POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	51	4	481–492	2003

Regular research paper

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CHANGES IN HERB LAYER HETEROGENEITY OF SCOTS PINE FORESTS ALONG THE NORTH-SOUTH TRANSECT

ABSTRACT: The purposes of the present paper are: a) to show the synusial structure of the herb layer of ten sites, located in Norway, Finland, Estonia, Latvia, Lithuania and Poland along the transect stretching between 50°28' and 70°09' N, and b) to characterise the species-area curves for all the sites studied.

The number of types of synusiae on the particular sites ranges from three to ten, though only one or two have the dominating character, that is, occupy at least 20% of surface. From the point of view of synusial differentiation three geographical groups of sites could be established: the most distinctly different are the northern sites. The second subset of sites, though featuring relatively weak internal mutual similarities, encompasses the sites located in the middle part of the transect. The third subset of sites, represents a more southern character.

For each of the sites separately the dependence between the number of vascular species of the herb layer and the area of the site considered (the species-area relationship) is described by the formula $y = ax^b$. Correlation coefficients between the model and the actual number of species are very high, from 0.902 to 0.998.

KEY WORDS: synusial differentiation, herb layer, number of species, life forms, species-area curve

1. INTRODUCTION

The horizontal differentiation of the herb layer constitutes one of the most important structural characteristics of the forest phytocoenoses. On the one hand, it influences the spatial heterogeneity of various processes, for instance, production and decomposition of the organic matter. On the other hand, it can be treated as a measure of the habitat micro-heterogeneity, with particular distinction of the topography, fertility and humidity differentiations (Hornberg *et al.*, 1997). One of the manners of describing the horizontal differentiation of the herb layer is the analysis of types of synusiae. The notion of synusium is used here to denote the grouping of species characterised by the similarity of the life forms and similar ecological requirements within a single layer of the association. The synusiae are sometimes considered to be the basic spatial and functional units within the framework of a phytocoenosis (Mavriscev, 1980; Gillet, 1986; Julve and Gillet, 1994; *Vegetation Classification Standard*, 1997). The term of microhabitat is being used also in a similar meaning (Guo, 1998).

Side by side with the synusial heterogeneity there is another important structural characteristic of the herb layer, namely the relation between the number of species observed, and the size of the observation area (Barnett and Stohlgren, 2001).

The purposes of the present report are: a) to show the synusial differentiation of the herb layer of ten sites located along the North-South transect under study, elaboration of the typology of the synusiae analysed and determination of the influence of geographical location and climatic conditions on the horizontal heterogeneity of the herb layer; and b) to characterise the curve of the dependence "number of species vs. surface area" for all the sites studied. The phytosociological and floristic characterisation of the study sites is shown in a separate report (Solon, 2003, in this volume).

2. METHODS

The basis of the description of the synusial structure of the herb layer was provided by the field charting within the surface of dimensions 11 m by 11 m, selected as the most typical for each of the ten study sites, located along the North-South transect (see Breymeyer, 2003a, in this volume). The floristic descriptions were elaborated for each of the individual synusiae. Each description encompassed the surface of 4 m^2. The quantitative characteristics of the species (area coverage) were estimated according to the modified 12-point scale, on which "r", "+", and "1" denote, respectively, 0.1%, 0.5%, and up to 10%, while the remaining values, from 2 through 10, denote the successive ten per cent intervals. These floristic descriptions were the basis for the identification of the types of synusiae. The typological tables put together contain only those species, whose cover measure was at least once higher than 10%. The species of the vascular plants were designated on the basis of the key of Szafer *et al.*, 1969, and the names used followed the elaboration of Rothmaler (1976). The field charting and the plant species descriptions were done in 1997. The sole exception was the Norwegian site, for which this was done in 2000. There were altogether 117 floristic records elaborated in the synusiae (nine on the NO1 site and 12 on each of the remaining sites). The similarities of the floristic compositions between the particular synusiae and the similarities of the particular sites with respect to the appearance of the types of synusiae were calculated with the Canberra distance and presented with the help of the dendrogram obtained from the Ward clustering method.

The variability of the number of species of vascular plants in the herb layer on the surfaces of different area magnitude was determined on the basis of a) the floristic descriptions elaborated for 20 squares of dimensions 1 m x 1 m, and one surface of 4 x 5 m; b) the data contained in the phytosociological relevés for the areas of 100 and 400 m^2 (see Solon, 2003). It was assumed that the character of the relation of "number of species vs. area" is defined by the formula $y = ax^b$.

The interdependencies between, on the one hand, the geographical location and the climatic measurements (the independent variables), and, on the other hand, the number and cover of synusiae (as a measure of the horizontal heterogeneity of the herb layer), were characterised on the basis of correlation and regression analysis. The climatic characteristics adopted were the long-term average annual precipitation, the long-term mean annual temperature (see Breymeyer, 2003a, b), and the indices of Lang and Martonne.

The Lang index (Lang, 1915) is defined as L = (annual precipitation / mean annual temperature), while the Martonne index (Martonne, 1926) has the form M = [annual precipitation / (mean annual temperature + 10)].

3. RESULTS

3.1. MAIN TYPES OF SYNUSIAE

The similarities of the 117 descriptions of synusiae, taken from the ten study sites are presented in Fig. 1. This similarity-based dendrogram indicates the appearance of three groups of synusiae, within which similarity exceeds 0.55. A more detailed analysis, accounting for the ecological character of the species and their quantitative proportions, makes it possible to distinguish four main groups encompassing 22 types of synusiae.

The first group (group A), the least similar to all the other ones, associated with the sites NO1 and FN1, encompasses the synu-

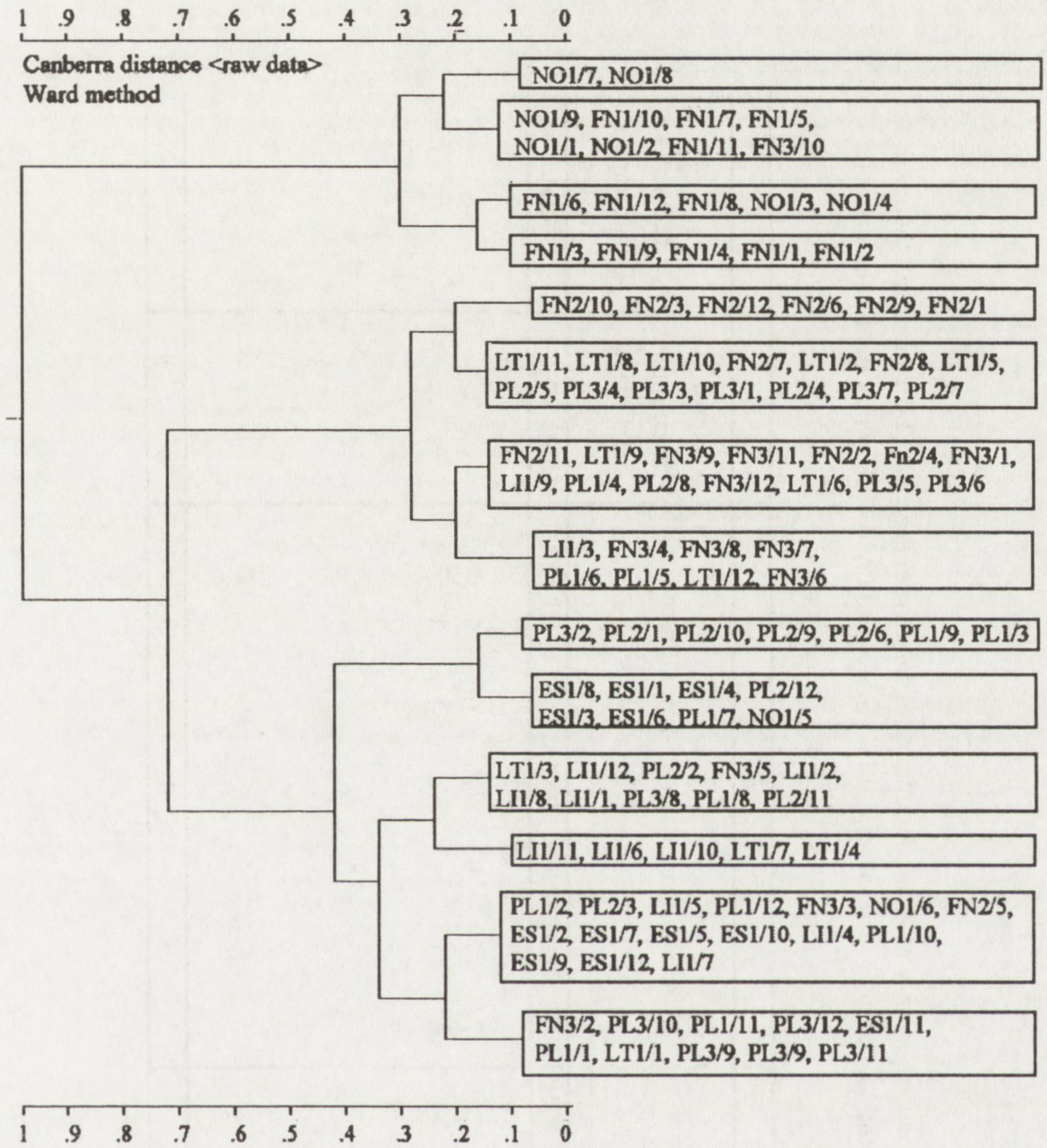


Fig. 1. Dendrogram of similarity of the species composition of the synusiae based on Canberra distance and Ward method. Codes: sample site/description number (e.g. FN1/6 means: the sixth field description (out of 12) on the FN1 site).

siae with a high share of *Empetrum nigrum*, or featuring a very low plant coverage (Table 1). Within this group five types of synusiae can be distinguished, differing by the domination of particular species. The second group (group B) encompasses the dwarfshrub – mossy synusiae, most common for the sites of the transect (Table 2). Within this group we can distinguish eight weakly pronounced types of synusiae. The third group (group C) is composed of the synusiae with a high share of *Vaccinium myrtillus* (Table 3). Depending upon the abundance of other species of the dwarfshrubs three different types of synusiae can be distinguished within this group. The last group (group D) contains the synusiae, in which the most important role is played by the mosses (Table 4). The further subdivision into six types within this group results from the area shares of the grassy and dwarfshrub species.

3.2. THE SYNUSIAL COMPOSITION OF THE STUDY SITES

Individual study sites are characterised by specific spatial heterogeneity of the herb layer (Fig. 2). The number of types of synusiae on the particular sites ranges from three to ten, with the most frequent number of types being four and five, though only one or two (on the site FN3 – three) have the dominating character, and occupy at least 20% of surface (Table 5). Notwithstanding the local specificity it is possible to draw conclusions concerning geographical variability of distribution of synusiae from the particular groups. Thus, occurrence of types representing group A is limited to just the sites NO1 and FN1, while group D contains the synusiae of a more southern character, which do not appear on the sites NO1, FN1 and FN2, while being most intensively differentiated and playing an important

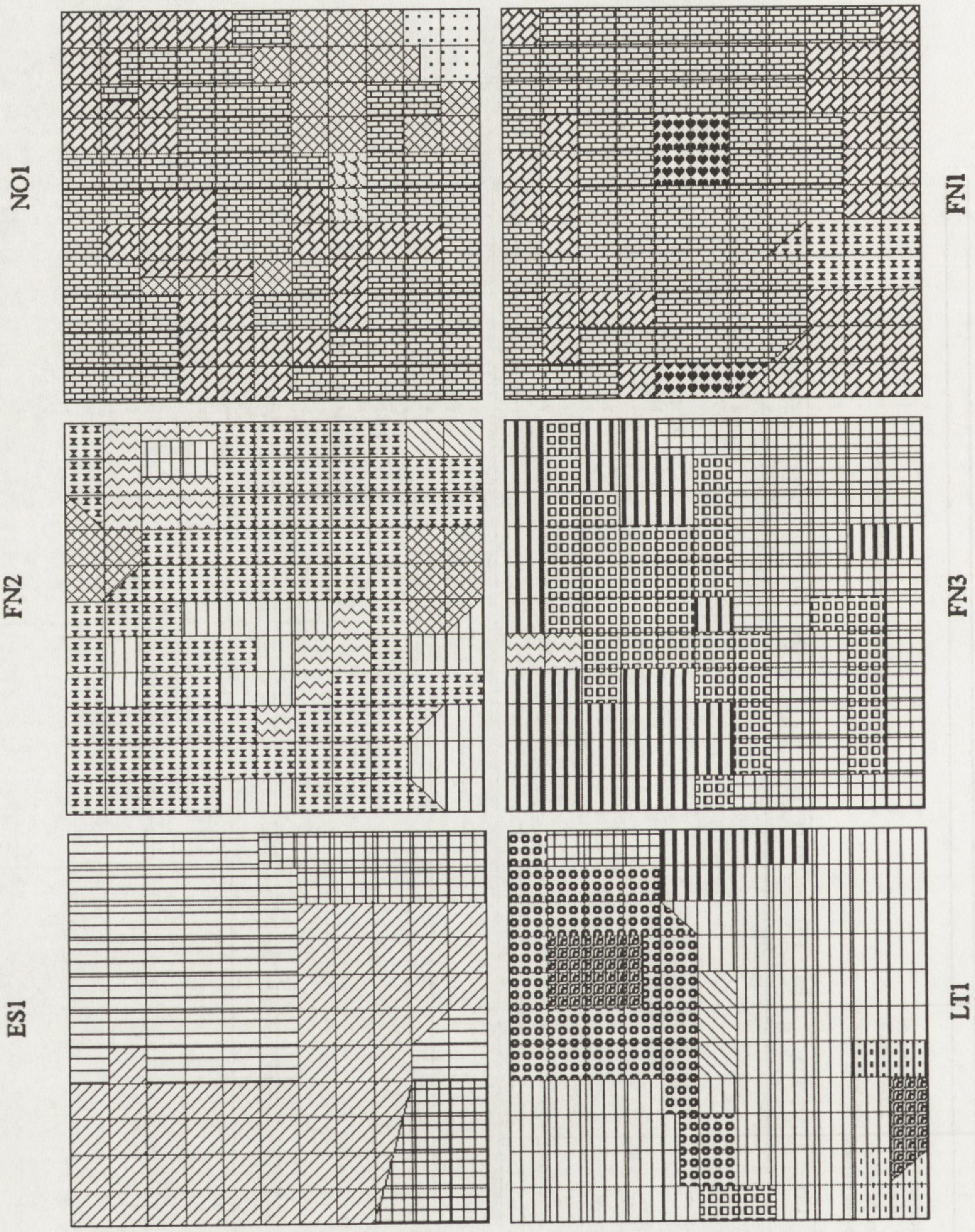
Table 1. Floristic composition of synusiae types belonging to the first group (group A), mainly with the dominance of *Empetrum nigrum*. (Type number - the same as in legend for Fig. 2; species coverage according to the 12-point scale: "r", "+", and "1" denote, respectively, 0.1%, 0.5%, and up to 10%, while the remaining values, from 2 through 10, denote the successive ten per cent intervals

type number	1		2						3							21		22
type name	Empetrum type		Vaccinium vitis-idaea-Empetrum type						Lichen -Vaccinium vitis-idaea-Empetrum type							loose Vaccinium vitis-idaea type		Lichen-Deschampsia type
study site	FN1	FN1	NO1	NO1	FN1	FN1	FN1	FN1	FN1	NO1	NO1	FN1	FN1	FN1	FN1	NO1	NO1	NO1
mosses		6	4	2	+		1	+	+	1	+	3			2	+	+	2
lichens		1	1	+	3	3	2	1	2	7	9	7	6	5	2			6
Empetrum nigrum	9	8	5	3	5	5	2	2	4	+	1	+	3	3	1			2
Vaccinium vitis-idaea	2	3	4	3	5	7	6	9	4	1	+	1	1	2	1	1	+	2
Vaccinium myrtillus			+	+						1	+							
Deschampsia flexuosa										+							+	3
Pinus sylvestris															+			
Vaccinium uliginosum											+							
Arctostaphylos alpina				3														
bare soil	+	+			2	+	3	1	3	1	+	1	4	3	4	8	9	

Table 2. Floristic composition of synusiae types belonging to the second group (group B) with the co-dominance of dwarfshrubs and mosses (Explanations: see Table 1).

type number	4				5	6	7																
type name	Vaccinium vitis-idaea-Empetrum type with mosses				Vaccinium vitis-idaea-Deschampsia type with mosses	Vaccinium vitis-idaea-Festuca type with mosses	Vaccinium vitis-idaea type with mosses																
study site	FN2	FN1	FN2	FN2	LT1	LT1	FN2	FN2	FN2	LT1	PL3	LT1	LT1	FN2	FN2	PL3	PL3	PL2	PL2	LT1	PL3	PL3	PL2
mosses	10	7	10	10	6	7	10	10	10	8	8	9	8	9	10	7	8	8	8	2	8	8	8
lichens		3		1			1	4		1													
Empetrum nigrum	5	6	3	2			1		3														
Vaccinium vitis-idaea	8	3	6	7	6	8	7	6	6	6	7	8	7	8	8	7	8	7	7	7	6	6	7
Vaccinium myrtillus											1										3		
Calluna vulgaris	2			2		1	2		2		1											1	1
Festuca ovina					1	5				1										2			
Deschampsia flexuosa					6																		
Calamagrotis epigeios																							
Melampyrum pratense					1																1		
Luzula pilosa																							
bare soil		1			1	1										3	1	2	2	2	2	1	1

type number	10						11			14					17											
type name	dwarfshrub-Pleurozium type						Calluna-Pleurozium type with Vaccinium vitis-idaea			Pleurozium type with Vaccinium vitis-idaea					Pleurozium-Calluna-Vaccinium vitis-idaea type											
study site	LI1	LI1	PL1	PL1	PL1	PL1	FN3	FN2	PL1	LT1	PL3	FN2	PL3	PL1	FN3	FN3	FN3	FN3	FN3	FN3	LT1	PL1	PL2	PL2	FN3	FN3
mosses	7	8	7	8	7	9	8	10	8	7	7	9	7	8	6	9	9	8	8	9	8	6	7	6	8	8
lichens		2					2	1				1			1	1	1	3	1	3						
Empetrum nigrum								2																		
Vaccinium vitis-idaea	5	3	2	5	3	2	4	5	2	5	5	4	4	3	5	2	3	5	5	3	4	2	5	2	3	2
Vaccinium myrtillus	1	1	1	1	4	1										1										
Calluna vulgaris	2	3	2	2	3	4	6	5	4						2	2	3	1	1	1	3	2	2	3	3	1
Festuca ovina		1																								
Deschampsia flexuosa																										
Calamagrotis epigeios						1																				
Melampyrum pratense			1	1	2																					
Luzula pilosa				1					3																	
bare soil	2	2	2	1	1	1	2		1	2	3		2	7	2		1	1	1		1	2	3	4	1	1



role on the sites LT1, LI1 and PL1 (Table 5). Likewise, the dendrogram of similarities of the study sites with respect to the area shares of the particular groups of synusiae indicates clearly the influence of geographical location on the composition of groups and their mutual likeness (Fig. 3). The most distinctly different are the northern sites, and in particular the sites NO1 and FN1, with the site FN2 being somewhat similar to them. The second subset of sites, though featuring relatively weak internal mutual similarities, encompasses the sites FN3, ES1, LI1 and PL1 located in the middle part of the transect. The third subset of sites, representing a more southern character, is composed of the sites PL2 and PL3. The site LT1, formally assigned also to this subset, displays an only marginally smaller similarity to the sites LI1 and PL1.

The geographical location is also associated with the spatial heterogeneity of the herb layer. It namely turns out that the sites characterised by the same number of the synusial types occurring on them feature higher spatial heterogeneity when located farther South (Fig. 4).

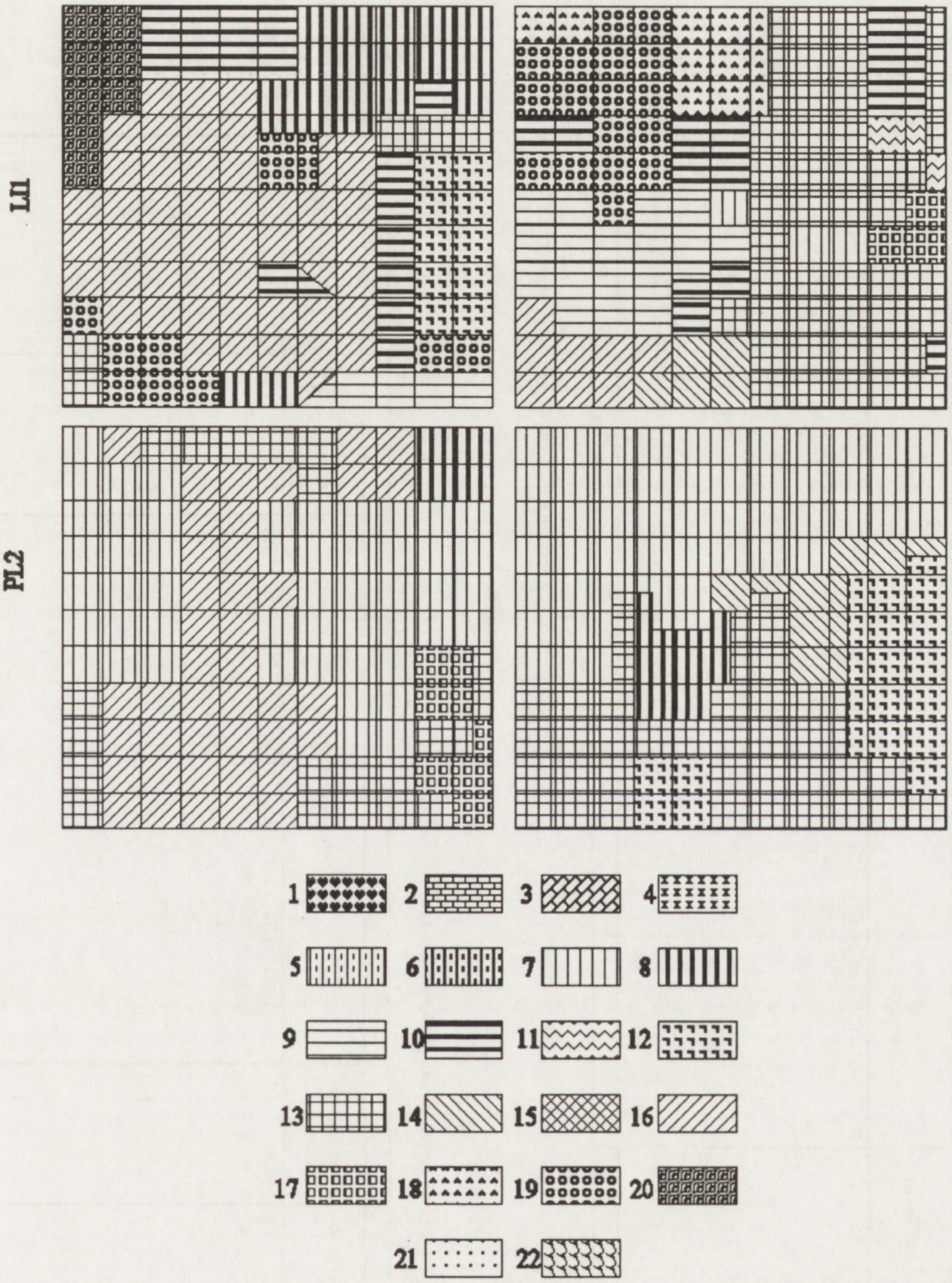


Fig. 2. Synusial heterogeneity of the study sites. 1–22: types of synusiae: 1 – Empetrum type; 2 – Vaccinium vitis-idea-Empetrum type; 3 – Lichen-Vaccinium vitis-idea-Empetrum type; 4 – Vaccinium vitis-idaea-Empetrum type with mosses; 5 – Vaccinium vitis-idaea-Deschampsia type with mosses; 6 – Vaccinium vitis-idaea-Festuca type with mosses; 7 – Vaccinium vitis-idaea type with mosses; 8 – loose Vaccinium vitis-idaea-Pleurozium type; 9 – Vaccinium myrtillus-Pleurozium type; 10 – dwarfshrub-Pleurozium type; 11 – Calluna-Pleurozium type with Vaccinium vitis-idaea; 12 – loose Calluna-mosses type; 13 – Pleurozium type; 14 – Pleurozium type with Vaccinium vitis-idaea; 15 – Pleurozium-Empetrum-Vaccinium type; 16 – Pleurozium-Vaccinium type; 17 – Pleurozium-Calluna-Vaccinium vitis-idaea type; 18 – Calamagrostis type; 19 – Festuca-mosses type; 20 – Pleurozium-Festuca type with lichens; 21 – loose Vaccinium vitis-idea type; 22 – Lichen-Deschampsia type (compare Tables 1–4).

Table 3. Floristic composition of synusiae types belonging to the third group (group C) with the dominance of *Vaccinium myrtillus* (Explanations: see Table 1).

type number	9						15				16													
type name	Vaccinium myrtillus-Pleurozium type						Pleurozium-Empetrum-Vaccinium type				Pleurozium-Vaccinium type													
study site	ES1	ES1	ES1	PL1	ES1	ES1	NO1	NO1	FN2	FN2	ES1	ES1	ES1	ES1	ES1	PL2	PL2	PL2	PL2	LI1	LI1	PL1	PL2	PL2
mosses	8	8	7	8	7	6	8	9	8	10	9	8	9	8	7	9	7	7	8	8	8	8	7	6
lichens							1	+		1										1	2			
Empetrum nigrum							2	2	3	1														
Vaccinium vitis-idaea	2	3	1	1	1	2	+	2	4	4	2	1	1	2	2	5	2	4	4	2	2	3	3	3
Vaccinium myrtillus	6	6	6	6	6	6	6	1			2	2	3	2	3	3	5	3	4	2	3	2	1	4
Calluna vulgaris										1														
Festuca ovina																					1			
Melampyrum pratense	2		1	1	1	1					1		1	1										
Diphasiastrum complanatum																		2						
bare soil		2	1		1	2	+				1	1		1			2	4	2	1	2	1	1	3

Table 4. Floristic composition of synusiae types belonging to the fourth group (group D) with the dominance of mosses (Explanations: see Table 1).

type number	8						12		13										18		19				20	
type name	loose Vaccinium vitis-idaea-Pleurozium type						loose Calluna-mosses type		Pleurozium type										Calamagrostis type		Festuca-mosses type				Pleurozium-Festuca type with lichens	
study site	LT1	FN3	FN3	LI1	LI1	PL2	PL3	LI1	FN3	ES1	LT1	LI1	PL1	PL3	PL3	PL3	PL3	ES1	PL1	PL1	LI1	LI1	LI1	LT1	LT1	LI1
mosses	5	4	4	5	5	4	5	5	7	10	8	8	7	8	7	8	7	8	7	9	8	6	7	7	5	5
lichens	1	1	7		1						+										1				4	1
Vaccinium vitis-idaea	4	2	2	2	3	4		1				2	1					1		1	1	1	1			1
Vaccinium myrtillus		+					1			1					1			1	4				1			
Calluna vulgaris							2	1						1					1							1
Festuca ovina																					4	5	4	3	3	2
Deschampsia flexuosa																								3		
Calamagrotis epigeios																			3	2						
Pinus sylvestris		1														1										
Melampyrum pratense								1											1	1						
Picee excelsa																						2				
Luzula pilosa																			1							
bare soil	3	3	5	3	3	3	2	3	3		2	2	3	1	1	1	2	2	2		3	1	2	2	2	3

Table 5. Area (in m^2) occupied by different synusiae types on 121 m^2 sampling plots of study sites.

	site	NO1	FN1	FN2	FN3	ES1	LT1	LI1	PL1	PL2	PL3
synusium group[1]	synusium type[1]		1								
A	21	3.5									
A	22	2									
A	2	64.5	72								
A	3	34	36								
A	1		6.5								
C	15	17		9.5							
C	9					43.5		4.5	17.5		
C	16					56.5		48.25	8	41	
B	4		6.5	77							
B	11			12	2				2		
B	14			2			3		5		8.5
B	7			20.5			65.5		3	50	51.25
B	17				37		2		3	6.5	
B	5						3.5				
B	6						2				
B	10							16.5	13.5		
D	13				45	21	3	5	42.5	19.5	36.75
D	8				37		6	18.5		4	6.5
D	20						7.5	8			
D	19						28.5	10.25	17		
D	12							10			18
D	18								9.5		
number of types		5	4	5	4	3	9	8	10	5	5
Shannon's diversity index of synusiae		1.64	1.39	1.56	1.69	1.48	2.04	2.56	2.76	1.85	1.94

[1]compare Table 1–4 and Fig. 2.

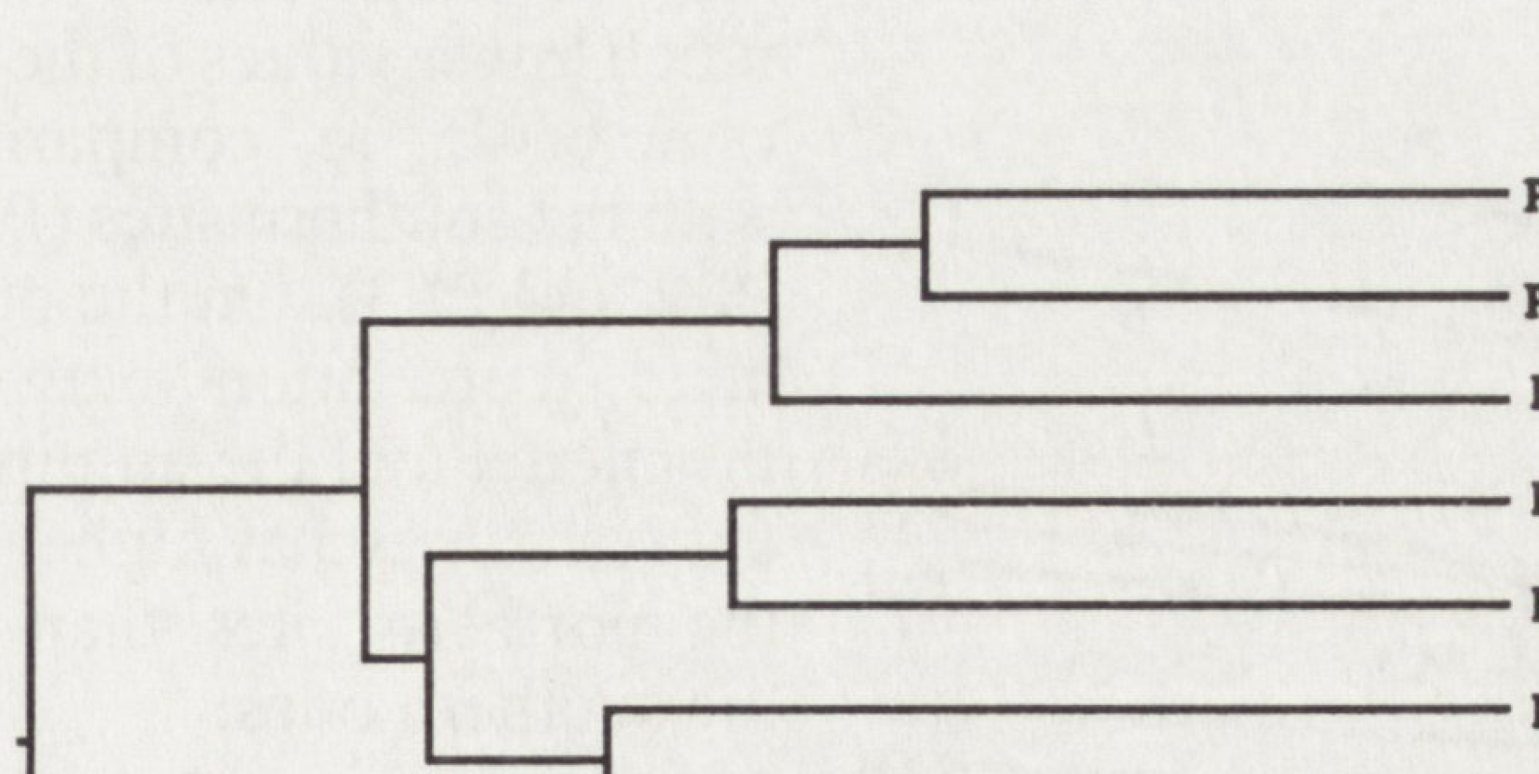


Fig. 3. Dendrogram of similarity of synusial composition of the herb layer on study sites based on Canberra distance and Ward method.

3.3. CHANGES OF THE SPECIES NUMBER

The relation between the geographical location and the number of vascular plants occurring on the areas of various size is not unambigous (Fig. 5). On the one hand, a statistically significant decrease is observed of the number of species within the 100 and 400 m^2 plots along with the latitude. On the other hand, latitude has no essential influence on the number of species observed on the areas of 1 or 20 m^2.

The previously mentioned climatic factors have no influence on

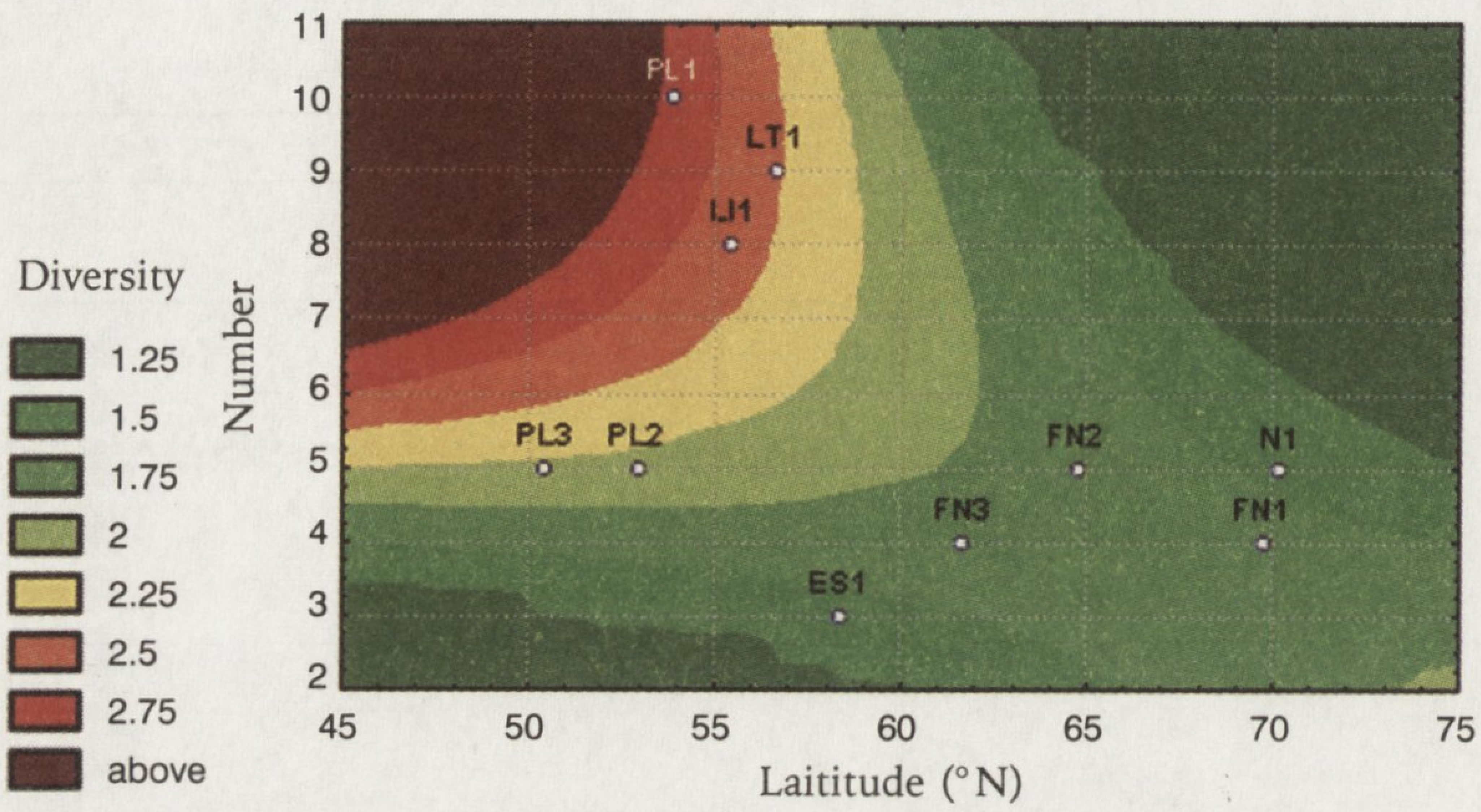


Fig. 4. The number of synusium types in the herb layer and the Shannon's index of synusial diversity of the study sites.

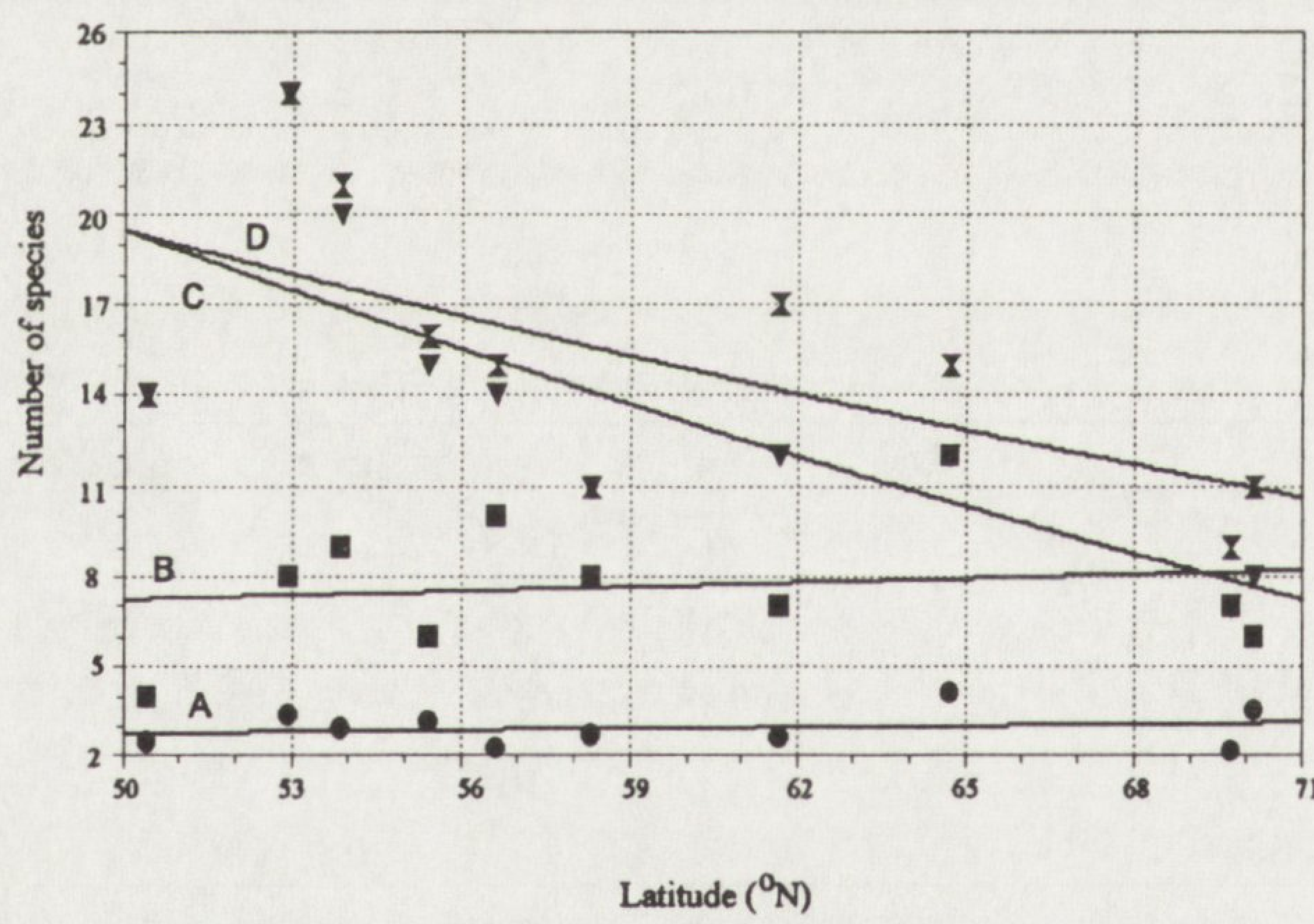


Fig. 5. Regression lines for the number of species in the herb layer against the latitude: A – for 1 m^2 ($y = a + bx$; $a = 1.96$, $b = 0.02$, correlation coefficient 0.18); B – for 20 m^2 ($y = a + bx$; $a = 4.98$, $b = 0.05$, correlation coefficient 0.14); C – for 100 m^2 ($y = a + b \times \ln x$; $a = 155.91$, $b = -34.87$, correlation coefficient 0.78); D – for 400 m^2 ($y = a + b \times \ln x$; $a = 118.09$, $b = -25.21$, correlation coefficient 0.63).

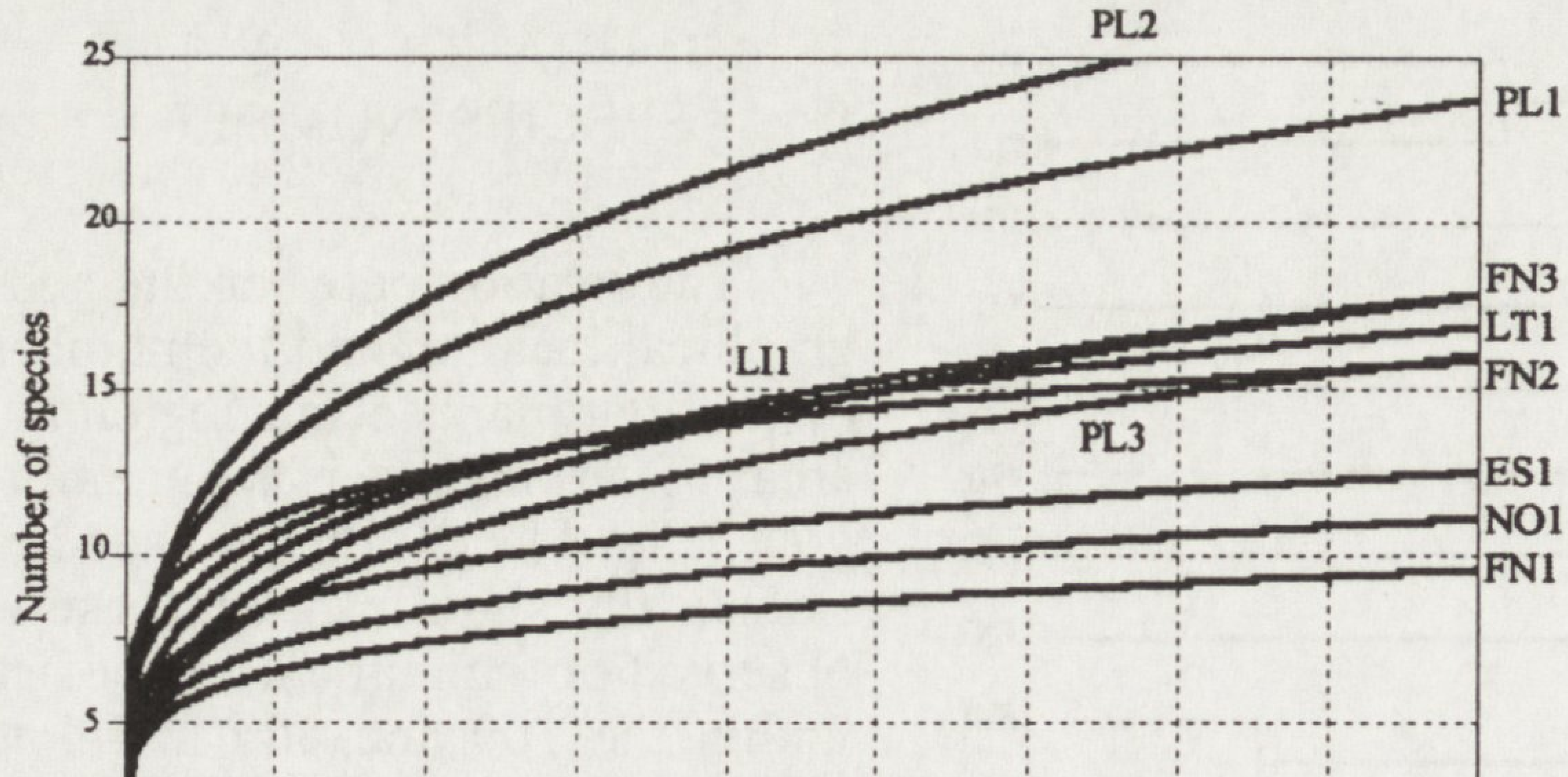


Fig. 6. Regression lines for the number of species in the herb layer against the area (m^2) for all the study sites. See Table 6 for the equation parameters.

the species richness of the sites. In particular, there is no statistically significant correlation between the number of species (on the surface of any area) and the annual total precipitation as well as the Martonne index. On the other hand, a weak association (correlation coefficient $r = 0.63$) is observed between the number of species per 1 m^2 and the Lang index ($y = -433.26 + 196.43x$).

For each of the sites separately the dependence between the number of vascular species of the herb layer and the area of the site considered (the "number of species vs. area" relationship) is described by the power form $y = ax^b$. The values of the exponent b are contained in the interval from approximately 0.16 to approximately 0.29, with the correlation coefficients between the model and the actual numbers of species being very high, from 0.902 to 0.998 (Fig. 6 and Table 6). It should be noted in this context that the northern sites (NO1, FN1 and FN2) are characterised by the much lower values of the parameter b, in comparison with the southern sites (PL1, PL2 and PL3). On the other hand, correlation between the model and the empirical data is somewhat higher for the northern sites than for the southern ones.

4. DISCUSSION AND CONCLUSIONS

Within the fresh pine forest ecosystems the herb layer is not homogeneous, but rather split up into fragments forming the setting of

Table 6. Parameters of regression lines (according to the model $Y = ax^b$) for the number of species (y) on the area (x) for all study sites

Site	a	b	Correlation coefficient
NO1	3.37	0.19	0.99
FN1	3.27	0.17	0.93
FN2	5.92	0.16	0.92
FN3	2.96	0.29	0.99
ES1	4.21	0.18	0.93
LT1	4.6	0.21	0.94
LI1	3.55	0.26	0.94
PL1	4.67	0.27	0.94
PL2	4.81	0.28	0.91
PL3	2.73	0.29	0.9

separate micro-areas, differing by the domination of the particular species and life forms. The method based upon the synusiae is useful in the description and characterisation of such spatial forms. It can complete, and in some cases also replace, other methods of description, applied in the typology of forest associations (Du Rietz, 1930; Lippmaa, 1935; Gillet, 1986; Freléchoux *et al.*, 2000).

Taking as the basis the dominating species, the life forms, and the degree of area coverage by vegetation, and accounting for the results of cluster analysis in the form of dendrogram, we can distinguish four main groups of synusiae, encompassing their 22 types. A part of these types are limited in their occurrence to just northern Scandinavia, while other ones are common to the pine forests of the remaining part of the transect. In particular, the synusiae with the domination of bilberry (*Vaccinium myrtillus*), and the purely mossy synusiae, with the domination of *Pleurozium schreberi*, are especially frequent. Their presence was also registered on the parallel transect stretching from the vicinity of Berlin to eastern Belarus' (Roo-Zielińska and Solon, 1998; Solon and Roo-Zielińska, 1998).

The increase of the number of the herb layer species, observed along with the increase of the area analysed, has a similar character for all the sites and is conform to the so-called allometric rule, represented through the formula $y=ax^b$. Similar relationships have been described many times, and the values of the exponent parameter obtained in the study range roughly between 0.17 and 0.33; such values being among the ones most often quoted in the literature (Stanley *et al.*, 2000). The sites especially rich in species feature, in general, higher values of the exponent b, which, again, is a commonly observed regularity (Barnett and Stohlgren, 2001).

Taking into consideration the synusial differentiation and the variability of the parameter appearing in the dependence of the number of species upon the size of the area analysed, we can deduce a clear division of the sites studied, located along the given transect, into three groups. The first of them encompasses the northernmost sites (NO1 and FN1), to which the site FN2 is much alike. The second, well separate group is composed of the southern sites, and especially PL2 and PL3. The heterogeneity of the herb layer on the remaining sites has an intermediate character.

ACKNOWLEDGEMENTS: The following organizations provided financial and/or in-kind support for this project: US Environmental Protection Agency, Washington D.C., USA; Finnish Forest Research Institute; University of Oulu, Oulu, Finland; Turku Universty, Kevo Subarctic Research Station, Finland; Estonian Academy of Science, International Center for Environmental Biology; Latvian Forestry Research Institute; Vytautas Magnus University, Kaunaus, Lithuania; Institute of Geography and Spatial Organization, Polish Academy of Sciences, Warsaw, Poland; Bowling Green State University, Bowling Green, OH USA; Michigan Technological University, Houghton, MI USA; Forest Research Institute, Warsaw, Poland; and collegues helping us in completion of climatic data for transect stands: drs G. Bjørbæk, E. Kubin, J. Haggman, J. Halminen, H. Parn, M. Sipols, R. Juknys.

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Received after revising June 2003