similar climatic conditions throughout the area;
- c. more or less uniform and well-known species pool coming from the same latitude (*cf.* Willing, Lyons 2000; Lomolino 2000c, 2001a), which is important for comparability of obtained results;
- d. varying number of moss and liverwort species in the available material.

a. Homogeneity of the data

The study area has for many years been investigated by a team of geobotanists representing one institution (Wrocław University), which ensures that the methods used in and approaches to the field research and data analysis are very similar, if not identical. Junior researchers of each institution learn the basics of geobotany from their senior colleagues, and then impart the knowledge gained on their successors. This guarantees the continuity of the research method and the manner of data interpretation, while the constant information exchange, including that unpublished, is also a conducive factor. In the case of the SPAR studies, it is particularly essential to use methodologically uniform input data, since using data acquired with different methods may result in erroneous conclusions.

b. Climatic conditions

The south-western part of Poland is climatically diverse, yet it reveals certain common features when seen from the country-wide perspective. Firstly, there is a distinct influence of oceanic climate, which is manifest as increased precipitation and higher mean annual temperatures. South-western Poland shares these characters with the regions of Ziemia Lubuska and Western Pomerania. Simultaneously, the Polish part of the Bohemian Arc (Sudetes), which shields the whole region from the south, is responsible for the occurrence of climatic phenomena that are typical of southern Poland (and also of the Carpathian

arc), such as föhn winds or temperature inversions. In consequence, the flora of the area is characterized by a high proportion of Atlantic components, with co-occurring montane species (Kącki *et al.* 2003), and also by the presence of a number of plant communities of west- or south-European character (Kącki *et al.* 2005). In spite of the undoubted variation of the region, mainly altitudinal, it forms a definable and uniform biogeographical unit. At the same time its diversity (topographical, climatic, altitudinal and habitat-related) ensures that any possible models to be obtained are referable to a territory more varied than a single geobotanical unit, and will enable tracing correlations between the area size and the number of species for different types of lowland and montane habitats.

c. Species pool

SPAR models which enable predicting the number of species occurring on land plots are, as a rule, limited to areas of uniform habitat and strictly defined geographical character. Each model has different equation coefficients, resulting from analysis of empirical data. The model used to make predictions must, based on empirical data for a given area, be confined within its boundaries. Only after the model has been verified for a given plot is it possible to attempt its application to the neighbouring areas.

d. Number of moss and liverwort species

I limited my investigations to vascular plants, since the distribution patterns for vascular and cryptogamous plants are substantially different (*cf.* Rosenzweig 1995, and references cited therein). Besides, only a small part of the phytosociological research was carried out in co-operation with bryologists. In such cases the phytosociological tables are significantly richer in species of cryptogamous plants.

3.2. Basic data

The next part of the research, the result of which are presented in the tables and appendices, focused on the estimation of the relationship between the area size and the number of vascular plants species which occur in particular plant communities or habitat types, understood as higher phytosociological units (of the rank of alliance, exceptionally order or even class).

The data base included basic information available in phytosociological tables published for SW Poland in 1960–2002. Patches classified at the level of class or order, sporadically documented in the literature, or ones that were impossible to locate in the system of plant communities of Poland, were excluded. The data base comprised: the name of the association or community, the total number of species in a table, the total area covered by phytosociological relevés

and, additionally, the mean numbers of species per releve and the mean area of the releve. Cryptogamous plants were excluded from all tables, which required prior re-calculation and subtraction of their number and percentage for each releve. The research covered all literature-documented plant communities from SW Poland – in all 750 phytosociological tables including 223 associations and plant communities.

The analysis used data on 173 syntaxa compiled in 667 tables – the remaining syntaxa were represented by single tables (fewer than five), or tables of insufficient number of phytosociological releves (three or fewer). The data on the tables used and those omitted are contained in Appendix VII.

The only applicable measure of diversity was the number of vascular plant species. Phytosociological tables do not provide sufficient data to calculate the Fisher index, Simpson concentration coefficient or other biodiversity indices. All taxa of vascular plants included in the tables were taken into account, except for unfixed hybrids and taxa identified only to the genus level. In the available literature, the genus *Taraxacum* is determined to the level of section, like some records in the tables of the genus *Rubus*. In these cases, occurrence of one taxon was noted. Representatives of other genera of problematic taxonomy (*Alchemilla*, *Rosa*, *Hieracium*) in the tables for the study area were determined to the level of species, according to the keys or lists of species available at pertinent periods (Szafer *et al.* 1979; Tutin *et al.* 1964–1980; Mirek *et al.* 2002), which made it possible to compare their species richness. The nomenclatural differences pertaining to particular species are not significant since on each occasion a given name referred only to one taxon.

The data from the combined table (see Appendix VII, Table 7_1), based on the 667 phytosociological tables, were afterwards divided into derived tables, each of which represented a single plant community or – in the case of a smaller number of data – a higher phytosociological unit. I analyzed the correlations exclusively for the cases where five or more tables were available. The names of plant communities and syntaxonomic classification follow W. Matuszkiewicz (2001) and J. M. Matuszkiewicz (2001), except for the treatment of class *Asplenietea trichomanis* (Świerkosz 2004). Single tables were excluded from the analysis due to their deviating significantly from the community type – this particularly concerns poorly explored compound associations which require further phytosociological study with respect to internal diversity. Each time such exclusion is justified.

3.3. Methods of analysis

Statistical analyses were performed with Statistica 7.1, in modules Non-linear Estimation, Non-parameter Statistics and Basic Statistics and Tables.

The analyses of the relationship of the number of species and the area size for particular plant communities or higher syntaxonomic unit were carried out

in the Non-linear Estimation module of Statistica 7.1, with the application of the Gleason equation (1922) as modified by May (1975):

Equation 6

$$S = a + b * \log(A)$$

and the classical power function (Arrhenius 1921, 1923):

Equation 7

$$\log(S) = \log c + z * \log(A)$$

usually transformed to its simpler form:

Equation 8

$$S = cA^z$$

Where:

S – number of species;

A – area size;

a, b, c and z – data-derived coefficients

Each community description (Appendix I and II) is provided with the data source along with indispensable statistical information (N, mean values, distribution of S and A).

Coefficients B and z are usually called *slope-coefficients* since they determine the slope of the SPAR curve in log-log space. Coefficient c in power function is called the *initial trajectory*, and A in semi-log model is the *intercept of the curve* in arithmetic space (Lomolino 2001a).

In the Arrhenius and the Gleason equations it is possible to apply any logarithm (Rosenzweig 1995). Like in the classical equation, the natural logarithm is often used here. However, application of the decimal logarithm enables an easy interpretation of the equation coefficients relative to the size of the area which is expressed in decimal system units. The unit size for which the calculations were made was a hectare. The choice of this unit has also practical reasons, since it enables a simple application of the obtained results to field studies.

Each time a residual analysis (normal distribution expected) was performed and the distribution of values expected relative to the residual values was checked (even dispersal around $x=0$ expected).

Using coefficients calculated from the Gleason equation, the results were shown in the semi-log space, which allows defining the regression equation and the determination coefficient (Appendix I and II). Although the number of species is a discrete variable, this procedure is commonly used in SPAR research and its application finds sufficient support in the pertinent literature (*cf.* May 1975). Based on Preston's (1960, 1962a, 1962b) papers – normal distribution of the data was assumed.

Vegetation maps used for analyses are based on published maps, as well as on data collected by author during field surveys. Scanned maps were imported into GIS environment, georeferenced and then vectorized. It was adopted that all vegetation patches smaller than 0.1 ha are represented by points and the larger ones by polygons. Each of vegetation types distinguished on digitized maps were ascribed to one of 58 analysed vegetation units.

4. Results

4.1. Models of α -diversity

Statistical procedures carried out on available phytosociological data from Lower Silesia allowed to recognize 58 single SPAR distributions, both for single phytosociological units (associations or even their geographical forms) or higher synataxonomic units (alliances, orders or even classes). Due to the character of the available data, values obtained for single units were much more precise and of greater statistical significance.

The results are presented in Tables 2 and 3.

Table 2

Number of analyzed data and complete results of the Gleason plot and power function for the 58 SPAR relationships (arranged by a value of A coefficient)

Habitat	N	Gleason plot	Power function
1	2	3	4
Bog coniferous woodland	5	$20.7974+5.37988*\log_{10}A$	$1.330563+0.150861*\log A$
<i>Lemnetea</i> class	8	$39.3477+9.362343*\log_{10}A$	$1.640206+0.185833*\log A$
<i>Potamion</i> all.	5	$43.1912+13.67196*\log_{10}A$	$1.873035+0.3611626*\log A$
<i>Leucobryo- & Molinio-Pinetum</i> ass.	15	$50.28233+26.27757*\log_{10}A$	$1.68564+0.2943156*\log A$
Alpine <i>Vaccinio-Piceion</i> forest (700 m a.s.l.)	6	$50.3892+26.92266*\log_{10}A$	$1.78051+0.4466903*\log A$

1	2	3	4
<i>Nymphaeion</i> all.	7	51.55305+21.5263*log ₁₀ A	1.9517+0.4873155*logA
<i>Phragmition</i> ser. 1	8	66.97593+21.27667*log ₁₀ A	1.954853+0.295008*logA
<i>Luzulo luzuloidis-Fagetum</i> ser. 1	11	70.4304+37.66856*log ₁₀ A	1.95067+0.460108*logA
<i>Asplenietea trichomanis</i> cl. (natural comm.)	8	73.0829+21.261*log ₁₀ A	2.45922+0.484182*logA
<i>Pino-Quercetum</i> ass.	9	79.3582+39.6025*log ₁₀ A	1.89108+0.29148*logA
<i>Luzulo pil.-Fagetum & Abietetum polonicum</i> ass.	9	79.476+50.4831*log ₁₀ A	1.9412+0.503647*logA
<i>Quercion robori-petraeae</i> cl.	14	79.914+28.7238*log ₁₀ A	1.9353+0.121591*logA
<i>Magnocaricion</i> all.	18	86.8763+25.4149*log ₁₀ A	2.0701+0.2841473*logA
<i>Ribeso-Alnetum</i> ass. ser. 1	7	87.0432+22.9018*log ₁₀ A	1.94475+0.136326*logA
<i>Salix</i> thickets	6	87.4514+28.3996*log ₁₀ x	2.248033+0.4129606*logA
<i>Phragmition</i> all. ser. 2	13	88.3771+22.6322*log ₁₀ A	2.012773+0.201219*logA
Forest plantation	12	89.0682+40.41797*log ₁₀ A	2.055397+0.4206234*logA
<i>Luzulo luzuloidis-Fagetum</i> ass. ser. 2	5	89.9216+33.77827*log ₁₀ A	2.035955+0.292404*logA
<i>Galio-Carpinetum</i> ass. Odra Valley	12	99.51223+36.3765*log ₁₀ A	1.99478+0.1978045*logA
<i>Trifolio-Geranietea</i> cl.	11	99.6015+27.0857*log ₁₀ A	2.26044+0.3069024*logA
<i>Melico-Fagetum</i> ass.	8	100.0177+56.66156*log ₁₀ A	2.011893+0.3536274*logA
<i>Tortulo-Cymbalarietalia</i> ordo	11	100.091+29.8236*log ₁₀ A	2.38972+0.412894*logA
<i>Arnoseridi-Scleranthetum</i> ass.	9	100.442+53.3111*log ₁₀ A	2.16048+0.529634*logA
<i>Bidentetea tripartiti</i> cl.	8	100.5087+31.8144*log ₁₀ A	2.21255+0.344139*logA
<i>Rhamno-Prunetea</i> cl.	9	102.8583+32.43686*log ₁₀ A	2.13221+0.285733*logA
Pioneer sandy swards	14	104.517+26.82645*log ₁₀ A	2.122565+0.2305655*logA
<i>Salici-Populetum</i> ass.	5	105.829+41.26823*log ₁₀ x	2.046844+0.252254*logA
<i>Polygonion avicularis</i> all.	18	106.855+32.0857*log ₁₀ A	2.42216+0.4252333*logA
<i>Molinion</i> all.	5	107.289+31.3814*log ₁₀ A	2.101256+0.220994*logA
<i>Ficario-Ulmetum</i> ass. Odra Valley	15	108.7264+49.67*log ₁₀ A	2.05396+0.306368*logA
<i>Caucalidion</i> all.	4	108.809+29.7553*log ₁₀ A	2.05702+0.167907*logA
<i>Ribeso-Alnetum</i> ass. ser. 2	5	113.844+24.78755*log ₁₀ A	2.056584+0.1122517*logA
<i>Aphanion</i> all.	8	113.95+42.8006*log ₁₀ A	2.1871+0.36788*logA
<i>Sisymbrietalia</i> ordo	21	115.6623+29.33453*log ₁₀ A	2.146163+0.206817*logA
<i>Tilienio-Acerenion</i> sall.	13	116.4793+50.3718*log ₁₀ A	2.142204+0.340818*logA
<i>Tilio-Carpinetum</i> ass.	5	116.794+61.13824*log ₁₀ A	2.06826+0.279381*logA
<i>Galinsogo-Setarietum</i> ass.	7	117.346+52.3623*log ₁₀ A	2.212835+0.405959*logA
<i>Dentario-Fagetum</i> ass.	18	117.9893+51.5522*log ₁₀ A	2.163175+0.372067*logA
<i>Arrhenatherion</i> all.	7	118.486+37.04115*log ₁₀ A	2.17372+0.2716225*logA
<i>Galio-Carpinetum</i> north ser.	16	119.923+85.1767*log ₁₀ A	2.06289+0.395269*logA
<i>Chenopodietea</i> class p.p.	6	120.5515+46.6393*log ₁₀ A	2.27352+0.4173684*logA
<i>Papaveretum argemones</i> ass.	9	131.6187+83.8319*log ₁₀ A	2.312407+0.659235*logA

1	2	3	4
<i>Fraxino-Alnetum</i> ass.	24	138.146+64.36627*log ₁₀ A	2.14935+0.3322536*logA
<i>Sedo-Scleranthetalia</i> ordo	10	141.6824+41.5411*log ₁₀ A	3.11668+0.634825*logA
<i>Ficario-Ulmetum</i> ass. (Sudetes foothills)	6	142.441+58.3965*log ₁₀ A	2.178056+0.2610573*logA
<i>Calthion</i> all.	13	143.845+46.9044*log ₁₀ A	2.366295+0.346467*logA
Thermophilous forest	8	145.5066+65.6929*log ₁₀ A	2.22877+0.335965*logA
<i>Vicetium teraspermae</i> ass.	11	150.3944+76.3576*log ₁₀ A	2.31755+0.466157*logA
<i>Echinochloo-Setarietum</i> ass.	18	150.739+85.27047*log ₁₀ A	2.364686+0.574823*logA
<i>Betulo-Adenostyletea</i> cl. (600-900 m a.s.l.)	5	153.502+60.70193*log ₁₀ A	2.53117+0.497017*logA
<i>Galio-Carpinetum</i> ass. (Sudetes foothills)	12	155.4563+86.83956*log ₁₀ A	2.2205+0.4081297*logA
<i>Alliarion</i> all.	6	163.2033+67.9784*log ₁₀ A	2.985906+0.781554*logA
<i>Eu-Arction</i> all.	11	173.529+57.69574*log ₁₀ A	2.6889+0.525343*logA
Synanthropic shrubs	7	174.114+75.6983*log ₁₀ A	2.64006+0.61561*logA
<i>Carici-Fraxinetum</i> ass. & <i>Stellario-Alnetum</i> ass.	14	175.0917+81.71495*log ₁₀ A	2.414206+0.4668243*logA
<i>Acerenion</i> sall.	7	188.1473+109.2406*log ₁₀ A	2.854465+0.946405*logA
<i>Onopordion</i> all.	7	188.7303+68.65533*log ₁₀ A	2.461195+0.375508*logA
<i>Festuco-Brometea</i> cl. p.p.	6	243.6343+86.49707*log ₁₀ A	2.59994+0.3804796*logA

Table 3

Coefficients A, B, c, z and r for each type of habitat described⁶.

Habitat	Gleason plot			Power function		
	A	B	r	C	Z	r
1	2	3	4	5	6	7
Bog coniferous woodland	20.80	5.38	0.74	1.33	0.15	0.75
<i>Lemnetea</i> class	39.35	9.36	0.71	1.64	0.19	0.72
<i>Potamion</i> all.	43.19	13.67	0.92	1.87	0.36	0.97
<i>Leucobryo- & Molinio-Pinetum</i> ass.	50.28	26.28	0.65	1.69	0.29	0.69
Alpine <i>Vaccinio-Piceion</i> forest (from 700 m)	50.39	26.92	0.69	1.78	0.45	0.68
<i>Nymphaeion</i> all.	51.55	21.53	0.89	1.95	0.49	0.94
<i>Phragmition</i> ser. 1	66.98	21.28	0.93	1.95	0.30	0.87
<i>Luzulo luzuloidis-Fagetum</i> ser. 1	70.43	37.67	0.94	1.95	0.46	0.94
<i>Asplenietea trichomanis</i> cl. (natural comm.)	73.08	21.26	0.92	2.46	0.48	0.97
<i>Pino-Quercetum</i> ass.	79.36	39.60	0.87	1.89	0.29	0.88
<i>Luzulo pil.-Fagetum & Abietetum polonicum</i>	79.48	50.48	0.94	1.94	0.50	0.77

⁶ Bolded r better fits the data.

1	2	3	4	5	6	7
<i>Quercion robori-petraeae</i> cl.	79.91	28.72	0.63	1.93	0.21	0.54
<i>Magnocaricion</i> all.	86.88	25.41	0.85	2.07	0.28	0.81
<i>Ribeso-Alnetum</i> ass. ser. 1	87.04	22.90	0.94	1.94	0.14	0.94
<i>Salix</i> thickets	87.45	28.40	0.83	2.25	0.41	0.87
<i>Phragmition</i> all. ser. 2	88.38	22.63	0.91	2.01	0.20	0.85
Forest plantation	89.07	40.42	0.83	2.06	0.42	0.80
<i>Luzulo luzuloidis-Fagetum</i> ass. ser. 2	89.92	33.78	0.75	2.04	0.29	0.81
<i>Galio-Carpinetum</i> ass. Odra Valley	99.51	36.38	0.97	1.99	0.20	0.96
<i>Trifolio-Geranietea</i> cl.	99.60	27.09	0.78	2.26	0.31	0.79
<i>Melico-Fagetum</i> ass.	100.02	56.66	0.92	2.01	0.35	0.94
<i>Tortulo-Cymbalarietalia</i> ordo	100.09	29.82	0.92	2.39	0.35	0.90
<i>Arnosseridi-Scleranthetum</i> ass.	100.44	53.31	0.83	2.16	0.53	0.90
<i>Bidentetea tripartitae</i> cl.	100.51	31.81	0.74	2.21	0.34	0.69
<i>Rhamno-Prunetea</i> cl.	102.86	32.44	0.85	2.13	0.29	0.87
Pioneer sandy swards	104.52	26.83	0.85	2.12	0.23	0.83
<i>Salici-Populetum</i> ass.	105.83	41.27	0.96	2.05	0.25	0.97
<i>Polygonion avicularis</i> all.	106.86	32.09	0.87	2.42	0.43	0.84
<i>Molinion</i> all.	107.29	31.38	0.81	2.10	0.22	0.76
<i>Ficario-Ulmetum</i> ass. Odra Valley	108.73	49.67	0.96	2.05	0.31	0.94
<i>Caucalidion</i> all.	108.81	29.76	0.56	2.06	0.17	0.50
<i>Ribeso-Alnetum</i> ass. ser. 2	113.84	24.79	0.71	2.06	0.11	0.75
<i>Aphanion</i> all.	113.95	42.80	0.77	2.19	0.37	0.90
<i>Sisymbrietalia</i> ordo	115.66	29.33	0.59	2.15	0.21	0.54
<i>Tilienio-Acerenion</i> sall.	116.48	50.37	0.85	2.14	0.34	0.84
<i>Tilio-Carpinetum</i> ass.	116.79	61.14	0.82	2.07	0.28	0.82
<i>Galinsogo-Setarietum</i> ass.	117.35	52.36	0.90	2.21	0.41	0.87
<i>Dentario-Fagetum</i> ass.	117.99	51.55	0.92	2.16	0.37	0.92
<i>Arrhenatherion</i> all.	118.49	37.04	0.90	2.17	0.27	0.94
<i>Galio-Carpinetum</i> north ser.	119.92	85.18	0.90	2.06	0.40	0.87
<i>Chenopodietea</i> class p.p.	120.55	46.64	0.83	2.27	0.42	0.92
<i>Papaveretum argemones</i> ass.	131.62	83.83	0.53	2.31	0.66	0.62
<i>Fraxino-Alnetum</i> ass.	138.15	64.37	0.90	2.15	0.33	0.86
<i>Sedo-Scleranthetalia</i> ordo	141.68	41.54	0.86	3.12	0.63	0.72
<i>Ficario-Ulmetum</i> ass. (Sudetes foothills)	142.44	58.40	0.78	2.18	0.26	0.76
<i>Calthion</i> all.	143.85	46.90	0.88	2.37	0.35	0.85
Thermophilous forest	145.51	65.69	0.85	2.23	0.34	0.84
<i>Vicetum teraspermae</i> ass.	150.39	76.36	0.69	2.32	0.47	0.67
<i>Echinochloo-Setarietum</i> ass.	150.74	85.27	0.54	2.36	0.57	0.57

1	2	3	4	5	6	7
<i>Betulo-Adenostyletea</i> cl. (600-900 m a.s.l.)	153.50	60.70	0.86	2.53	0.50	0.90
<i>Galio-Carpinetum</i> ass. (Sudetes foothills)	155.46	86.84	0.92	2.22	0.41	0.91
<i>Alliarion</i> all.	163.20	67.98	0.96	2.99	0.78	0.95
<i>Eu-Arction</i> all.	173.53	57.70	0.81	2.69	0.53	0.73
Synanthropic shrubs	174.11	75.70	0.85	2.64	0.62	0.86
<i>Carici-Fraxinetum</i> ass. & <i>Stellario-Alnetum</i> ass.	175.09	81.71	0.92	2.41	0.47	0.87
<i>Acerenion</i> sall.	188.15	109.24	0.98	2.85	0.95	0.97
<i>Onopordion</i> all.	188.73	68.66	0.80	2.46	0.38	0.79
<i>Festuco-Brometea</i> cl. p.p.	243.63	86.50	0.87	2.60	0.38	0.86

4.2. Species-area relationships for different habitat types

As shown in Tables 2 and 3, which summarize the calculations (see also Appendix I and II), there exist many single SPAR relationships, specific for various habitat types. There are very species-poor or very species-rich habitats, some with the number of species increasing very slowly, others – very quickly.

4.2.1. Forest habitats

Forest habitats are the best investigated, and almost 35% of basic tables (282 data records) concern forest communities. Thus the analysis of forest habitats can be more detailed.

Most data (174) come from well or very well preserved patches of the *Quercus-Fagetum* forest, in many cases within nature reserves, national parks or areas only slightly disturbed by forestry (like the Odra River Valley). In most cases, the SPAR relationships are very clear, their statistical significance is very high, and the determination coefficient values vary from 0.90 to 0.98.

The great variety of data allows not only to recognize the SPAR pattern for each community, but also for the smaller units, different due to their geographical location and history of human impact. Such various forms were recorded for e.g. the oak-hornbeam and ash-elm-oak riparian forest.

4.2.1.1. Oak-hornbeam forest

Within the oak-hornbeam forest four smaller units could be distinguished: three of *Galio-Carpinetum* ass. (Odra Valley, Wał Trzebnicki and Sudetes foothills) and one *Tilio-Carpinetum* ass. series.

The character of the curve, determined by *B* coefficient, shows significant differences between these four series. The first one is represented mainly by the community patches located in nature reserves (Kanigóra, Grodziska Ryczyńskie, Zwierzyniec) or within areas with relatively low forestry impact

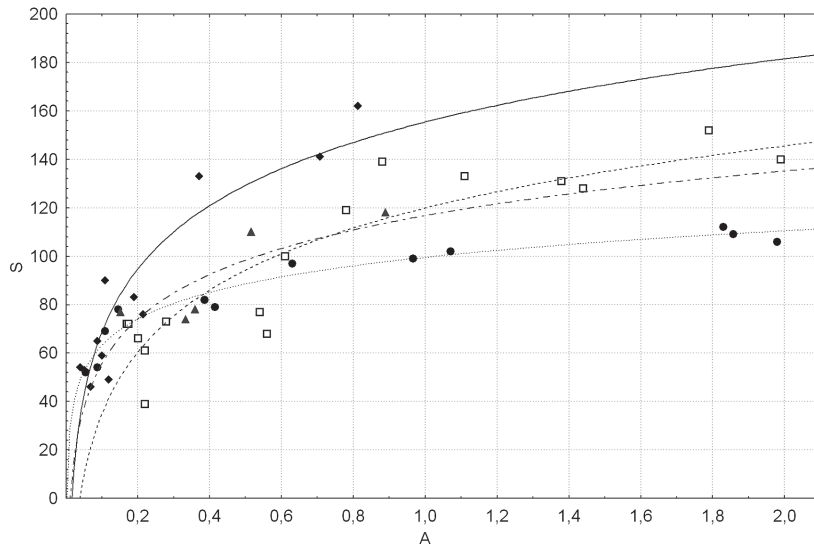


Fig. 4. SPAR relationships in four series of oak-hornbeam forests in Lower Silesia. Dots – *Galio sylvatici-Carpinetum* forest of the Odra River valley; squares – *Galio sylvatici-Carpinetum* forest of Wał Trzebnicki; diamonds – *Galio sylvatici-Carpinetum* forest of the Sudetes foothills; triangles – *Tilio-Carpinetum* forest, which in Lower Silesia has isolated south-western stands.

(other areas of the Odra and Bystrzyca river valleys). These are forests with a relatively long history of spontaneous evolution, and of almost natural origin, but with a high density of tree-tops and a small number of natural gaps. They are “closed” to incoming non-forest species, their species richness per hectare (A) is relatively low (99.5) and B coefficient is 36.4, but with a very high determination coefficient ($r^2=0.94$). The high r^2 means that the species composition of the Odra Valley oak-hornbeam forest is based mainly on core species.

The oak-hornbeam forest of Wał Trzebnicki has a different history. The forest is intensively managed, it has many gaps and it holds many thermophilous and nitrophilous species coming from the neighbouring communities such as meadows, tall herb communities or thermophilous swards. Its mean species richness A is high (119 species/ha), and the slope coefficient is almost 3 times higher than that of the preceding community ($B=85.18$). However, the determination coefficient of its Gleason equation is lower ($r^2=0.82$), which suggests a higher proportion of *common species*.

The oak-hornbeam forest south of the Odra line, situated within the Sudetes foothills, is extremely species-rich. The most probable explanation is that the effect of intensive management here is reinforced by the small size of the forest patches and the high soil fertility (most of the patches were found on basalts and greenstones). The slope coefficient is almost the same as the previous

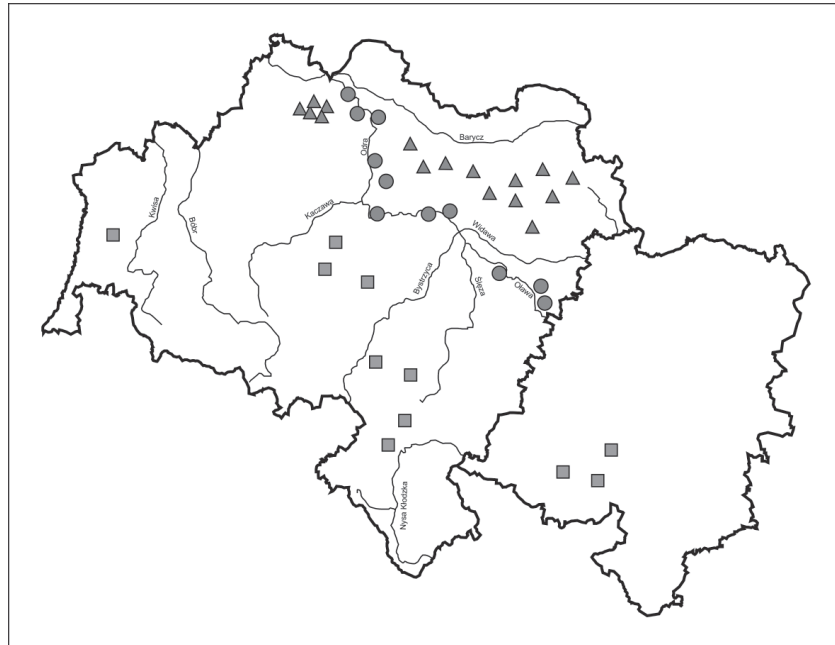


Fig. 5. Geographical distribution of three recognized series of *Galio-Carpinetum* forest (squares – Sudetes foothills series; circles – Odra Valley series, triangles - northern series of Wał Trzebnicki and adjacent areas).

one, but A is much higher ($A=155.45$), and the determination coefficient ($r^2=0.84$) is significantly lower than in the first series coming from little disturbed areas.

Due to their different history of anthropopressure, the three groups of the same forest association differ very much in species richness, and they are a good example of contiguous vector between the “closed” (almost natural forests of river valleys) and “open” (more intensively managed forest of the Sudetes which are split into small patches) communities.

4.2.1.2. Ash-elm-oak riverine forests (*Ficario-Ulmetum*)

The situation is very similar in the case of species richness of two series of *Ficario-Ulmetum*. The first SPAR pattern comes from the riverine forest (*Ficario-Ulmetum typicum*) in the Odra Valley. Like the Odra Valley series of *Galio-Carpinetum* ass., the forest is almost not managed, and many of its patches are within nature reserves or other protected areas. Its species richness is similar to that of the oak-hornbeam forests growing in the same biogeographical region ($A=108.7$; $B=49.7$), and the determination coefficient is very high ($r^2=0.92$). It probably means that the core species play the most important part in its species composition.

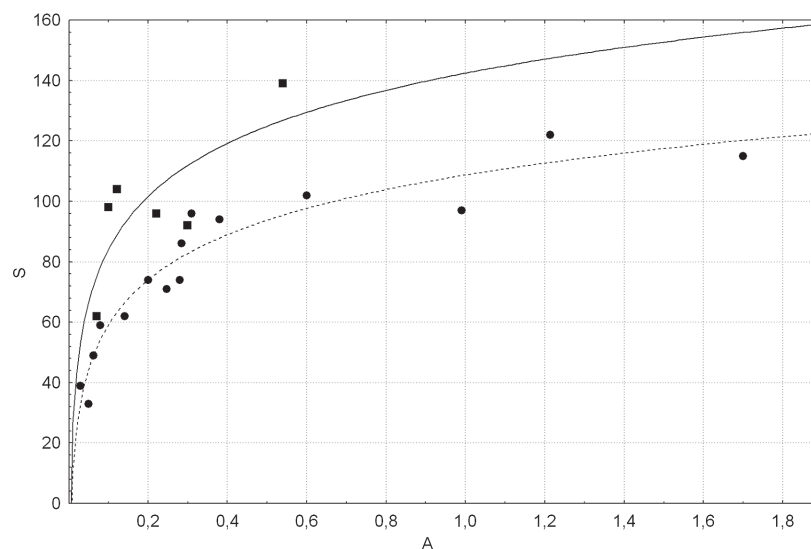


Fig. 6. Comparison of the SPAR relationship in two sets of data for riverine forest. Diamonds: *Ficario-Ulmetum typicum*, regularly flooded forms in the Odra valley; squares: *Ficario-Ulmetum chrysosplenietosum*, inland forms

The second SPAR pattern is typical of the subassociation *Ficario-Ulmetum chrysosplenietosum*, which is associated with small rivers and streams (the analysed data come from the Sudetes piedmont area, but the subassociation is also common in the Silesian lowland). This subtype is much richer in species than the previous one, which means that it is more “open” for the incoming species. In fact, the patches of *Ficario-Ulmetum chrysosplenietosum* are small, long and their perimeter/area ratio is much greater than in the typical form of this forest found in big river valleys. The determination coefficient is relatively low ($r^2=0.60$), which was observed also in the case of intensively managed oak-hornbeam forests and probably resulted from a high proportion of satellite species.

4.2.1.3. Acidophilous beech and beech-fir forest (*Luzulo nemorosae-Fagetum*, *Luzulo pilosae-Fagetum*, “*Abietetum polonicum*”)

Also in the case of *Luzulo nemorosae-Fagetum* it is possible to recognize two series of data, one poorer, with the SPAR relationship described by $A=70.43$, $B=37.67$, but with a very high determination coefficient ($r^2=0.94$); and another richer ($A=89.92$; $B=33.78$), but with a determination coefficient significantly lower ($r^2=0.75$).

It is unclear what causes this differentiation; the problem requires further studies. The most probable explanation is that this “unusually rich” form of

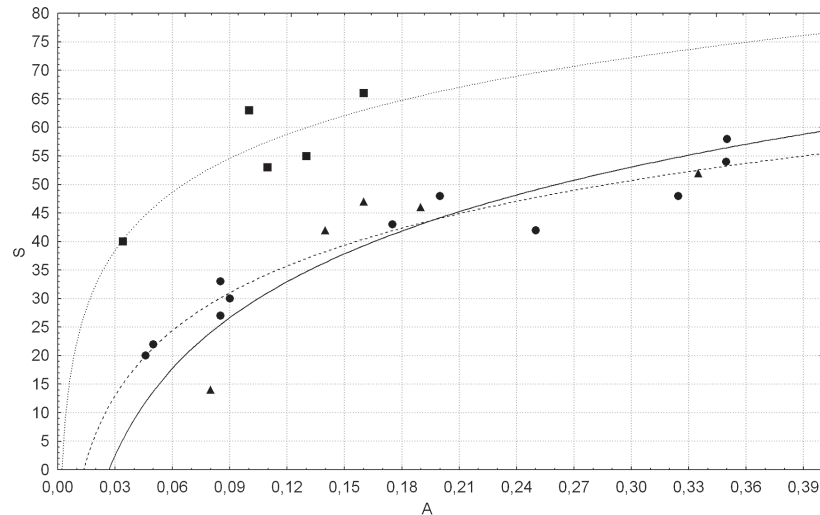


Fig. 7. Comparison of the SPAR relationship in three sets of data for acidophilous beech forests
 Circles: *Luzulo nemorosae-Fagetum* (“poor” series 1); triangles – *Luzulo pilosae-Fagetum*
 & “*Abietetum polonicum*”; squares – *Luzulo nemorosae-Fagetum* (“rich” series 2).

acidophilous forest is in fact a forestry-degraded form of other forest communities (e.g. rich beech forest or oak-hornbeam forest). This interpretation is supported by the result of calculations pertaining to:

- acidophilous beech and fir lowland forests, where A , B , and r^2 coefficients are almost the same as in the poor series of *Luzulo nemorosae-Fagetum*,
- well-preserved and almost natural *Galio-Carpinetum* forest, where A , B , and r^2 coefficients are almost the same as in the rich series of *Luzulo nemorosae-Fagetum*.

4.2.1.4. Sycamore-beech(-rowan) ravine forest (*Lunario-Aceretum* & *Sorbo-Aceretum* group)

This is a very unique type of habitat due to its almost natural origin and long history of spontaneous evolution. The light canopy with many gaps, fallen trees and open screes are conducive to occurrence of many different plants representing various ecological groups. Consequently, A coefficient is very high ($A=188.15$), and the slope coefficient indicates a very “open” community ($B=109$). The B value is one of the highest among all the investigated habitats.

4.2.1.5. Altitudinal differences – ash-alder and rich beech forest

These habitats show immanent differentiation, depending on association, which in the studied area is determined by altitudinal and geographical distribution.

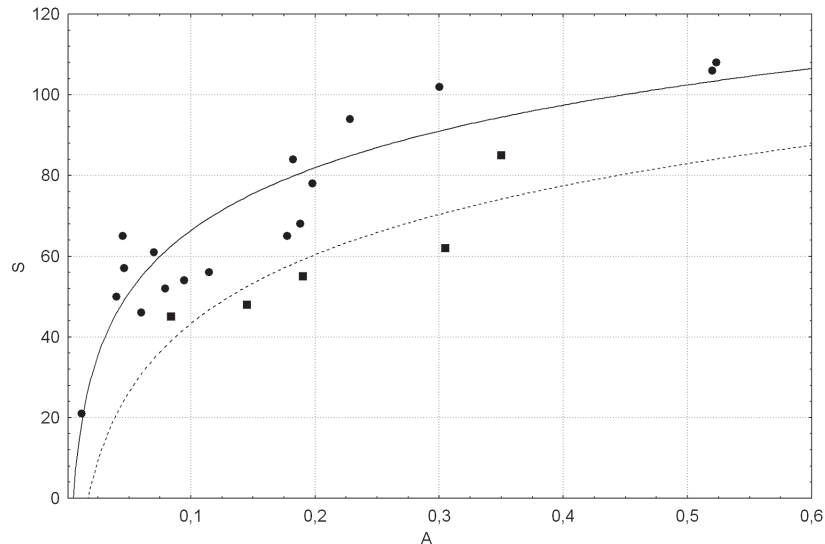


Fig. 8. Comparison of the SPAR relationship in two data sets for rich beech forest. Circles: *Dentario enneaphyllidi-Fagetum*, montane and submontane patches; squares: *Asperulo-Fagetum* (=Melico-Fagetum), lowland patches.

The lowland patches of ash-alder alluvial forest represent the association *Fraxino-Alnetum* while the montane and submontane patches are *Carici remotae-Fraxinetum* and *Stellario-Alnetum*. These two data sets are different – the montane and submontane patches are richer ($A=175.09$ vs 138.15), and their slope coefficient B is higher (81.71 vs 64.37). Their determination coefficient is similar (0.80 – 0.84).

The situation is analogous in the case of rich beech forest. The montane association (*Dentario enneaphyllidi-Fagetum*) is richer in species ($A=117.98$ versus 100.02) but its B coefficient is lower (51.55 vs 56.67). Also in this case the coefficients are very similar.

4.2.1.6. Ecological similarity between various kinds of broad-leaf forests

Comparison of SPAR relationships within groups of forest habitats under the influence of the same geographical sets of factors reveals an interesting situation. All the forest data which come from the Odra Valley show almost the same type of relationship. There is no good ecological explanation for it, since most ecological factors (such as the time of flooding, availability of nutrients, soil type, mean water level and others) are different for each habitat type. However, if this kind of relationship looks highly probable, in future studies we should check and consider the assumption that most well-preserved and almost natural forest communities in the region could have the same SPAR

relationship. It is supported by the results of Partel *et al.* (2001), who found that the mean α -diversity was significantly positively correlated with the number of core species. In natural communities (especially forest communities) the core species (plants growing in shady and humid habitats) play a more important role than satellite species.

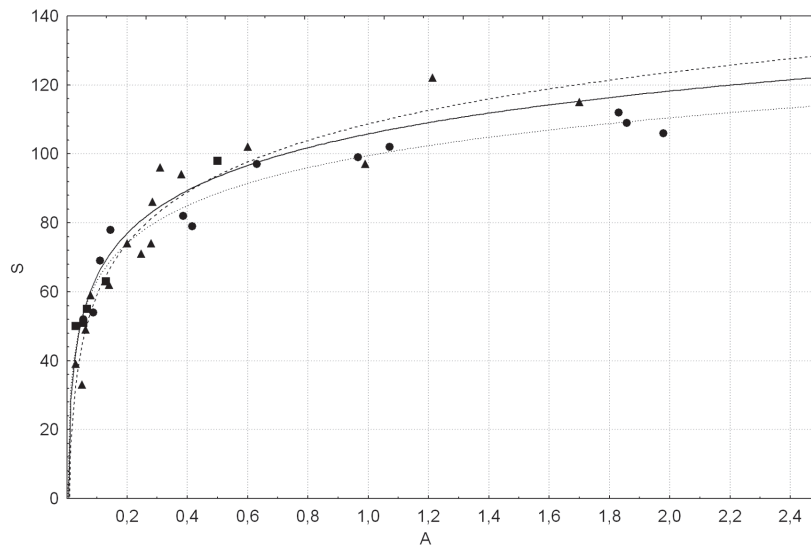


Fig. 9. Comparison of the SPAR relationship in three neighboring riverine forests in the Odra Valley.

Circles: *Galio-Carpinetum* (Odra Valley); squares: *Salici-Populetum*, triangles: *Ficario-Ulmetum* (Odra valley).

4.2.1.7. Alder peat-bog forest

Alder peat-bog forests (*Ribeso nigri-Alnetum*, incl. *Carici elongatae-Alnetum*) are also represented by two different series. Most of the patches show a typical pattern [$S=87.04+22.90*\log_{10}(A)$] with almost 90 species per hectare, but there are some patches of unusual richness with 15 more species per “first” hectare [$S=113.84+24.79*\log_{10}(A)$]. Like in the previous case, it is impossible to find any regional diversity because both the poor and the rich patches were located within the same areas (Kotlina Milicka, Pradolina Wrocławska). The explanation should be sought in the possibility that the rich patches could be open for the neighboring communities due to their small area and isolation, or – more convincingly – due to abiotic factors, e.g. occurrence of calcium in the ground water. Solving this problem will need further investigation.

4.2.2. Natural non-forest communities

The pattern characterizing the non-forest natural communities is very similar to the one discussed in the previous chapter.

4.2.2.1. Rock-dwelling communities (Cl. *Asplenieta trichomanis*, O. *Sedo-Scleranthetalia*)

Because all the available data come from very small patches, the obtained results are not directly applicable to real situations in the field (there are no patches of epilithic communities of 1 ha or more!). However, from the point of view of predicting the γ -biodiversity these results could be useful.

The high values of A and B coefficients ($A=73$ and $B=21$ in the *Asplenieta trichomanis* class, $A=141$ and $B=41$ in *Sedo-Scleranthetalia* epilithic communities) suggests that the occurrence of this vegetation type is very important for the analysis of γ -diversity, because even very small patches can add new species to the list of plants within the analyzed area.

A comparison between the natural and the synanthropic plant communities of the class *Asplenieta trichomanis* reveals that the latter are somewhat richer in species, and both their A and B coefficients are higher than in natural epilithic patches.

None of these types has a very high determination coefficient ($r^2=0.74$ to 0.84) which is not surprising considering the number of common species coming to patches of such communities.

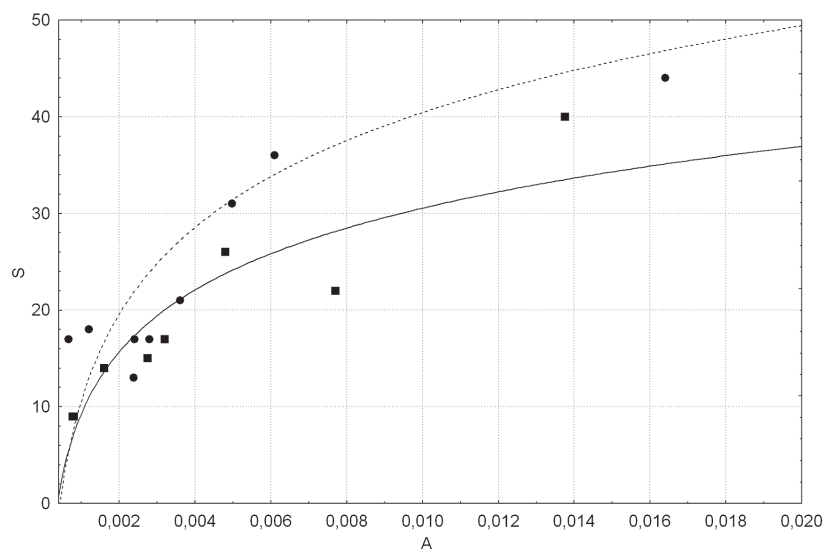


Fig. 10. Comparison between SPAR relationships of *Asplenieta trichomanis* class. Squares: natural epilithic communities; circles: wall synanthropic communities (*Tortulo-Cymbalarion* ordo)

4.2.2.2. Aquatic communities

Only two patterns are recognizable among aquatic communities. Pleustone communities (Cl. *Lemnetea*) are too unstable to yield statistically significant results.

However, the macrophyte still water vegetation of all. *Nymphaeion* and O. *Potametea* shows two similar diversity patterns (Fig. 11). Such communities are not very species-rich ($A=51.55$ and $A=43.19$), and their B coefficient is very low ($B=21.53$ and $B=13.67$), so that the SPAR curve flattens very quickly. The determination coefficient is rather high for *Potametea* communities ($r^2=0.84$), and lower for all. *Nymphaeion* ($r^2=0.79$)

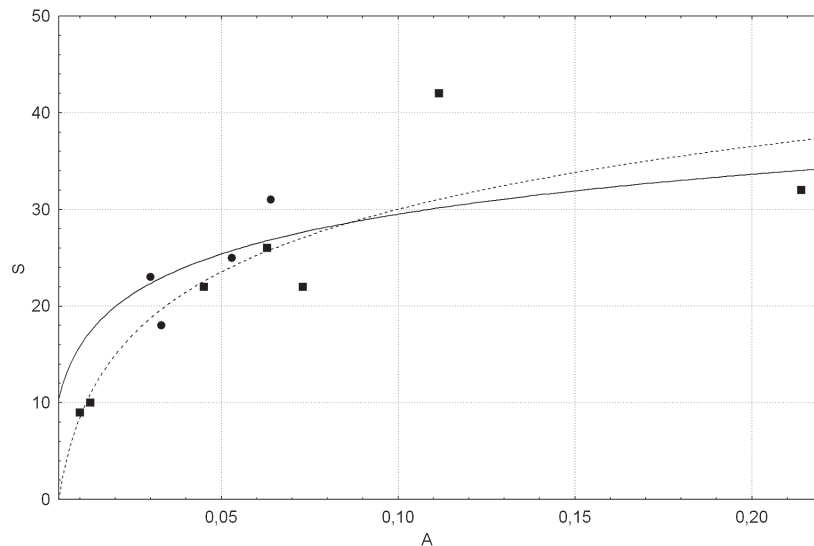


Fig. 11. Comparison of the SPAR relationship within the macrophyte still water vegetation. Circles: all. *Nymphaeion*; squares: *Potametea* ordo

4.2.2.3. River and lake shore communities

This category comprises grass-sedge, rush and muddy banks vegetation of the *Bidentea tripartiti* class. Their patterns are very similar; their A and B coefficients vary from 66 to 88 and from 21 to 25, respectively. Only communities of the *Polygono-Bidentetea* class are richer and their coefficients equal 100 (A) and 31 (B). The determination coefficient r^2 varies between 0.73 and 0.85.

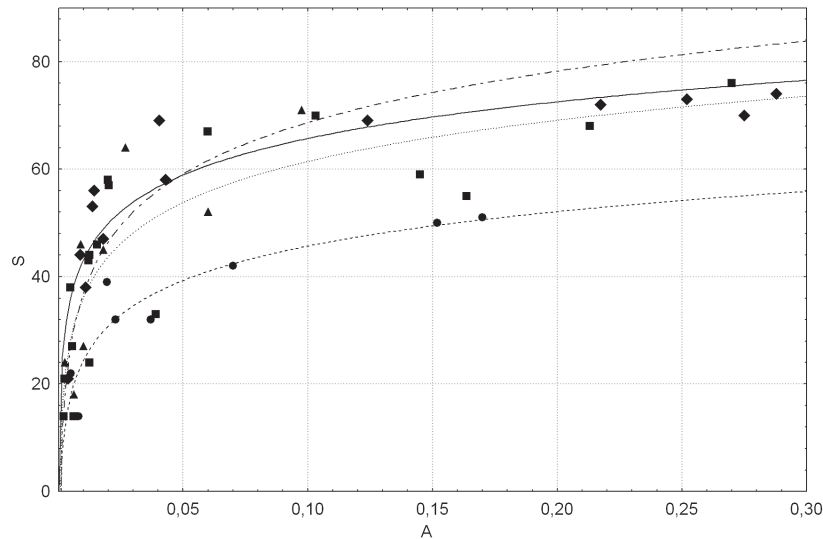


Fig. 12. Comparison of the SPAR relationship within two series of rush, grass-sedge and muddy bank vegetation

Squares: all. *Magnocaricion*; diamonds: all. *Phragmition* ser. 1; circles: all. *Phragmition* ser. 2; triangles: cl. *Bidentetea tripartiti*

4.2.3. Semi-natural non-forest communities

Seven semi-natural non-forest habitat types were examined. Only *Molinia* meadows showed no statistically significant correlation between the area and species number. For the remaining communities the results are significant.

The poorest communities are the pioneer sandy swards of the alliances *Vicio lathyroidis-Potentilletum* and *Koelerion glaucae* ($A=104.52$, $B=27.09$, $r^2=0.72955$) and dwarf swards of trodden habitats (all. *Polygonion avicularis*; $A=106.86$, $B=32.09$, $r^2=0.7511$). Likewise, lowland hay meadows (all. *Arrhenatherion elatioris*) are not very rich ($A=118.49$, $B=37.04$, $r^2=0.8027$). Species-rich habitats include wet meadows and tall herb communities (all. *Calthion* and *Filipendulo-Geranion*) of lowland areas ($A=143.85$, $B=46.9$, $r^2=0.7716$), as well as xerothermic swards representing the class *Festuco-Brometea* ($A=243.63$, $B=86.5$, $r^2=0.8705$).

Surprisingly, thermophilous lems (cl. *Trifolio-Geranietea*) in Lower Silesia are very species-poor ($A=99.6$, $B=27.08$, $r^2=0.6062$). The reason may be that in the region concerned this habitat type lacks many species typically occurring in south-eastern Poland.

In most habitat types discussed here the determination coefficient is about 0.80, which means that their species composition is quite stable, though it includes many satellite species.

4.2.4. Synanthropic communities

Most ruderal communities and their complexes (instances when various associations of the same higher physociological unit show the same SPAR patterns) are rich in species per unit area (100 to 188 species per hectare), but the determination coefficient and statistical significance of the results are low or very low (e.g. $r^2=0.35$ for the order *Sisymbrietalia*). Most of these habitats have many satellite species, and their structure is unstable, depending on the age and human impact. The exceptions are the wall vegetation of the order *Tortulo-Cymbalarietalia* ($r^2=0.84$, $p<0.001$) and the *Eu-Arction* alliance communities ($r^2=0.81$, $p<0.001$).

The segetal communities vary among themselves. Their A coefficient varies between 100 and 150, whereas r^2 ranges from 0.53 to 0.89. These communities depend greatly on the impact of agriculture, use of herbicides and probability of occurrence of satellite species.

4.3. Testing the γ -biodiversity model

To test the theoretical model of γ -diversity changes, I used the results of equations obtained in Appendix I and II of this paper and literature data on different types of study plots in south-western Poland (publications containing both lists of vascular plants and maps or detailed descriptions of communities which allowed to estimate the implicit area (in ha) occupied by particular communities or their complexes). It was necessary to limit the test to areas ranging from 1.25 to 137 ha, which included 13 nature reserves and 18 plots of 100 ha thoroughly studied in the Stołowe Mts. (Świerkosz 1998); larger areas were too insufficiently documented to be used in this study.

The theoretical model is described in Chapter 2.6. Testing the model was based on two independent data sets.

4.3.1. Equal-sized areas

To avoid an increasing area effect (Rosenzweig 1995), 18 equal-size areas (100 hectares each) were selected. All were situated in the Stołowe Mts. and were studied in detail by the author (Świerkosz 1998, unpubl.). The areas were chosen because of being the best studied and thus the probability of completeness of their species lists was high (Table 4, see also detailed analysis in Appendix VI). Please note that some of these 100-ha squares were used to prepare Figs 1 and 2 in this paper. For each coefficient ω was recalculated from the expected range of the model.

The best results were obtained for $\omega=0.29$ (the predicted and actual number of species differ by 10–11%) and for $\omega=0.30$ (difference 9–12%) as it was expected in Chapter 2.5.

Table 4

Comparison between the predicted and actual number of plant species on equal-sized 100-ha plots in the Stołowe Mts. (field data from Świerkosz 1998, unpubl.).

Tested area	S	A	H _n	S predicted ($\omega=0,24$)	Difference in %	S predicted ($\omega=0,25$)	Difference in %	S predicted ($\omega=0,26$)	Difference in %	S predicted ($\omega=0,27$)	Difference in %	S predicted ($\omega=0,28$)	Difference in %	S predicted ($\omega=0,29$)	Difference in %	S predicted ($\omega=0,30$)	Difference in %	S predicted ($\omega=0,31$)	Difference in %	S predicted ($\omega=0,32$)	Difference in %
Ostra Góra	264	98	6	266	-1	271	-3	276	-4	281	-6	286	-8	291	-10	296	-12	301	-14	307	-16
Duszniki	251	100	4	256	-2	260	-3	263	-5	267	-6	271	-8	274	-9	278	-11	282	-12	286	-14
N Łężno	262	100	6	248	5	253	4	257	2	262	0	267	-2	271	-4	276	-5	280	-8	235	-10
Niknaça Łąka	150	100	4	145	3	147	2	149	1	151	-1	153	-2	155	-4	157	-5	236	-7	240	-9
Wąwóz Czernicy	220	100	5	211	4	215	2	218	1	222	-1	225	-2	229	-4	233	-6	281	-7	286	-9
Łężno E	197	100	7	182	8	185	6	189	4	193	2	197	0	200	-2	204	-4	160	-6	162	-8
Kamień Popielny	252	100	7	220	13	224	11	229	9	233	7	238	6	243	4	247	2	208	-6	212	-8
Pośna	261	100	6	227	13	231	12	235	10	239	8	243	7	248	5	252	3	255	-2	260	-4
Danczówka	255	100	5	222	13	225	12	229	10	233	9	236	7	240	6	244	4	337	1	343	-1
Jeżowice	213	100	6	203	5	207	3	211	1	214	-1	218	-2	222	-4	226	-6	252	0	257	-2
Grodziec*	339	100	5	301	11	306	10	311	8	316	7	321	5	326	4	332	2	257	2	261	0
N Karłów	261	100	8	215	18	220	16	224	14	229	12	234	10	239	9	244	7	278	2	283	0
Central Karłów	282	100	8	240	15	245	13	250	11	255	9	261	8	266	6	272	4	248	3	252	1
Pasterka, pn	250	100	7	223	11	227	9	231	7	236	6	241	4	245	2	2	0	214	5	218	4
S Karłów	245	100	8	202	17	207	16	211	14	215	12	220	10	224	8	229	6	234	4	239	2
Ptasia Skala	226	100	5	191	15	194	14	198	13	201	11	204	10	207	8	211	7	249	5	254	3
Pasterka, pd	287	100	7	236	18	241	16	245	14	250	13	255	11	260	9	265	8	271	6	276	4
Białe Ściany	209	100	7	169	19	173	17	176	16	180	14	183	12	187	11	190	9	194	7	198	5

Explanation: S – number of species counted in the field
A – area of investigation

H_n – habitat number
* – data from Kwiatkowski, Struk 2003.

Table 5
Comparison between the actual and predicted species number in nature reserves of unequal size

No of site	Tested area (nature reserves)	S (in field)	A	Hn	Results																			
					S predicted ($\omega=0.24$)	Difference in %	S predicted ($\omega=0.25$)	Difference in %	S predicted ($\omega=0.26$)	Difference in %	S predicted ($\omega=0.27$)	Difference in %	S predicted ($\omega=0.28$)	Difference in %	S predicted ($\omega=0.29$)	Difference in %	S predicted ($\omega=0.30$)	Difference in %	S predicted ($\omega=0.31$)	Difference in %	S predicted ($\omega=0.32$)	Difference in %	S predicted ($\omega=0.33$)	Difference in %
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	Kanigóra	134	5.6	2	142.17	-6.10	143.16	-6.84	144.16	-7.58	145.16	-8.33	146.17	-9.08	147.18	-9.84	148.21	-10.60	149.24	-11.37	150.28	-12.15	151.32	-12.93
2	Puszcza Śnieżnej Białki	147	159.1	4	141.70	3.61	143.67	2.26	145.68	0.90	147.71	-0.49	149.78	-1.89	151.87	-3.31	153.99	-4.75	156.14	-6.21	158.32	-7.70	160.53	-9.20
3	Grodzisko Ryczyńskie	92	1.7	2	91.72	0.31	92.36	-0.39	93.00	-1.08	93.64	-1.79	94.30	-2.50	94.95	-3.21	95.61	-3.93	96.28	-4.65	96.95	-5.38	97.62	-6.11
4	Olszyny Niezgodzkie	247	74.2	7	222.17	10.05	226.53	8.29	230.98	6.48	235.52	4.65	240.15	2.77	244.87	0.86	249.68	-1.09	254.59	-3.07	259.59	-5.10	264.69	-7.16
5	Jodłowice	128	9.6	2	125.75	1.76	126.63	1.07	127.51	0.38	128.39	-0.31	129.29	-1.01	130.19	-1.71	131.09	-2.42	132.00	-3.13	132.92	-3.85	133.85	-4.57
6	Radunia	193	44.7	4	177.94	7.80	180.43	6.51	182.95	5.21	185.50	3.89	188.09	2.54	190.72	1.18	193.38	-0.20	196.08	-1.59	198.81	-3.01	201.59	-4.45
7	Góra Słęża	188	140.3	4	173.11	7.92	175.52	6.64	177.97	5.33	180.46	4.01	182.98	2.67	185.53	1.31	188.12	-0.06	190.75	-1.46	193.41	-2.88	196.11	-4.31

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
8	Uroczysko Obiszów	167	6.1	4	145.94	12.61	147.98	11.39	150.04	10.15	152.14	8.90	154.26	7.63	156.42	6.34	158.60	5.03	160.81	3.70	163.06	2.36	165.33	1.00
9	Krokusy w Górzyniu	167	3.9	5	141.15	15.48	143.44	14.11	145.77	12.71	148.14	11.30	150.54	9.86	152.98	8.39	155.46	6.91	157.99	5.40	160.55	3.86	163.15	2.30
10	Las Bukowy w Skarszynie	205	23.4	5	170.07	17.04	172.83	15.69	175.64	14.32	178.49	12.93	181.38	11.52	184.33	10.08	187.32	8.63	190.36	7.14	193.44	5.64	196.58	4.11
11	Zwierzyniec	190	9.1	3	163.69	13.85	165.50	12.89	167.33	11.93	169.18	10.96	171.05	9.97	172.94	8.98	174.85	7.97	176.78	6.96	178.73	5.93	180.71	4.89
12	Góra Miłek	260	137.3	6	210.61	19.00	214.42	17.53	218.30	16.04	222.24	14.52	226.26	12.98	230.35	11.40	234.52	9.80	238.76	8.17	243.07	6.51	247.47	4.82
13	Wzgórze Joanny	236	25.3	6	182.61	22.62	185.91	21.22	189.28	19.80	192.70	18.35	196.18	16.87	199.73	15.37	203.34	13.84	207.02	12.28	210.76	10.70	214.57	9.08

4.3.2. Different-sized areas

Thirteen independent sites are presented in Table 5 (see also Appendix IV). For each site the number and area of plant communities were counted, and the number of plant species of each community calculated using a single equation for each community. Then the presented model (Equation 5) was used to calculate the predicted number of species in each square. For each coefficient ω from the expected range (0.24 up to 0.32) the model was recalculated.

The best results were obtained for $\omega=0.31$ and $\omega=0.32$, as was supposed earlier in chapter 2.5. The differences between the actual and predicted values ranged from -12% to +12%. This indicates that the proposed model is a good predictor of the number of species actually existing in an area, the more so that the inventory of plant species counted in the field may sometimes be incomplete. For example, Anioł-Kwiatkowska & Weretelnik (1995a) recorded 97 higher plant species from the Kanigóra nature reserve, and other counts, performed by Kaćki & Dajdok (pers. comm.) yield the number of 134. Since the difference in the number of plant species obtained by various botanists in the field can be as wide as 50%, the discrepancy between the actual and model-generated values is not great.

5. Discussion

5.1. Simplification of the model

Compared to the curve obtained from canonical SPAR theory, the actual increase in species diversity looks like a very complex plot of sigmoid function (Fig. 3). The presented model is a simplification of a much more complex dependence, but as long as it fits the data and helps predict species diversity, it can be useful in conservation biology. Theoretically, the degree of the model's simplification should decrease with increasing number of habitats, but no such tendency was observed in the analyzed data. The problem needs further studies.

The model will also fail for rarely occurring sets of independent ecosystems such as a xerothermic sward bordering with peat-bog, or a calcareous rock surrounded by heaths, with no, or almost no common species. In such cases a simple sum of species found in these habitats (β -diversity level) will sufficiently describe the complete species set in a multi-habitat area (cf. Koleff *et al.* 2003). Such cases are nevertheless very rare.

5.2. Comparison of various models of species richness prediction

One of the most interesting models in the debates on the area-habitat issue has been proposed by Triantis *et al.* (2003). Their model, called *choros*, considers both the area and the number of habitats, modifying the classical equation $\log(S) = \log c + Z \log(A)$ to

$$\log(S) = \log c + Z \log(K)$$

where K is called the "choros" value, defined as

$$K = H * A$$

Where H is the number of habitats, a A is the area.

Having constructed the model, Triantis *et al.* (2003) compared various species-area relationships from 22 data sets and recalculated them using the "choros" coefficient. The use of the modified coefficient in the species-area equation gave a better fit, and the prediction value was much higher than that obtained when using A only. Their recalculated data sets included some on plant species, however z coefficient varied between 0.09 (data from Nilsson *et al.* 1988; after Triantis *et al.* 2003) and 0.51 (data from Deshayé, Morisset 1988; after Triantis *et al.* 2003), and thus was not useful for predicting the number of species. Whittaker & Fernandez-Palacios (2007) pointed to two problems with the model. The first is the *sensitivity of outcome to how habitats are defined*; the second involves standardisation of K parameter.

A very interesting *habitat-unit model of island biogeography* was proposed by Buckley (1982), where the three independent species area-relationships were applied to three main types of island habitats. Contrary to the model proposed here, values obtained for these relationships were summed for the whole island (in my model this sum is only a step in the modelling, and it is divided by the number of habitats, to obtain the mean number of species per habitat). He found a better fit for the number of species counted in the field than for the area-based prediction. In his later paper however he found the area to be the primary determinant of the total species number (Buckley 1985).

There are many so called *predictive* models based on various kinds of *multiple regression analysis* (or multiple logistic regression, e.g. Hill, Keddy 1992; Wohlgemuth 1998; Pollock *et al.* 1998; Ricklefs, Lovette 1999; Bastin, Tho-

mas 1999; Morand 2000; Sanchez, Parmenter 2002; Ma *et al.* 2002; Rejmánek, Rejmánková 2002; Bio *et al.* 2002; Harrison *et al.* 2006) but none of them is really predictive. They are applicable mainly each to one data set, analysed directly, and explain the current plant species richness using various factors rather than predicting the species number. Though in many cases (e.g. Bio *et al.* 2002) the model gives a good prediction of probability of occurrence of some plant species due to their ecological requirements, it is useless for predicting the number of plant species per unit area. Comparable results, though with the use of *indirect gradient analyses* (CA and CCA), were obtained for the distribution of alpine plant species in the Tirol alpine-nival ecotone (Gottfried *et al.* 1998)

One of the most interesting models of this group is the *Interim General Model* (O'Brien 1998), which tries to integrate climate variables, water and energy dynamics to predict the richness of woody plants over extensive areas such as Africa or South America. The water-energy model was also tested by Whittaker *et al.* (2007) in Europe, but only using generalized additive models (GAMs).

The last decade has brought many models using advanced techniques and new statistical procedures, such as *Geographic Information System* (Kadmon, Danin 1997; Loo de *et al.* 1998; Rutledge *et al.* 2004), *boosted regression trees* (Thuiller *et al.* 2006), rarefaction method (Koellner *et al.* 2004) or various kinds of computer modelling (Pyšek *et al.* 2002; Desmet, Cowling 2004; Elith *et al.* 2006), but it is quite a different kind of modelling, based on satellite images, topographic data, climatic features, soil and land use analysis of wide areas (whole countries or even geographical regions).

The most interesting models in this category is that of Waldhardt *et al.* (2004), combining advanced GIS techniques with extensive field exploration. The predictive power of their model is roughly the same as that of the model presented here (deviating from actual values by about 10%), at least for plot sizes of more than 0.25 ha. Smaller plots are overestimated due to a methodological artifact (cf. Waldhardt *et al.* 2004, p. 221). The method used in this study is however quite different because it is based on the probability of occurrence of species precisely counted in the field at the beginning of this study.

5.3. Habitat information conveyed by the Gleason plot

5.3.1. Species-poor and species-rich habitats (from *closed* to *open* plant communities)

The first important information yielded by the Gleason plot is the value of *A* coefficient. The coefficient conveys direct information on the number of plant species occurring in each habitat in the analyzed unit areas – when these ar-

as equal 1, \log_{10} of 1 is 0, and only A coefficient occurs in the equation. In this paper the analyzed unit area is a hectare, hence A conveys direct information on the species richness of 1 ha of each plant community. A coefficient varies very widely, from 20 to nearly 240, which means that in different habitats from 20 to 240 species (in the case studied) could occur per hectare.

The lowest A coefficient characterizes very specific communities such as peat-bogs, still water or rock-dwelling communities, which can hold only a very small number of species, adapted to particular conditions. However, there are important differences between these communities. The peat-bog or still water communities are occupied by a specific group of species which are associated only with this type of habitat (due to their ecological requirements), with no *satellite* species coming from the neighbouring habitats. In contrast, the rock-dwelling communities, besides such a group of core species (e.g. *Asplenium* sp. div.), include also many *satellite* species penetrating from the neighbouring communities such as forests, thermophilous swards or synanthropic communities (Świerkosz 2004). These common species however are not sufficiently dominant in the general species composition to be important in the counts of the total number of species. Each group of rock-dwelling communities releves contains only a few such “immigrants”, so that their presence in the whole analyzed material is insignificant. This situation was analyzed by Holt *et al.* (1999), who pointed out that in general communities with low trophic rank were closed to immigration and species-poor.

On the opposite pole of this “richness” scale are very rich communities such as xerothermic swards or ash-alder submontane forests. Their case is also different.

A xerothermic sward has a specific flora of higher plants which is very species-rich, with many unique components growing only in that particular type of habitat. Many species of extensively managed meadows and pastures accompany these core species, additionally increasing the richness.

The situation is still different in a submontane ash-alder forest. It holds only a few characteristic species, but numerous species from other ecological groups accompanying them (forest, meadow and spring species, submontane and nitrophilous tall herb communities, etc.).

This shows that both “closed” and “open” plant communities can occur within the same general habitat type (such as forest, meadow or grassland), since these types may have different histories, ecological features and varied human impact.

There exist two types of “open” plant communities.

The first includes communities which are really open for species from various ecological groups, due to their immanent differentiation, occurrence of a wide set of microhabitats or specific features of their species composition. Examples

are some *Festuco-Brometea* swards, thermophilous forests (*Quercetalia pubescentis-petraeae* ordo) or ravine forests of *Acerenion* suballiance. These types of communities, as shown by Cornwell & Grubb (2003), are recruited from both nutrient-rich (forest communities) and nutrient-poor soils (swards).

The characteristic feature of the second type of “open communities” is their species diversity with many common species coming from the neighbouring communities due to their synanthropization, small patch size or greater perimeter/area ratio compared to the “closed” communities. The “open” communities are richer in plant species, even when they belong to the same phytosociological units as their “closed” vicarious subassociations (case of oak-hornbeam or riparian forest, described in Chapter 4.). The majority of such species-rich communities (submontane ash-alder forest, thermophilous and nitrophilous tall herb communities, some synanthropic communities and their complexes, meadows and swards) are “open” to immigration of *common* species, due to their patch size, perimeter/area ratio or average intensity of anthropopressure (e.g. Whitehead, Jones 1968; Tabarelli *et al.* 1999; Moody 2000; Ma *et al.* 2002; Decocq *et al.* 2004). Also the intensity of management plays an important role. Traditionally managed meadows show a higher species richness compared to intensively cultivated ones (see also Myklestad, Sætersdal 2003).

The best exemplification of this problem is the occurrence of three different groups of oak-hornbeam forest (*Galio sylvatici-Carpinetum*) within the investigated material. Due to their different history of anthropopressure, the three groups of the same forest association differ very much in their species richness, and they are a good example of contiguous vector between the *closed* (nearly natural forests of river valleys) and *open* communities (more intensively managed forest of the Sudetes, divided into small patches and open to immigration of non-native species) (cf. Wu, Vankat 1991; Holt *et al.* 1999; Battles *et al.* 2001; Keeley 2002; Decocq *et al.* 2004). Only Lawesson *et al.* (1998) found an opposite relationship, because of the more intensive management in larger forest patches in Denmark, compared to smaller ones.

In conclusion:

1. The *A* coefficient is crucial for the distinction between the poor and the rich communities. It was confirmed by Partel *et al.* (2001) that the *intercept of the curve* is significantly positively correlated with the number of core species and responsible for the α -diversity; Keeley & Fotheringham (2003) found that it had “*some predictive value in ecological communities*”.

2. Its value conveys more information on species richness than the mean number of species per releve. The phytosociological relevés vary in size from 4 (pleustone or rock-dwelling communities) to 200 square metres (Chytry, Otypkova 2003), however relevés ranging from 1 to 1200 square metres are

sometimes encountered. Comparison of such material is impossible – the intercept of the curve can standardize this value

5.3.2. Rate of and reasons for the increase in biological diversity (the role of B and z coefficients)

Since the slope coefficient (z or B) changes regularly due to the increase in the combined area of patches investigated (as clearly shown by Crawley, Harral 2001), it is not advisable to analyze the slope as a constant value, independent from the area of plant communities taken into consideration. Counting the slope coefficient is useful only in a situation analogous to that discussed in the above mentioned paper, i.e. when the area of the plant community falls between 1 m² and 5 ha. Crawley & Harral (2001) give a value of z for this range of area size between 0.2 (1 m²) and 0.37 (25 ha), but with the maximum value of 0.53 to 0.57 for 1 ha and 4-ha plots, thus suggesting that “*Instead of one process determining changes in species richness across a wide range of scales, different process might determine plant biodiversity at different spatial scales*”. However, the maximum value is reached not only by simply increasing the area, but also by addition of new habitats, and when the number of habitats is full, the slope coefficients rapidly drop. Also Sagar *et al.* (2003) demonstrated that the z coefficient was significantly affected by scale, and decreased with increasing scale. A similar result was obtained by de Bello *et al.* (2007), who found that α -diversity followed a similar pattern as z coefficient. Only Weiher (1999) suggests independence of z coefficient.

Another interesting finding by Crawley & Harral (2001) is that in species-richer habitats (meadows and waste ground) the effect of changes in the *slope value* is significantly lower than in species-poor habitats (forest and bracken). These effects are due to the plant size (especially with very small patch areas), and to the more even distribution of species (comp. also Kilburn 1966).

The z coefficient may also be affected by habitat fragmentation and isolation (Brooks *et al.* 1997; Lomolino 2001a; Ovaskainen, Hanski 2003), or even by grazing (de Bello *et al.* 2007) and may increase, which results in flattening of the SPAR curve. It is also obviously latitude-dependent (Malyshev 1991 in Hill 2001), varying from 0.038 in the Arctic tundra to 0.224 in southern Africa. The value typical of central Europe (at wide scale) is $z \sim 0.15$.

The slope coefficient B in the investigated cases varied from 5.38 to 109.24, and z varied from 0.11 to 0.95. The maximum z values are higher than ever described in the mentioned papers. I did not study the *core/satellite* species, and thus have no grounds to claim that the slope coefficient is correlated with the number of satellite species, as should be assumed. However A and B coefficients are highly positively correlated ($r=0.82$), and c and z are correlated in the same way ($r=0.68$).

In conclusion: It means that they are interdependent, and the slope coefficient B independently does not play any important role in explaining plant species richness in the analyzed cases (as opposed to such correlation found by e.g. Kilburn 1966 or Niklas *et al.* 2003). The use of slope coefficient as an index of habitat heterogeneity is not justified either (see Wilson, Shmida 1984).

5.4. Discretion versus self-similarity of plant communities⁷?

For many years, almost since the advent of plant ecology, we have believed that plant communities really or “almost really” exist and have their own “species pattern” (Archibald 1949). Each community has distinct boundaries within which its species composition is more or less homogenous, and the transition between the communities is relatively quick. This belief was a cornerstone of every phytosociological concept. This hypothesis is known as a *discrete-community concept*, and it is quite a good explanation of local plant diversity, at least for the temperate zone (cf. Condit *et al.* 1996, who suggest that tropical forests lack well-defined communities).

On the other hand, many researchers, starting with Robert Whittaker, believe that these “really” existing communities are only artifacts, and plant species respond primarily to the environment, and not necessarily in any coordination with other, co-occurring species. Harte *et al.* (1999a, 1999b) maintain that the same pattern of heterogeneity is seen at all spatial scales, with no distinction between communities and their neighbourhood. Wilson & Chiarucci (2000, 2001) tried to support this theory, of the so-called “*self-similarity*”, by counting the number of species in wide areas (Tuscany, Italy) from small patches of oak-forest, but as rightly observed by Hills (2001) they failed. Their results were probably only an artifact because they disregarded the changes of the slope coefficient (z , as they used the power function) with increasing area (cf. Crawley, Harral 2001). Maddux (2003) tested this hypothesis mathematically, and clearly showed that the power law for the species-area relationship arose from the probability rule only under special circumstances which depended upon the specific bisection scheme used to break the landscape.

Green *et al.* (2003) found some support for fractal species-distribution, though they also suggested that across spatial scales between 0.008 and 64 square metres the species distribution was non-fractal. Some species used in their study had spatial structure depending on their ecological requirements. On the other hand, it may suggest that the self-similarity occurs only *inside* the communities, but not *between* them. Also other authors found more arguments against

⁷ The term self-similarity of plant communities comes from papers of Harte *et al.* (1999a), Wilson, Chiarucci (2000, 2001) and Connor, McCoy (2001); in many earlier papers a similar concept was described as continuous plant cover.

the *discrete-community theory* than against the competing one, both empirical (Sagar *et al.* 2003) and theoretical (Maddux, Athreya 1999; Maddux 2003). Yet, the debates still continue (Lomolino 2001a, 2001b, 2002; Lennon *et al.* 2002; He, Legendre 2002; Green *et al.* 2003; Ostling *et al.* 2000, 2003, 2004).

In conclusion:

This paper is not capable of providing a full answer to this complex question, but the results suggest that the borders between communities are sharp rather than soft, and the *self-similarity concept*, although very interesting and theoretically well justified, is of limited usefulness.

The main argument against the *self-similarity* concept, coming from my studies, is the big difference in the number of species per 1 ha (A coefficient in the Gleason plot) recorded for closely related communities (e.g. within various forest associations of the alliance *Alno-Padion*, even within three different forms of *Galio-Carpinetum*).

5.5. Applicability of the power function to small patches

Papers dealing with the SPAR usually express a conviction that the classical power function ($S=cA^z$) is useful only at bigger scales, e.g. plots of 1–3 ha (Gentry 1988; Tuomisto *et al.* 1995), ones exceeding 2 ha (Plotkin *et al.* 2000) or 3 ha (Sagar *et al.* 2003). Furthermore, Dony (1977) found a significant change in the slope coefficient for a plot of 0.25 ha (2500 square metres), suggesting that the Gleason plot is useful only up to this size scale, and the SPAR in wider areas should be described by power function.

Also Condit *et al.* (1996), using the power function, maintain that an area containing 1000 tree trunks in a tropical forest would yield a prediction for the number of species per 50 ha. Such an area varies from 1500 m² (*Dipterocarpaceae* forest in central Malaysia) to 0.5 ha (*Tectona grandis* dominated forest in Tamil Nadu, India). However, the methods of the grid-point system employed by Condit *et al.* (1996) and Plotkin *et al.* (2000a) have weak points, which were brilliantly discussed by Williamson (2003), and their results may not be as significant as they thought. Finally, Sagar *et al.* (2003) showed that the *slope coefficient* in power function was significantly correlated with the scale, and is decreased with increasing area.

In the cases analyzed however there are no distinct differences between the results obtained with the Gleason plot and with the power function (see Table 3). Determination coefficient r^2 calculated both from the first and the second equation are similar. In some cases the Gleason plot seems to generate better prediction of the species number, because it gives higher r in 33 relationships (against power law – better r in 21 cases). This means that power law may be useful not only for patches exceeding 1–3 ha, as was described in

the mentioned papers, but also for very small ones (as suggested by Kilburn in 1966). The power law was sometimes used for such areas not exceeding 2 square metres (e.g. Gonzales 2000). Keeley & Fotheringham (2003) found a better fit of the power model in the majority of Mediterranean communities, but the exponential model gave a better fit for communities with preponderance of annual plants.

5.6. Small island effect – does it work within habitats?

Preston (1962a, 1962b), in his basic study of the species-area relationship, was the first to notice the problem of “sigomidality” of the species-area curve. He observed this effect, albeit without providing any explanation. The problem occurred on too small islands, which were not able to hold too many individuals, and in some areas which did not show the canonical SPAR. Lomolino (2000c) and Lomolino & Weiser (2001), when looking for the border between big and small islands (both marine and terrestrial), found a break-point value T_1 (for plants) between $10^{1.7}$ and $10^{7.8}$ (50 and 6400 square metres, depending on the investigated archipelago). In their hypothesis an area smaller than the break-point value showed a *small island effect*, and the prediction of its species composition by the power function or semi-log equation was incorrect. The *small island effect* was confirmed in many cases (Lomolino 2000c) and described in detail at least for some invertebrate (Connor *et al.* 2000) and vertebrate communities (Connor *et al.* 2000; Lomolino, Perault 2000, 2001; Lomolino, Smith 2003a, 2003b), but it seems to be an intuitive concept and should be applicable also to plant communities.

This problem needs further studies, with a necessary search for data that would fit the sigmoidal-hill function proposed by Lomolino (2000c). However, as the species pool for each community is open (due to the occurrence of *common species*), the S_{\max} will always be only a theoretical construct as it approximates the asymptote (Lomolino 2000c; Williamson *et al.* 2001; Bartha, Ittzes 2001).

In conclusion: The area of most habitat patches analysed in this paper is within an exactly specified range (the area of a community varied from 1 square metre to a few ha), however the data analysis showed no break-point, contrary to what was predicted by Lomolino (2000c) or Lomolino & Weiser (2001). All the patches analysed showed features of islands beyond the upper limit of SIE, where plant species diversity appears to be more deterministic and can be predicted based on the area size and ecological factors. Probably, the reason is that the data were analysed not as related to independent islands, but as an element of the habitat, and the habitat’s capacity for holding the suitable number of species is constant *within* each community.

5.7. Consequences for the SLOSS problem

The SLOSS (*Single Large or Several Small* – Higgs, Usher 1980) problem has not really been defined yet or – at least – the definition seems insufficient. As shown by the sigmoidal SPAR models (Williams 1995; He, Legendre 1996, 2002; Lomolino 2000c, 2001b; Lomolino, Weiser 2001), the real problem of SLOSS may be defined at least for the moment when the area is wider than the T_2 value, and it allows for *in situ* speciation. The results of the current work permit to say that small habitat patches could play for plant species the same ecological role as a single well-preserved patch, of an area equal to combined small patches, at least when we consider the local higher plant diversity. This has also indirectly been indicated by the results of Price (2004) pertaining to the Maui Nui island complex, or by Oertli *et al.* (2002) in ponds of Switzerland. The real problem of SLOSS lies in the areas below the T_1 (“break-point” in the sense of Lomolino, Weiser 2001; Lomolino, Smith 2003a), where the habitat patches are unable to exist independently, as they are too sensitive to external and stochastic catastrophes; and beyond the T_2 (above the second break-point on the sigmoidal curve), where independent speciation could take place (e.g. Losos, Schluter 2000). Within the “terrestrial islands” such a problem seems to be non-existent, as far as they are able to preserve ‘specific features’ of their habitats⁸.

Obviously, there are more factors which should describe this relationship (e.g. isolation, edge effects, local habitat conditions – Lomolino *et al.* 1989; Lomolino 2001b; Connor, McCoy 2001), but the tendency seems to be general. Some of the data presented (e.g. Simberloff, Abele 1976; Cole 1981; Godefroid, Koedam 2003) show that the total number of species in a collection of small forest patches or islands is significantly higher than in one or two big islands, and the difference is not quantitative but qualitative in nature – big patches can hold some ancient forest species not occurring in smaller ones. The effect is important for conservation biology, but it may be created not only by the mere area size, but also by the history of such big patches. The biggest patches also reduce the risk of species extinction – it is an obvious consequence of the canonical *island biogeography theory* (Mac Arthur, Wilson 1963, 1967; Simberloff, Wilson 1969; Lomolino 2001a; Godefroid, Koedam 2003), but from the point of view of their species biodiversity the turnover is still in progress.

On the other hand, however, the largest islands examined by Cole (1981) and Chown *et al.* (1998) are more attractive to immigrating species due to

⁸ This consideration is justified mainly for organisms occupying small areas, such as plants, fungi, molluscs and many vertebrates, not for migrating species or mammals which need a minimum critical area to persist.

their higher probability of propagule transfer and habitat heterogeneity. In fact, all the investigations suggest that the more islands the more habitats; even when they have the same type of habitat, their internal heterogeneity increases with the expanding area.

Though larger areas can hold more species and will be more attractive to *core* species, the patch size is not the only factor determining the biodiversity. On the other hand the quality of local flora (ratio of core species to ubiquitous species) was not studied here, and many authors (cf. Whittaker, Fernandez-Palacios 2007, p. 276–178) proved the occurrence of edge effect, which dramatically changes the quality of the flora in small patches. Connor *et al.* (2000) suggest that (in case of animals) a few large patches of a suitable habitat could accommodate more species than a regional network of small and large habitat patches.

In conclusion: As mentioned earlier, I did not confirm the *small island effect* concerning plant species number. There is no reason to suppose that the SLOSS problem is really relevant to preservation of good quality habitat patches, in their internal species capacity. The same result was obtained for plants of forest patches in Belgium (Honnay *et al.* 1999; Piessens *et al.* 2004) and montane mammals of southwest U.S.A (Patterson 1986). The '*key-habitat*' concept in Scandinavian forest protection (Mönkkönen 1999) or in distribution of forest birds in the Andaman Islands (Davidar *et al.* 2001) also refers to this assumption. In the case of Mediterranean communities also several medium size reserves could support more species than one large area (Venegas *et al.* 2008).

6. Conclusions

1. Each plant community has a defined species *capacity* (or *saturation*), depending on its immanent diversity of biotic and abiotic factors. The possibility to predict the number of species in this community depends exclusively on the patch size. Each set of patches of a plant community represented in one phytosociological table can be treated as an exemplification of one uniform habitat island of a size comparable to the combined acreage of the patches. Individual SPAR relationships exist for various kinds of habitats treated as single syntaxonomic units, their parts, or higher units such as alliance or order.

2. Fifty eight SPAR relationships were recognised in the investigated area (south-western Poland), either for single phytosociological units (associations or even their geographical forms) or for higher syntaxonomic units (alliances, orders or even classes). Depending mainly on the available material, the values obtained for single units were much more precise and of greater statistical significance.

3. The most meaningful results were obtained for forest communities, in most cases determination coefficient r^2 exceeded 0.8 and its statistical significance was very high. Within well-defined and properly described forest communities the influence of area *per se* explains 90% of its number of higher plant species per plot.

4. The highest determination coefficient was obtained for communities with a relatively long history of spontaneous evolution, and of almost natural origin, in most cases protected in nature reserves or within areas with relatively low forestry impact. Such communities have at the same time lower *intercept of the curve A* compared to more intensively managed communities.

5. Among the non-forest natural communities the best results of high statistical significance were obtained for some rush, sedge and rock-dwelling communities. The determination coefficient r^2 also exceeded 0.72 for these habitat types.

6. The SPAR relationships of seminatural and synanthropic communities were in most cases weaker than for the forests and natural non-forest communities. The number of plant species per plot size depended on the level of anthropopressure in each habitat patch, and many satellite species occurred there.

7. The relationship between the number of habitats and the number of common species had allometric properties. The value of coefficient ω varied from 0.24 to 0.32.

8. A simple γ -diversity prediction model was proposed, explained and tested based on 18 equal-sized plots in the Stołowe Mts. and 13 unequal-sized areas (south-western Poland nature reserves). For the equal-size areas ($\omega=0.29$ or $\omega=0.3$) the difference the actual and predicted species number did not exceed 12%. For the unequal-sized areas ($\omega=0.30$ – 0.32) the difference did not exceed 12% either.

9. The A coefficient for the analysed data varied from 20.08 to 243.63, and c varied from 1.33 up to 3.12. Their values are crucial for distinguishing between poor and rich communities. The *intercept of the curve* (or *initial trajectory* in power law) is significantly positively correlated with the number of core species and is responsible for the α -diversity.

10. The A coefficient is a better approximation of community plant species richness, than the mean number of species per releve, used previously in phytosociology.

11. The slope coefficient B in the investigated cases varied from 5.38 to 109.24, and z varied from 0.11 to 0.95. The maximum z value was higher than ever described in pertinent literature. I did not study the problem of *core/satellite* species, and thus have no grounds to claim that the slope coefficient is correlated with the number of satellite species. However A and B coefficients are highly positively correlated ($r=0.82$), and c and z are correlated in the same

way ($r=0.68$). It means that they are inter-dependent, and the slope coefficient B alone does not play any important role in the explanation of plant species richness in the analyzed cases.

12. In the cases analysed there was no distinct difference between the results obtained with the Gleason plot and the power function (see Table 3). Determination coefficients r^2 calculated from the first and the second equation were similar. The Gleason plot seemed to be a better predictor of the species number in more cases, because it gave higher r in 31 relationships (against power law – better r in 23 cases). It means that power law may be useful not only for patches exceeding 1–3 ha, as described in many papers, but also for very small ones.

13. All the patches analysed show features of islands beyond the upper limit of *small island effect area*, where plant species diversity appears to be more deterministic and can be predicted based on the area size and ecological factors. Probably, the reason is the fact that the data were analysed not as related to independent islands, but as an element of the habitat, and the habitat's capacity for holding the suitable number of species is constant *within* each community

14. Since I did not confirm the *small island effect* concerning the number of plant species, there is no reason to suppose that the SLOSS problem is relevant to preserving good quality habitat patches, in their internal species capacity. Larger areas could hold more species and would be more attractive to *core* species, but the patch size is not the only factor determining its biodiversity. On the other hand, the quality of local flora (ratio of core species to ubiquitous species) was not studied here.

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Streszczenie

Wstęp

Sformułowane przez Arrheniusa (1921, 1923a, 1923b) oraz Gleasona (1922, 1925) równania opisujące zależność pomiędzy przyrostem powierzchni, a wzrostem liczby gatunków należą do najstarszych modeli matematycznych stosowanych w ekologii, a ich użyteczność dla tej gałęzi wiedzy rzadko bywa kwestionowana. Pierwsze obserwacje dotyczące takiej zależności występują już w literaturze XIX wiekowej, jednak dopiero w latach 20-tych ubiegłego wieku zależność ta uzyskała swoje sformułowanie matematyczne.

Popularność modeli SPAR jest tak szeroka, że często określa się je jako jedno z głównych praw ekologicznych – znalazły zastosowanie w teorii wysp, teorii metapopulacji oraz ochronie przyrody, jako jedno z głównych narzędzi, pozwalających na przewidywanie prawdopodobieństwa wymierania gatunków jako rezultatu postępującej fragmentacji środowiska przyrodniczego.

W chwili obecnej wyróżniamy trzy główne podejścia do modeli SPAR.

Pierwszy wynika z głównych założeń biogeografii wysp, gdzie zależność pomiędzy powierzchnią wyspy, a liczbą gatunków (także izolowanego fragmentu siedliska) wynika głównie z samego wzrostu powierzchni wyspy i nie jest związana dodatkowo z innymi czynnikami.

Druga koncentruje się na zróżnicowaniu siedlisk, jako głównym powodzie występowania takiej zależności i zgodności modeli SPAR ze stanem obserwowanym w przyrodzie. Za jej duchowego ojca uważa się Forstera, przyrodnika towarzyszącego w podróży słynnemu kapitanowi Cookowi.

Trzecia koncepcja, znana pod nazwą „passive sampling hypothesis”, uznaje za główną przyczynę funkcjonowania modeli SPAR losowe rozmieszczenie osobników badanych grup w przestrzeni – jest rzeczą oczywistą, że większe fragmenty przestrzeni (wyspy lub płyty siedliska) będą zawierały większą liczbę osobników, a co za tym idzie także i gatunków.

Szeroka zgoda panuje tylko co do dwóch podstawowych twierdzeń: że liczba gatunków faktycznie wzrasta wraz z wielkością powierzchni oraz, że szybkość tego przyrostu maleje wraz ze wzrostem tejże powierzchni. Jednak natura oraz szczegółowy opis tej zależności pozostają nadal przedmiotem wielu dyskusji i sporów.

1. Główny cel badań

Możliwa korelacja pomiędzy liczbą gatunków a powierzchnią poszczególnych zbiorowisk roślinnych oraz ich mozaiki, posiada nie tylko znaczenie teoretyczne,

ale także doniosłe znaczenie praktyczne, umożliwiające wykorzystanie uzyskanych modeli w planowaniu ochrony różnorodności gatunkowej obszarów o niedostatecznie poznanej roślinności oraz dla określenia stopnia degeneracji poszczególnych obszarów pod wpływem antropopresji.

Do najważniejszych celów niniejszej pracy należy więc zaliczyć:

- określenie możliwości sformułowania modelu, który pozwoli na przewidywanie liczby gatunków roślin naczyniowych w zróżnicowanych układach zbiorowisk roślinnych o różnych powierzchniach – zarówno poszczególnych zbiorowisk, jak i różnych powierzchniach całkowitego obszaru;
- opis modeli SPAR dla poszczególnych zbiorowisk roślinnych znanych z terenu Polski pd.-zach., z maksymalną dokładnością, jaką można wysnuć ze zróżnicowanych danych podstawowych;
- weryfikacja proponowanego modelu predykcyjnego przy użyciu danych uzyskanych z poszczególnych relacji SPAR dla dobrze rozpoznanych florystycznie i fitosocjologicznie obszarów z terenu Polski pd.-zach.
- dyskusja nad konsekwencjami zaprezentowanego modelu i jego funkcjonowania w praktyce, w kontekście różnych aspektów zależności SPAR omawianymi obecnie w światowej literaturze dotyczącej tego zagadnienia.

2. Modelowanie α - i γ -różnorodności

2.1. Krok pierwszy – czy zawsze możliwe jest bezpośrednie zastosowanie modeli SPAR

Wszystkie dotychczas badane modele species-area relationship posiadały wyraźnie określony obszar oraz grupę istniejących (a czasem wymarłych) organizmów i w większości przypadków modele wykazywały istotny statystycznie wzrost liczby gatunków zgodnie z powiększaniem się obszaru. Za każdym razem można przyjąć także, że modele te posiadały swoją wartość prognostyczną, jednak każdorazowo wartość ta dotyczyła wybranego obszaru i wybranej grupy gatunków – nie miała więc charakteru predyktywnego, gotowego do przeniesienia na inny teren. Łatwo udowodnić to twierdzenie podstawiając do klasycznego wzoru Gleasona, przedstawiającego zależność SPAR w formie logarytmicznej, zbiór niejednorodnych danych dotyczących obszarów o różnej powierzchni i różnej florze naczyniowej (tabela 1). Jak wynika z rysunku 1 oraz rysunku 2 – próba określenia zależności SPAR dla wybranych 28 dobrze zbadanych powierzchni na terenie Polski pd.-zach. wydaje się nie spełniać przewidywanej zależności. Nawet jeśli przyglądamy się rys. 1 i rys. 2 zależność ta wygląda słabo, natomiast próba określenia równania regresji dla modelu (przy założeniu logarytmicznej zależności obu wartości) wykazuje nie tylko bardzo niski

współczynnik determinacji, ale także brak jego istotności statystycznej ($p=0.087$, $r^2=0.1$). Nie znaczy to oczywiście, że zależność opisywana przez setki naukowców od 80 lat nie istnieje dla tego zbioru danych – jednak jej opis nie jest prostą pochodną obszaru badanych obiektów.

Większość dotychczas badanych obszarów dotyczyła obiektów o charakterze jednorodnym pod względem siedliskowym – kiedy badane są układy, na które składa się wiele różnych zbiorowisk roślinnych, zależność ta staje się bardziej złożona.

2.2. Krok drugi – każde zbiorowisko roślinne posiada własny model species-area relationship.

Podczas gdy zdefiniowanie podstawowych cech zależności SPAR nie jest rzeczą trudną, to dokładne określenie tego, co jest, a co nie jest siedliskiem, jakie należy rozpatrywać w odniesieniu do różnych grup organizmów, nie jest już takie proste. Po pierwsze, zdefiniowanie siedliska zależy od samego charakteru grupy taksonomicznej, dla której staramy się określić zależność SPAR. Czym innym jest siedlisko dużego gatunku ssaka, przekraczające nieraz 1000 km², a czym innym lądowego mięczaka, który może spędzić całe życie na obszarze nie przekraczającym powierzchni kilku metrów kwadratowych.

Z praktycznego punktu widzenia, najprościej jest definiować siedliska gatunków roślin naczyniowych, będących przedmiotem zainteresowania niniejszej pracy, po prostu jako poszczególne zbiorowiska roślinne. Nasza obecna wiedza na ich temat pozwala większość ze zbiorowisk (lub ich zespołów) określić jako unikalne „jednostki biotyczne”, których struktura gatunkowa jest rezultatem warunków abiotycznych, wzajemnych zależności pomiędzy gatunkami, historią flory danego regionu, stopnia antropopresji oraz szeregu innych czynników. Zbiorowiska roślinne stanowią więc swoistą odpowiedź przyrody na czynniki środowiskowe i antropogeniczne, co czyni z nich (niezależnie od stopnia izolacji i charakteru samego zbiorowiska) przykłady „wysp środowiskowych” w sensie powszechnie nadawanym temu pojęciu w literaturze przedmiotu.

Większość autorów badających zależności pomiędzy występowaniem liczby gatunków a zmiennością siedliskową (choć z uwagi na rozbieżności badanych grup systematycznych definicje „siedliska” bardzo różniły się w poszczególnych pracach) dowiodło występowania takiej zależności, a jedynie pojedyncze prace zaprzeczały jej występowaniu. W wielu wypadkach dotyczyło to płatów lub wysp o niewielkich rozmiarach, na których występują naturalne fluktuacje liczby osobników (a więc także gatunków) powodowane przez „*small island effect*”.

Większość z danych zawartych w literaturze przedmiotu, szczególnie od czasu sformułowania hipotezy „*metacommunity*”, zdaje się potwierdzać fakt, że każda

wyspa siedliskowa, a więc w omawianym przypadku – sąsiadujące ze sobą zbiorowiska roślinne, posiadają własny, specyficzny zbiór gatunków o liczbie dążącej do osiągnięcia wysycenia (*saturation*), z których przynajmniej część jest swoista dla danego zbiorowiska. Pozwala to sformułować hipotezę, iż dla każdego ze zbiorowisk możliwe jest opisanie immanentnego modelu species-area relationship. Co więcej – założenia hipotezy „*metacommunity*” oraz niektóre z wyników badań prowadzonych na wyspach oceanicznych, pozwalają także założyć, że liczba gatunków występujących na sąsiadujących ze sobą, lecz komunikujących się „wyspach”, jest w przybliżeniu równa liczbie gatunków występujących na obszarze, stanowiącym równowartość obszaru połączonych ze sobą wysp.

2.3. Krok trzeci – wstępne uwagi do możliwości przewidywania różnorodności gatunkowej w złożonych układach siedliskowych.

Przejście od różnorodności gatunkowej wybranego ekosystemu (siedliska, zbiorowiska roślinnego) do sumy liczby gatunków na bardziej złożonym obszarze, nie jest prostą sumą gatunków występujących w badanych pojedynczo zbiorowiskach. Najważniejszymi problemami, jakie należy rozwiązać przy modelowaniu γ -różnorodności są:

- założenie istnienia miary różnorodności gatunkowej zależnej od liczby siedlisk;
- rozpoznanie dużych różnic w bogactwie gatunkowym poszczególnych zbiorowisk, zależnym od warunków abiotycznych i stopnia antropopresji;
- występowanie gatunków wspólnych dla różnych typów zbiorowisk roślinnych, co uniemożliwia przedstawienie liczby gatunków większego, niejednorodnego obszaru jako sumy gatunków w poszczególnych zbiorowiskach
- „*small island effect*”, który może być źródłem błędów w określaniu liczby gatunków w zbyt małych lub izolowanych płatach.

2.4. Krok czwarty – od różnorodności gatunkowej pojedynczego zbiorowiska do różnorodności gatunkowej układów wielozbiorowiskowych.

Jak podkreślano w poprzednim rozdziale, obliczenie liczby gatunków w dowolnym obszarze przez proste określenie możliwej liczby gatunków dla pojedynczych typów zbiorowisk, a następnie ich sumowanie w układach wielozbiorowiskowych nie jest możliwe wskutek występowania dużej liczby gatunków wspólnych.

Jako miarę różnorodności gatunkowej, uśrednionej dla zbiorowisk występujących na danym terenie, zaproponowano średnią liczbę gatunków na zbiorowisko. Nie mówi nam ona wiele o realnej różnorodności każdego z typów siedlisk, jednak jest dobrym przybliżeniem pozwalającym na użycie w następnych etapach wnioskowania.

Oczywiście miara ta ma swoje wady. Można bowiem wyobrazić sobie układ wielozbiorowiskowy, w którym poszczególne typy zbiorowisk są tak różne, że nie mają żadnych gatunków wspólnych, ponadto znacząco różnią się liczbą gatunków (np. płaty torfowisk sąsiadujące z murawami kserotermicznymi). Na szczęście w przyrodzie układy takie są bardzo rzadkie.

2.5. Krok piąty – liczba gatunków wspólnych jest związana z liczbą zbiorowisk.

Tylko skrajnie nieliczne gatunki roślin naczyniowych są ściśle związane z określonym typem siedliska. Duża część z nich występuje w obrębie jednego ze zbiorowisk (*core species*), sporadycznie jednak przechodząc także do innych, a wiele występuje jako gatunki towarzyszące, niespecyficzne dla żadnego określonego zbiorowiska lub tylko dla ich grupy (np. gatunki ogólnoleśne, czy pospolite gatunki termofilne). Gatunki te określone są w niniejszej pracy jako „wspólne” (*common species*).

Jak wielokrotnie udowodniono to w literaturze przedmiotu, występowanie gatunków wspólnych lub też ich niewielkich grup bardzo utrudnia przeprowadzenie aproksymacji różnorodności gatunkowej dla większych obszarów.

Przyjęto więc, że liczba gatunków wspólnych jest związana z liczbą zbiorowisk na badanym terenie, oraz że zależność ta przybiera charakter allometryczny. Zależności allometryczne wielokrotnie wykazały swoją skuteczność w badaniach ekologicznych, a poczynając od równania Arrheniusa mają także długą tradycję w badaniach geobotanicznych i wielokrotnie były tu stosowane.

Zaproponowano współczynnik ω o wartości zbliżonej do kanonicznej wartości współczynnika z w równaniu Arrheniusa (0.26), zakładając, że współczynniki te posiadają wspólne cechy związane ze wzrostem liczby gatunków w zależności od obszaru lub liczby siedlisk.

2.6. Krok ostatni – najprostszy możliwy model.

Zaproponowano prosty model wiążący teoretyczną liczbę gatunków uzyskanych z modeli SPAR dla każdego z typów zbiorowisk, dla którego możliwe będzie pozyskanie danych z liczbą gatunków wspólnych i liczbą siedlisk (równanie 5).

3. Testowanie modelu

Dla sprawdzenia możliwości predykcyjnych przewidywanego modelu konieczne było:

- określenie modeli species area-relationship dla poszczególnych typów zbiorowisk, w oparciu o zbiór danych pozyskanych z literatury źródłowej;
- wybór dobrze zbadanych obszarów, skąd znana jest zarówno liczba gatunków roślin naczyniowych, jak i mapy roślinności rzeczywistej;
- sprawdzenie funkcjonowania modelu poprzez podstawienie do niego danych pochodzących z badań terenowych.

3.1. Zasięg geograficzny obszaru pochodzenia danych

Badania zależności pomiędzy powierzchnią siedlisk, a występującą na niej liczbą roślin prowadziłem dla obszaru Dolnego Śląska i Opolszczyzny (Polska pd.-zach.). Obszar ten obejmuje około 33.000 km², co stanowi około 10% powierzchni Polski.

Badania postanowiłem ograniczyć do jednego, określonego regionu geograficznego i wyłącznie do roślin naczyniowych z uwagi na:

- względną jednorodność pochodzących z jego obszaru danych;
- zbliżone warunki klimatyczne całego obszaru;
- jednorodne i dobrze rozpoznane "*species pool*", składające się z gatunków typowych dla niewielkiego wycinka szerokości geograficznej, co jest istotne dla uzyskania jednorodnych rezultatów w badanych modelach;
- zmienną liczbę gatunków mszaków i wątrobowców w tabelach fitytosocjologicznych.

A. Jednorodność danych

Dany teren badany jest od wielu lat przez zespół geobotaników wywodzących się z jednego ośrodka (Uniwersytet Wrocławski), co pozwala założyć, że stosowane przez nich techniki i podejście metodyczne do prac terenowych i opracowania kameralnego danych są, jeśli nie identyczne, to bardzo do siebie zbliżone. Młodzi pracownicy naukowcy każdego ośrodka uczą się podstaw geobotaniki od starszych kolegów i sami następnie przekazują je następcom. Gwarantuje to ciągłość metody i sposobu interpretacji danych, czemu sprzyja ponadto stała wymiana informacji, także niepublikowanej. W przypadku badań nad SPAR uzyskanie jednorodnych metodycznie danych wyjściowych jest szczególnie istotne, gdyż dane pozyskane różnymi metodami mogą doprowadzić do błędnych wniosków.

B. Klimat

Polska południowo-zachodnia jest regionem zróżnicowanym pod względem klimatycznym, jednak na tle klimatycznej mapy Polski ujawnia pewne cechy

wspólne. Należą do nich przede wszystkim wyraźne wpływy klimatu oceanicznego, przejawiające się w postaci podwyższonych opadów i wyższych średnich temperatur rocznych. Cechy te Polska pd.-zach. dzieli z Ziemią Lubuską i Pomorzem Zachodnim. Jednocześnie Łuk Hercyński, osłaniający całą region od strony południowej, jest przyczyną powstawania zjawisk klimatycznych specyficznych dla południa Polski (a więc także dla łuku Karpat) jak wiatry fenowe lub inwersje temperatury. Powoduje to, że szata roślinna Polski pd.-zach. charakteryzuje się m.in. dużym udziałem gatunków elementu atlantyckiego oraz współwystępujących z nimi gatunków górskich, a także obecnością szeregu zbiorowisk roślinnych o charakterze zachodnio- i południowoeuropejskim. Mimo niewątpliwej różnorodności, związanej głównie z wysokością nad poziomem morza przyjąłem, że badany obszar stanowi zdefiniowaną i zamkniętą jednostkę biogeograficzną. Zróżnicowanie obszaru (pod względem topograficznym, klimatycznym, wysokościowym i siedliskowym) zapewnia jednocześnie, iż ewentualne modele będą odnosiły się do terenu bardziej urozmaiconego niż jedna tylko jednostka geobotaniczna i pozwolą na prześledzenie zależności obszaru i liczby gatunków dla różnych typów siedlisk nizinnych i górskich.

C. „Species pool”

Modele SPAR umożliwiające prognozowanie liczby gatunków na obszarach lądowych są z reguły ograniczone w swoim zasięgu do obszarów o jednolitym charakterze siedliskowym i jednoznacznie określonym charakterze geograficznym. Każdy z modeli posiada inne współczynniki równań, które otrzymuje się poprzez analizę danych empirycznych. Model służący do prognozowania musi, bazując na danych empirycznych z określonego terenu, zamykać się jednocześnie w jego granicach. Dopiero po sprawdzeniu modelu w danym terenie możliwe są próby jego aplikacji na obszary sąsiadujące.

D. Liczba gatunków mszaków i wątrobowców

Badania ograniczyłem do roślin naczyniowych, gdyż wzory rozmieszczenia roślin naczyniowych i zarodnikowych bardzo się różnią, ponadto tylko niewielka część badań fitosocjologicznych prowadzona była z udziałem specjalistów z zakresu bryologii. W tym przypadku tabele fitosocjologiczne są znacznie bogatsze w gatunki roślin zarodnikowych.

3.2. Dane źródłowe

Część pracy oparta o dane źródłowe, której wyniki prezentowane są w tabelach i załącznikach, obejmuje określenie relacji pomiędzy powierzchnią, a liczbą gatunków roślin naczyniowych, jaka występuje w poszczególnych zbiorowiskach roślinnych lub typach zbiorowisk, pojmowanych jako wyższe jednostki fitosocjologiczne (w randze związku, wyjątkowo rzędu lub nawet klasy).

Badania rozpocząłem od stworzenia bazy danych, w której zawarłem podstawowe dane z tabel fitosocjologicznych opublikowanych z terenu Polski pd.-zach. w latach 1960–2002. Nie uwzględniałem sporadycznie dokumentowanych w literaturze zbiorowisk kałużowych, klasyfikowanych na poziomie klasy lub rzędu, bądź niemożliwych do umiejscowienia w systemie zbiorowisk roślinnych Polski. Dane te obejmowały: nazwę zespołu lub zbiorowiska, łączną liczbę gatunków w tabeli, łączną powierzchnię zdjęć fitosocjologicznych oraz – dodatkowo średnie liczby gatunków w zdjęciu i średnie powierzchnie zdjęć. Ze wszystkich tabel każdorazowo wyłączałem rośliny zarodnikowe, co wymagało przeliczania i odjęcia ich liczby i udziału w poszczególnych zdjęciach. Badaniami objąłem wszystkie udokumentowane w literaturze zbiorowiska roślinne z terenu Polski pd.-zach. – łącznie 750 tabel fitosocjologicznych reprezentujących 223 zespoły i zbiorowiska roślinne. W analizie wykorzystano dane dotyczące 173 syntaksonów zebrane w 667 tabelach – pozostałe reprezentowane były w postaci pojedynczych tabel (mniej niż 5) lub w tabelach o niedostatecznej liczbie zdjęć fitosocjologicznych (trzy i mniej). Podsumowanie danych o tabelach użytych w analizie oraz z niej wykluczonych znajduje się w Appendix VII do niniejszej pracy.

Przyjąłem, że liczba gatunków w danym zespole lub zbiorowisku pozostaje w zależności od powierzchni, niezależnie od tego, czy stwierdzone płaty zbiorowiska znajdują się obok siebie, czy też są rozdzielone terytorialnie – podstawy takiego założenia wynikają z teorii „*metacommunity*” oraz kilku prac naukowych, w których wykazano, iż liczba gatunków występujących w archipelagu izolowanych wysp jest zbliżona do liczby gatunków występujących na jednolitym obszarze o powierzchni równej łącznej powierzchni wysp. Tym samym każda tabela fitosocjologiczna reprezentuje tu jedną wyspę siedliskową, a ich wartość dla analiz SPAR powinna być równoważna z jednolitym obszarem o podanej powierzchni, zajęтым przez jednorodny zespół roślinny.

Jedyną możliwą w zastosowaniu miarą różnorodności była liczba gatunków roślin naczyniowych. Tabele fitosocjologiczne nie zawierają danych wystarczających dla obliczenia indeksu Fishera, współczynnika koncentracji Simpsona lub innych miar różnorodności biologicznej. Liczono wszystkie występujące w tabelach taksony roślin naczyniowych, poza nieutrwalonymi mieszańcami oraz taksonami oznaczonymi tylko do rodzaju. Rodzaj *Taraxacum* w dostępnym materiale literaturowym jest podawany z dokładnością do sekcji, podobnie jak niektóre występujące w tabelach notowania rodzaju *Rubus*. W tym przypadku notowano wystąpienie jednego taksonu. Inne rodzaje o trudnej systematyce (*Alchemilla*, *Rosa*, *Hieracium*) są w tabelach z badanego terenu oznaczane z dokładnością do gatunku, zgodnie z dostępnymi w danych okresach kluczami lub listami gatunków (Szafer *et al.* 1979, Tutin *et al.* 1964–1979, Mirek *et al.* 2003), co pozwoliło na uwzględnienie ich pełnej zmienności gatunkowej. Różnice

w nomenklaturze dotyczącej poszczególnych gatunków nie są w tym przypadku znaczące, gdyż każdorazowo pod określoną nazwą notowany był tylko jeden takson.

Dane zebrane w tabeli zbiorczej (Appendix VII), obejmującej podsumowanie danych uzyskanych z 667 tabel fitosocjologicznych, zostały następnie podzielone na tabele potomne, z których każda reprezentowała jeden zespół roślinny lub, w przypadku mniejszej liczby danych – wyższą jednostkę fitosocjologiczną. Analizowałem wyłącznie zależności dla 5 i więcej dostępnych tabel. Nazwy zbiorowisk roślinnych i klasyfikacja syntaksonomiczna wg W. Matuszkiewicza (2001) i J. M. Matuszkiewicza (2001), poza ujęciem klasy *Asplenieta trichomanis* (Świerkosz 2004). Pojedyncze tabele zostały wyłączone z analizy, wskutek występowania znacznych odchyłeń od typu zbiorowiska – szczególnie dotyczy to słabo zbadanych zespołów, które wymagają dalszych badań fitosocjologicznych nad ich wewnętrznym zróżnicowaniem. Każdorazowo wyłączenie takie jest uzasadnione.

3.3. Metody analizy

Analizy statystyczne wykonywano przy wykorzystaniu narzędzi programu Statistica 7.1, w modułach Estymacja nieliniowa, Statystyki nieparametryczne oraz Podstawowe statystyki i tabele.

Analizy stosunku liczby gatunków do powierzchni dla poszczególnych zbiorowisk roślinnych lub wyższych jednostek syntaksonomicznych prowadziłem w module Estymacji nieliniowej programu Statistica 7.1, przy zastosowaniu równania Gleasona (1922) w modyfikacji Maya (1975), oraz równań Arrheniusa.

Przy opisie każdego zbiorowiska (Appendix I i II) podano źródła danych oraz niezbędne dane statystyczne (N , średnie, rozkład S i A). Każdorazowo przeprowadzono analizę reszt w zakresie rozkładu reszt (oczekiwany rozkład normalny) oraz sprawdzono rozkład wartości przewidywanych względem resztowych (oczekiwany równomierny rozrzut wokół $x=0$).

W równaniach Arrheniusa i Gleasona możliwe jest wykorzystanie dowolnego logarytmu. Często używany jest tu logarytm naturalny (jak w klasycznych równaniach), jednak użycie logarytmu dziesiętnego pozwala na łatwą interpretację współczynników równania w odniesieniu do powierzchni, której jednostki pochodzą z systemu dziesiętnego.

Jednostką powierzchni, w której prowadzono obliczenia jest hektar. Jednostkę tę przyjąłem również ze względów praktycznych, gdyż umożliwia ona prostą aplikację otrzymanych wyników do badań terenowych.

Po uzyskaniu współczynników wynikających z równań Gleasona i Arrheniusa, wyniki przedstawiono w przestrzeni semi-logarytmicznej, co pozwala na okreś-

lenie równania regresji oraz współczynnika determinacji (Appendix I i II). Procedura ta, mimo, że liczba gatunków jest zmienną dyskretną, jest powszechnie stosowana w badaniach SPAR i jej zastosowanie ma dostateczne poparcie w literaturze przedmiotu. W oparciu o prace Prestona (1960, 1962a) przyjęto założenie o normalnym rozkładzie danych.

4. Wyniki

W analizowanym materiale wyróżniono 58 pojedynczych modeli species-area relationship, zarówno dla wybranych syntaksonów (a nawet ich lokalnych odmian geograficznych), jak i dla wyższych jednostek syntaksonomicznych, na poziomie związku, rzędu, a w pojedynczych przypadkach także klasy. Wartości uzyskane dla pojedynczych jednostek syntaksonomicznych są bardziej precyzyjne i mają wyższe istotności statystyczne, jednak tylko dla części z nich udało się uzyskać wystarczającą liczbę danych (tabel fitosocjologicznych) dla przeprowadzenia analizy.

Wyniki analiz przedstawione są w tabeli 2 (nazwy wyróżnionych jednostek, liczba danych, równania Gleasona i Arrheniusa) oraz tabeli 3, gdzie przedstawiono współczynniki A i B (dla równania Gleasona), c i z (dla równania Arrheniusa) oraz współczynniki korelacji dla obu równań.

Do testowania modelu teoretycznego zmian γ -różnorodności wykorzystano wyniki równań uzyskane w części pierwszej oraz dane literaturowe dotyczące różnego typu obszarów w Polsce pd.-zach., dla których dysponujemy zarówno spisem gatunków roślin naczyniowych, jak i mapą lub szczegółowym opisem zbiorowisk roślinnych, pozwalającym na określenie bezwzględnej powierzchni (w ha) zajętej przez poszczególne zbiorowiska lub ich związki. Z konieczności ograniczono się do obszarów w granicach od 1.25 do 137 ha, wśród których znajduje się 13 rezerwatów przyrody oraz 18 kwadratów o powierzchni 100 ha, szczegółowo badanych w Górach Stołowych (Świerkosz 1998). Większe obszary nie posiadają dostatecznej dokumentacji, którą można byłoby wykorzystać w niniejszych badaniach.

Zarówno dla obszarów o jednolitej powierzchni, jak i dla obszarów o różnych powierzchniach uzyskano wyniki różniące się od uzyskanych z badań terenowych w granicach +/- 12%, przy współczynniku ω , mieszczącym się w przewidywanym wcześniej przedziale wartości (0.24 do 0.32).

5. Dyskusja

5.1. Uproszczenia modelu

Proponowany model jest oczywiście uproszczeniem stanu rzeczywistego, ponieważ rzeczywisty wykres przyrostu liczby gatunków wraz z dodawaniem kolejnych typów zbiorowisk przypomina wykres funkcji sigmoidalnej (ryc. 3). Teoretycznie uproszczenie to powinno zmniejszać się wraz z przyrostem liczby typów zbiorowisk.

Proponowany model nie może być także użyteczny w rzadkich, jednak spotykanych w przyrodzie przypadkach, gdy sąsiadujące ze sobą typy zbiorowisk są tak silnie izolowane ekologicznie, że nie będą posiadały żadnych gatunków wspólnych.

5.2. Porównanie modelu z innymi, pozwalającymi na przewidywanie różnorodności gatunkowej

Porównano prezentowany model z wieloma innymi próbami przewidywania różnorodności gatunkowej, opartymi na różnych modelach matematycznych i metodach wnioskowania oraz pozyskiwania i obróbki danych. W literaturze przedmiotu nie znaleziono rozwiązania podobnego do zaprezentowanego w niniejszej pracy – natomiast najbardziej precyzyjne z dotychczas zaproponowanych modeli mają podobną skalę dokładności (do 10%).

5.3. Informacje na temat typów zbiorowisk, które można uzyskać ze wzoru Gleasona

5.3.1. Zbiorowiska bogate i ubogie w gatunki

Pierwszą z ważnych informacji, jakiej dostarcza równanie Gleasona, jest wartość współczynnika A , w wielu pozycjach literatury wskazywana jako wysoce skorelowana z liczbą „core species”. Niska wartość współczynnika A charakteryzuje zbiorowiska o wysokim stopniu specjalizacji wchodzących w ich skład gatunków (torfowiskowe, naskalne, wodne). Wysoką wartość współczynnika zauważyć możemy w dwóch różnych grupach zbiorowisk. Z jednej strony są to zbiorowiska charakteryzujące się wysoką wewnętrzną złożonością mikrosiedlisk (zbiorowiska ciepłolubne, lasy stokowe), z drugiej zaś zbiorowiska o charakterze otwartym dla gatunków pospolitych, czy to wskutek niewielkiej powierzchni płatów, ułatwiającej wnikanie gatunków ze zbiorowisk sąsiadujących, czy też stopnia antropopresji, ułatwiającej wkraczanie gatunków pospolitych. Doskonałą egzemplifikacją tego zjawiska jest występowanie trzech różnych modeli species-area relationship dla trzech odmian geograficznych *Galio*

sylvatici-Carpinetum, od uboższych w gatunki, lecz z przewagą „core species” grądów doliny Odry, aż po bogate w gatunki niespecyficzne grądy Pogórza i Przedgórze Sudeckiego, podlegające intensywnej gospodarce leśnej i o niewielkich powierzchniach izolowanych płatów.

5.3.2. Szybkość przyrostu gatunków na jednostkę powierzchni (rola współczynnika B oraz z)

Jak wielokrotnie analizowano to w literaturze przedmiotu, współczynnik B oraz z są silnie zależne od skali analizowanych płatów, ich fragmentacji oraz izolacji. Ponadto są one silnie skorelowane z wartościami współczynnika A lub c . Współczynniki te nie niosą więc samodzielnie dodatkowej informacji o charakterze zbiorowiska, choć pojawiały się sugestie, iż są one skorelowane z liczbą „satellite species”.

5.4. Zbiorowiska roślinne – wyraźne czy rozmyte

Uzyskane wyniki sugerują istnienie wyraźnie określonych typów zbiorowisk roślinnych, różniących się od siebie składem gatunkowym, dla których możliwe jest przewidywanie przyrostu gatunków zgodnie z modelami area-species relationship dla każdego z typów zbiorowisk oddzielnie.

5.5. Zastosowanie funkcji Arrheniusa dla małych płatów zbiorowisk

Większość z dotychczas publikowanych prac sugerowała, że zastosowanie równania Arrheniusa dla małych płatów (o powierzchniach mniejszych niż 0.25 aż do 3 ha, w zależności od autora) nie jest uzasadnione. Wyniki uzyskane w niniejszej pracy sugerują, że równanie Gleasona częściej przynosi wyniki o wyższej wartości współczynnika determinacji niż równanie Arrheniusa (33 versus 21), jednak oba mogą być stosowane do płatów mniejszych niż dotychczas sugerowano.

5.6. Czy *small island effect* jest zauważalny w przypadku typów siedlisk roślinnych

W niniejszej pracy nie stwierdzono występowania *small island effect* (*SIE*) w obrębie analizowanych płatów różnych typów zbiorowisk roślinnych, mimo że najmniejsze z analizowanych powierzchni, w przypadku zbiorowisk naskalnych lub pleustonowych wynosiły 1 m². Wszystkie analizowane płaty wykazały przynależność do obszaru powyżej punktu przełamania *SIE* (T_p), co oznacza, że każde ze zbiorowisk roślinnych ma odrębny *break point* T_p , poniżej którego efekty *SIE* mogą wystąpić, i że zbiorowiska o zakresie powierzchni mniejszej niż punkt przełamania *SIE* nie są analizowane w literaturze fitosocjologicznej.

5.7. Konsekwencje dla problematyki SLOSS

Wyniki niniejszej pracy sugerują, że w przypadku ochrony zbiorowisk roślinnych, zestaw gatunków typowych dla danego zbiorowiska może zostać utrzymany zarówno w jednym, dużym płacie zbiorowiska, jak i w szeregu wysp siedliskowych o łącznej powierzchni zbliżonej do dużego, jednorodnego płatu, jeśli tylko ich minimalna powierzchnia umożliwia utrzymanie gatunków typowych dla zbiorowiska.

6. Podsumowanie i wnioski

1. Każde zbiorowisko roślinne posiada określoną pojemność gatunkową (*species capacity*), zależną od specyficznego zestawu czynników biotycznych i abiotycznych. Liczba gatunków roślin naczyniowych określonego typu zbiorowiska zależy wyłącznie od wielkości płatu. Indywidualne modele species-area relationship można określić dla dowolnej jednostki syntaksonomicznej – zespołu, jego wariantu lokalnego, a także wyższych jednostek, takich jak związek czy rząd.

2. W analizowanym materiale wyróżniono 58 modeli SPAR dla poszczególnych jednostek syntaksonomicznych różnego rzędu. Modele o najwyższej precyzji określono dla pojedynczych jednostek syntaksonomicznych, dla których dysponowano wystarczającą liczbą danych.

3. Dla zbiorowisk leśnych w większości przypadków uzyskano wysoce precyzyjne modele o współczynniku determinacji r^2 przekraczającym 0.9 i o wysokim poziomie istotności statystycznej ($p < 0.01$).

4. Najwyższe współczynniki determinacji uzyskano dla zbiorowisk leśnych o charakterze naturalnym (lasy chronione w rezerwach lub też podlegające niskiej presji gospodarki leśnej, z uwagi na specyficzne warunki siedliskowe). Jednocześnie lasy te charakteryzują się niższą różnorodnością gatunkową (niższy współczynnik A) niż lasy wykorzystywane w gospodarce leśnej, z uwagi na mniejszy udział gatunków sporadycznych i satelitarnych, niezwiązanych bezpośrednio z typem zbiorowiska.

5. Spośród naturalnych zbiorowisk nieleśnych najbardziej precyzyjne modele SPAR o wysokim współczynniku determinacji i wysokiej istotności statystycznej uzyskano dla zbiorowisk naskalnych oraz szuwarów i trzcinowisk.

6. Modele SPAR uzyskane dla zbiorowisk półnaturalnych i synantropijnych mają niższe wartości współczynnika determinacji oraz istotności statystycznej, co wiąże się zapewne z trudnym do przewidzenia, nieukierunkowanym wpływem antropopresji.

7. Zaproponowano możliwość występowania zależności pomiędzy liczbą gatunków wspólnych w poszczególnych zbiorowiskach i liczbą tych zbiorowisk.

Założono, że zależność ta ma charakter allometryczny, a potęgą równania jest współczynnik ω o wartościach mieszczących się w przedziale 0.24–0.32.

8. Zaproponowano prosty model umożliwiający przewidywanie różnorodności gatunkowej w układach wielozbiorowiskowych (γ -różnorodność). Model przetestowano na 18 obszarach o powierzchni 100 ha pochodzących z Gór Stołowych oraz 13 obszarach o różnych powierzchniach (rezerваты z obszaru Dolnego Śląska). Dla obszarów o jednolitych powierzchniach optymalny współczynnik ω wyniósł 0.30, a różnice w liczbie gatunków znanej z terenu oraz przewidywanej przez model nie przekroczyły 12%. Dla obszarów o różnych powierzchniach optymalny współczynnik ω wyniósł 0.31, a różnice w liczbie gatunków znanej z terenu oraz przewidywanej przez model nie przekroczyły 12%.

9. Współczynnik A (*intercept of the curve*) z równania Gleasona waha się dla analizowanych zbiorowisk pomiędzy 20.08 a 243.63, zaś współczynnik c (*initial trajectory*) równania Arrheniusa od 1.33 do 3.12. Wartość ta jest podstawą dla rozróżnienia pomiędzy ubogimi, a bogatymi w gatunki zbiorowiskami.

10. Współczynnik A wydaje się być lepszym wskaźnikiem bogactwa gatunkowego typów zbiorowisk niż powszechnie stosowana w fitysocjologii miara średniej liczby gatunków w zdjęciu fitysocjologicznym.

11. W analizowanych danych współczynnik B z równania Gleasona waha się od 5.38 do 109.24, zaś z z równania Arrheniusa pomiędzy 0.11 a 0.95. Współczynniki te są dodatnio skorelowane ze współczynnikami A i c , co pozwala sądzić, że nie mają one samodzielnego znaczenia dla analizowania bogactwa gatunkowego badanych płatów.

12. W analizowanych danych nie zauważono istotnych różnic pomiędzy modelami SPAR dla poszczególnych jednostek syntaksonomicznych obliczanymi według równania Gleasona i Arrheniusa. Pierwsze z nich odznaczają się wyższymi współczynnikami determinacji w 33 modelach, drugie zaś w 21. Mimo więc, że równanie Gleasona daje bardziej precyzyjne rezultaty, to używanie równania Arrheniusa dla małych płatów (poniżej 1–3 ha) w świetle uzyskanych wyników jest dopuszczalne.

13. Wszystkie analizowane płaty leżą prawdopodobnie powyżej granicy, za którą dostrzegalne są zaburzenia modeli SPAR generowane przez „*small island effect*”.

14. Ponieważ nie zauważono oddziaływania „*small island effect*”, wyniki niniejszej pracy sugerują, że w przypadku ochrony zbiorowisk roślinnych zestaw gatunków typowych dla danego zbiorowiska może zostać utrzymany zarówno w jednym, dużym płacie zbiorowiska, jak i w szeregu wysp siedliskowych o łącznej powierzchni zbliżonej do dużego, jednorodnego płatu, jeśli tylko ich minimalna powierzchnia umożliwia utrzymanie gatunków typowych dla zbiorowiska.