

## DIVERSITY AND NICHE CHANGES OF SHRUB SPECIES WITHIN FOREST MARGIN\*

By

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In a forest margin, ecotone formed along the meeting contact of a turkey-oak forest and a vineyard the change of diversity (species-individual, species-relative cover), equitability and evenness of the shrub species were studied from the edge of the forest margin towards the inside of the forest by means of transects. The change of niche-width and overlap of the species were examined in a niche-axis in the transects in the same direction. The niche-axis may correspond to the "light conditions". According to the change of diversity of species-relative cover the "ordering" of the shrub layer is increasing towards the inside of the forest. In the outer zone of the forest margin neither species have a competitive advantage. Proceeding towards the inside of the forest some species (*Cornus mas*, *Acer tataricum*, *Ligustrum vulgare*) take up the greater part of the niche-space and have a competitive advantage over the other species. As a response to the closing of the canopy layer the majority of the species will narrow their niche-width. From the results it can be drawn that in the examined forest the maximum width of the forest margin may be approximately 8 meters. Beyond this distance towards the inside of the forest the conditions of shrub-structure are already characteristic of the inside of the forest.

### Introduction

An intermediate zone, the ecotone may often form in the zone of forest and unforested areas. The ecotones are rich in species because a part of species of both contact communities may appear in them. Apart from these species there are also ones which can be found more frequently only in the ecotones. The environmental effects are changing from the outer zone of the margin towards the inside of the community so the behaviour of the species can be studied along gradients by means of transects.

The vegetation of the forest margin plays a special role in the life of the forest. It often behaves as a "filter" and "protector" against the effects coming from outwards assuring in this way the (relative) undisturbed function and development of the inside of the forest (JAKUCS 1972).

The species composition, structures and functions of the vegetation of the forest margin are different to a certain extent from those of the forest and open (treeless) communities, respectively, bordering the forest. This difference can be seen, for example, in that some shrubs and herbs are growing more quickly and have more products than those living inside the forest (GHISELIN 1977, RANNEY 1977). In the forest shade tolerant species are prevailing, in the margin shade- and light-tolerant species are mixed; in the forest mesofrequent species can often be found, in the margin meso- and xerofrequent species also occur beside the previously mentioned ones (MCINTOSH 1957, RANNEY 1977, WALES 1972). These phenomena show

\* Síkfőkút Project, No. 73.

that light, wind and soil-moisture have an essential part amongst microclimatic factors. The soil of the forest margin is different from that of the forest also in its supply with nutrients, chemical reaction and amount of humus (JAKUCS 1972, MCINTOSH 1957, MÉSZÁROS and JAKUCS 1981).

This study demonstrates the change in diversity and niche of the shrub species of the vegetation of a deciduous oak forest from the margin of the forest towards the inside of the forest.

### The examined forest and forest margin

The forest (*Quercetum petraeae-cerris*), which in many respects can be considered homogeneous in a great extension, is a 70–75 year old stand of coppice origin. The MAB sample area in Hungary ("Sikfőkút Project"; JAKUCS 1973, 1979, PAPP and JAKUCS 1976).

The northern edge of the forest is in contact to a vineyard. In this edge an unbroken closed zone of margin vegetation, well observable also physiognomically, can be found. In the outer part — about 4 meters in width — of this zone the shrubs reach a height of even 3 meters and herbs can hardly be found under them. Above the thick shrub layer the cover of the foliage of the trees is 60% on average (in the inside of the forest it is 80%; JAKUCS, HORVÁTH and KÁRÁSZ 1975). The cover of the foliage above the margin is given by the trees standing in the edge of the closed forest, not by the ones rooting in the margin. The zone of shrub is constituted partly by species which are constant and dominant in the inside of the forest also (*Ligustrum vulgare*, *Cornus sanguinea*, *Acer tataricum*, *Quercus petraea*, *Euonymus europaeus*, *Euonymus verrucosus*), and partly by ones which have very low constancy and dominancy in the inside of the forest or are present not at all (*Crataegus monogyna*, *Viburnum antana*, *Prunus spinosa*; see: KÁRÁSZ 1976).

### Method of sampling

3 transects of 4 times 8 meters and 2 transects of 4 times 12 meters were designated perpendicularly to the forest margin. The transects were divided into plots of 4 meters (Fig. 1). In these plots the percentage of cover of the shrub species was estimated in heights of 0.3, 1.0, 1.5, 2.0 and 3 meters, and the number of the individuals belonging to shrub species counted.

### Method of evaluation

SHANNON-WEAVER's formula was used to calculate the diversity (H: SHANNON and WEAVER 1949). Beside it the equitability,  $J = H/\log S$  where S means the number of species, as well as the evenness (NOSEK 1976) were also given. The evenness was calculated by the formula:

$$V = \frac{H - H_{l,\min}}{H_{l,\max} - H_{l,\min}}$$

Values H, J and V, of species-individual and species-relative cover were calculated.  $H_{l,\min}$  value of species-individuals was calculated so that one individual was attached to species  $n-1$  and the remaining individuals, to one species (NOSEK 1976). To calculate  $H_{l,\min}$  value of the species-relative cover, a cover of 99% was attached to one species while the remaining 1% was evenly distributed among the other species (PRÉCSÉNYI 1981). The mentioned characteristics will be given from the edge of the forest margin towards the inside of the forest and also according to height levels.

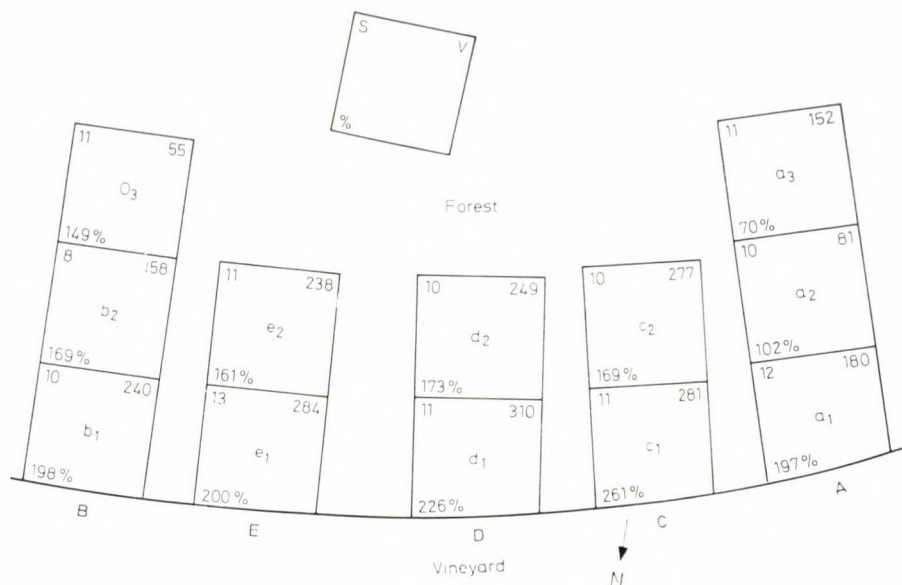


Fig. 1. Placing of the transects. S = number of species; N = Number of individuals; % = cover (sums of the cover from level to level)

SØRENSEN'S (1948) similarity index was used for the floristic comparison of the plots.

The niche-width and overlap of the species were estimated in each plot of 16 m<sup>2</sup> on the basis of the values of relative cover falling to the height categories (0.3 m, 1.0 m, etc.), then the niche-widths and overlaps calculated in the plots, which were in equal distance from the outer edge of the margin (0 to 4 meters, 4 to 8 meters, 8 to 12 meters), were averaged for the evaluation. LEVINS' (1968) formulas were used for the calculation of the niche-width and overlap:

$$B_i = \frac{1}{\sum p_{ij}^2}; \quad \alpha = \alpha_{hi} = \frac{\sum p_{hj} p_{ij}}{\sum p_{hj}^2}; \quad \beta = \alpha_{ih} = \frac{\sum p_{hj} p_{ij}}{\sum p_{ij}^2}$$

On the basis of the overlap values the community effect was estimated by row-average of the community matrix for the zones of the margin vegetation while the species effect, by its column-average (VANDERMEER 1972).

## Results

Before presentation of the results a few remarks on physiognomy are needed: proceeding inwards the transects, the total cover of individual of the shrubs is decreasing (Fig. 1 and Tables 1 and 2). In the plots of 8 to 12 meters (*a*<sub>3</sub>, *b*<sub>3</sub>) already their cover and number of individual, too, come close to the values characterizing the inside of the forest (KÁRÁSZ 1976). Towards the inside of the forest the foliage of the trees are closing more and more, at the same time the cover of the shrub level is loosening.

The maximum value of the cover of the shrub layer is vertically about in 1 m height from 0 to 4 meters and 4 to 8 meters away of the outer edge of the margin (on average 75.5% and 53.5%, respectively) and in plots 8 to 12 meters away from the edge of the margin it is in a height of 1.5 meters (on average 32.0%).



Table 1

Cover (%) of the shrub species estimated

	A					B				
	30 cm	1	1.5	2	3	30 cm	1	1.5	2	3
		m					m			
0-4 m										
<i>Cornus sanguinea</i>	25	30	35			10	6	2		
<i>Rosa canina</i>	10	10	20	5		1				
<i>Frangula alnus</i>	2									
<i>Euonymus europaeus</i>	3	5				4	1			
<i>Acer tataricum</i>		5	5	5		5	25	25	25	12
<i>Euonymus verrucosus</i>	5	3				8	5			
<i>Ligustrum vulgare</i>	15	3				15	7	3		
<i>Prunus avium</i>		3				1	1			
<i>Crataegus oxyacantha</i>	1									
<i>Prunus spinosa</i>	1					10	15	3		
<i>Berberis vulgaris</i>		2								
<i>Cornus mas</i>	1	3								
<i>Quercus cerris</i>						1				
<i>Viburnum lantana</i>										
<i>Crataegus monogyna</i>						1	3	3	3	3
<i>Pyrus pyraster</i>										
<i>Sorbus domestica</i>										
4-8 m										
<i>Cornus sanguinea</i>		7				3	12	15	3	
<i>Rosa canina</i>						1				
<i>Frangula alnus</i>		3								
<i>Euonymus europaeus</i>	1					1				
<i>Acer tataricum</i>	1	1	1	10		7	15	25	20	3
<i>Euonymus verrucosus</i>	10	8	15	12		5	4			
<i>Ligustrum vulgare</i>	2					10	15	15		
<i>Crataegus oxyacantha</i>	4	8	8	8						
<i>Prunus spinosa</i>	1					3	5	5		
<i>Cornus mas</i>						1				
<i>Quercus petraea</i>	1									
<i>Acer campestre</i>	1									
<i>Quercus cerris</i>						1				
<i>Viburnum lantana</i>										
<i>Crataegus monogyna</i>										
<i>Pyrus pyraster</i>										
<i>Lonicera xylosteum</i>										
8-12 m										
<i>Cornus sanguinea</i>						3	5			
<i>Rosa canina</i>	1	2					1			
<i>Frangula alnus</i>	2					1				
<i>Acer tataricum</i>	1	6	20	5		1	2	3		
<i>Euonymus verrucosus</i>	6	2				1				
<i>Ligustrum vulgare</i>	10					10	15	5	1	
<i>Prunus avium</i>	1	1								
<i>Crataegus oxyacantha</i>	1									
<i>Prunus spinosa</i>	1					1	1			
<i>Cornus mas</i>						5	20	30	20	15
<i>Quercus petraea</i>	1		2							
<i>Acer campestre</i>								2	3	
<i>Quercus cerris</i>	1					1				
<i>Viburnum lantana</i>	3	2	1							
<i>Pyrus pyraster</i>						1	2			
<i>Rhamnus catharticus</i>			1							

*in various heights in plots of 16 m<sup>2</sup>*

C					D					E				
30 cm	1	1.5	2	3	30 cm	1	1.5	2	3	30 cm	1	1.5	2	3
	m					m					m			
2	7	3	1		0.5	10				2.5	4	7		
2	10	15	7		2	10	20	5		2	25	15	5	
1	2	3			1	3				1	1	2		
3	10	7	3		3	10	15	20		2	7	2		
2	5				5	5				5	8	3		
25	10	10			30	20	7			10	15			
10	10				0.5	3				5				
	15	25	20			2	10	7	5	1				
1	15	15	5		7	20				10	7	10		
2										1				
2	3	5	5		1	2				1				
					1	1				2	10	20	10	5
											0.5	0.5		
20	25	10	7		1	15				20	22			
0.5	5	7								0.5	1			
											1			
5										1.5	0.5			
2	10	5			5	7				2	7	12	5	
3	5				2	8				8	15	10		
10	3				30	20	2			5	2			
5	10	15	5		0.5					0.5	8	10	18	8
2	7				1	4	2			0.5				
						3	30	35						
						3	0.5							
1	3													
0.5	3				1	1								
					0.5					2				
					0.5	0.5				0.5	0.5			

Table 2

Number of individuals of the shrub species in plots of 16 m<sup>2</sup> of the transects

Transect	A			B			C		D		E	
	0-4	4-8	8-12	0-1	4-8	8-12	0-4	4-8	0-4	4-8	0-4	4-8
	m			m			m		m		m	
<i>Cornus sanguinea</i>	78	14	—	28	44	4	7	87	11	15	29	75
<i>Rosa canina</i>	11	—	4	2	2	3	24	3	20	—	36	4
<i>Frangula alnus</i>	7	8	6	—	—	5	—	—	—	—	—	1
<i>Euonymus europaeus</i>	19	1	—	13	1	—	4	16	5	—	4	11
<i>Acer tataricum</i>	16	3	37	30	17	10	34	22	23	9	10	11
<i>Euonymus verrucosus</i>	12	34	10	42	48	1	10	19	17	39	55	95
<i>Ligustrum vulgare</i>	29	4	59	93	23	20	121	83	207	146	84	20
<i>Prunus avium</i>	2	—	5	3	—	—	47	—	2	—	10	—
<i>Crataegus oxyacantha</i>	1	8	1	—	—	—	2	9	1	—	2	13
<i>Prunus spinosa</i>	1	6	1	26	21	4	21	32	21	31	41	3
<i>Berberis vulgaris</i>	1	—	—	—	—	—	—	—	—	—	—	—
<i>Conus mas</i>	3	—	—	—	1	1	—	—	—	1	—	—
<i>Quercus petraea</i>	—	2	4	—	—	—	—	—	—	1	—	—
<i>Acer campestre</i>	—	1	—	—	—	1	—	—	—	—	—	—
<i>Quercus cerris</i>	—	—	2	2	1	3	3	2	—	—	7	—
<i>Viburnum lantana</i>	—	—	22	—	—	—	8	—	2	4	3	—
<i>Crataegus monogyna</i>	—	—	—	1	—	—	—	4	—	1	2	2
<i>Pyrus pyraeaster</i>	—	—	—	—	—	3	—	—	1	—	—	3
<i>Rhamnus catharticus</i>	—	—	1	—	—	—	—	—	—	—	—	—
<i>Sorbus domestica</i>	—	—	—	—	—	—	—	—	—	—	1	—
<i>Lonicera xylosteum</i>	—	—	—	—	—	—	—	—	—	2	—	—

Table 3

Floristic similarity of the plots

	a <sub>2</sub>	a <sub>3</sub>	b <sub>1</sub>	b <sub>2</sub>	b <sub>3</sub>	c <sub>1</sub>	c <sub>2</sub>	d <sub>1</sub>	d <sub>2</sub>	e <sub>1</sub>	e <sub>2</sub>
a <sub>1</sub>	0.73	0.67	0.73			0.78		0.78		0.72	
a <sub>2</sub>		0.64		0.63			0.70		0.67		0.76
a <sub>3</sub>					0.61						
b <sub>1</sub>				0.84	0.67	0.84		0.76		0.87	
b <sub>2</sub>					0.80		0.84		0.60		0.70
c <sub>1</sub>							0.86				
d <sub>1</sub>									0.64		
e <sub>1</sub>											0.75

### Floristic similarity of the plots

#### *Similarity within transect*

The plots following each other in the transects show a high floristic similarity, except plots  $e_{1-2}$  (Table 3). The similarity of the plots farther from each other (e.g.  $a_{1-3}$ ) is slightly less than that of the above mentioned ones. The plots of transect "B" following each other ( $b_{1-2}$ ,  $b_{2-3}$ ) show a high similarity.

**Table 4**

*Floristic similarity of the plots in various heights*

	m	a <sub>2</sub>	a <sub>3</sub>	b <sub>2</sub>	b <sub>3</sub>	c <sub>2</sub>	d <sub>2</sub>	e <sub>2</sub>
a <sub>1</sub>	0.3	0.59	0.60					
	1.0	0.43	0.57					
	1.5	0.33	0.29					
	2.0	0.40						
a <sub>2</sub>	0.3		0.63					
	1.0		0.40					
	1.5		0.29					
b <sub>1</sub>	0.3			0.84	0.63			
	1.0			0.77	0.53			
	1.5			0.89	0.44			
	2.0			0.50				
b <sub>2</sub>	0.3				0.78			
	1.0				0.67			
	1.5				0.50			
c <sub>1</sub>	0.3					0.80		
	1.0					0.74		
	1.5					0.67		
	2.0					0.50		
d <sub>1</sub>	0.3						0.63	
	1.0						0.60	
	1.5						0.25	
e <sub>1</sub>	0.3							0.82
	1.0							0.67
	1.5							0.36

### *Similarity between transects*

The floristic similarity of the equidistant plots of the respective transects was also examined (e.g.  $a_1$ - $b_1$ ;  $a_2$ - $b_2$ ; etc., Table 3). The values of the plots of 0 to 4 meters ( $a_1$ ,  $b_1$ , etc.) exceed those of the plots of 4 to 8 meters ( $a_2$ ,  $b_2$ , etc.). Proceeding inwards the forest the value of similarity is generally decreasing, however, it remains above 0.5 without exception.

### *Change of the similarity within transect according to the height*

The floristic similarity of the plots is decreasing with the increase of the height (Table 4). In most instances the floristic similarity suddenly decreases in heights from 0.3 m to 1.0 m and 1.0 to 1.5 meters, respectively. It can be explained partly by that the majority of the shrubs reaches a height of 0.3 to 1 m and partly by that the number of common species is decreasing due to the various light conditions.

## Diversity

### *Species-individual diversity*

Proceeding from the outer edge of the margin inwards the forest in transect "A" the diversity, equitability and evenness are hardly changing (Table 5). In plot  $a_1$  the *Cornus sanguinea*, in plot  $a_2$  the *Euonymus europaeus* while in plot  $a_3$  the *Ligustrum vulgare* are represented by most individuals.

**Table 5**  
*Species-individual diversity (H), equitability (J) and evenness (V)*

Transect	A	B	C	D	E	Average
0-4 m						
H	0.7783	0.7553	0.7720	0.5507	0.8585	0.7430
J	0.7212	0.7553	0.7413	0.5288	0.7707	0.7035
V	0.6714	0.7263	0.7129	0.4824	0.7430	0.6672
4-8 m						
H	0.7766	0.7200	0.7734	0.5747	0.7050	0.7099
J	0.7766	0.7546	0.7734	0.5747	0.6770	0.7113
V	0.6994	0.7152	0.7502	0.5266	0.6359	0.6655
8-12 m						
H	0.7634	0.8562				0.8098
J	0.7074	0.8222				0.7648
V	0.6457	0.7167				0.6812



In transect "B" the diversity and equitability of the plot ( $b_3$ ) in the direction of the inside of the forest are greater than those of the other two plots. The evenness is almost the same in the three plots. The reason of the increase in diversity is that there is no such a prominent value in the number of individuals in plot  $b_3$  than in the other two plots. The low diversity, equitability and evenness in transect "D" are due to the great number of individuals of *Ligustrum vulgare*.

In the inside of the forest the species-individual diversity of the shrubs is 0.9378, their equitability is 0.7788, calculating on KÁRÁSZ's (1973) data. In the transects lower values H are obtained but the equitability — excepting transects "D" and "E" — is approximately the same.

### *Species-relative cover diversity*

In plots of 16 m<sup>2</sup> the species-relative cover diversity, equitability and evenness were examined partly on the basis of addition of the cover percentages estimated from species to species in various heights (Table 6) and partly vertically, on the basis of the cover percentages estimated from species to species in the height levels (Table 7).

The species-relative cover diversity, equitability and evenness calculated on the basis of the species cover summed from level to level are increasing towards the inside of the forest in transect "A" and decreasing in the other transects. The highest values for H, J and V were obtained in transect "C" while the lowest ones, in transect "B".

**Table 6**

*Species-relative cover diversity (H), equitability (J) and evenness (V)*

Transect	A	B	C	D	E	Average
0-4 m						
H	0.7210	0.7216	0.9236	0.8600	0.8828	0.8218
J	0.6681	0.7216	0.8869	0.8258	0.7925	0.7790
V	0.6603	0.7119	0.8830	0.8199	0.7858	0.7722
4-8 m						
H	0.6619	0.6514	0.8202	0.7054	0.7371	0.7152
J	0.6619	0.6827	0.8202	0.6774	0.7078	0.7100
V	0.6501	0.6712	0.8139	0.6664	0.6978	0.6999
8-12 m						
H	0.7864	0.5655				0.6760
J	0.7287	0.5430				0.6359
V	0.7197	0.5275				0.6236

**Table 7**  
*Species-relative cover diversity (H), equitability (J) and evenness (V) in the plots in various heights*

		a <sub>1</sub>	a <sub>2</sub>	a <sub>3</sub>	b <sub>1</sub>	b <sub>2</sub>	b <sub>3</sub>	c <sub>1</sub>	c <sub>2</sub>	d <sub>1</sub>	d <sub>2</sub>	e <sub>1</sub>	e <sub>2</sub>
0.3 m	H	0.7182	0.7026	0.8505	0.8419	0.8090	0.7585	0.7112	0.7647	0.6201	0.4622	0.9273	0.6786
	J	0.7527	0.7780	0.8167	0.8419	0.8478	0.7949	0.7112	0.7647	0.6201	0.4844	0.8592	0.6786
	V	0.7437	0.7696	0.8104	0.8364	0.8423	0.7875	0.7011	0.7565	0.6068	0.4657	0.8546	0.6674
1.0 m	H	0.7496	0.6241	0.6158	0.7184	0.6460	0.6114	0.9426	0.8352	0.8927	0.7820	0.8067	0.6924
	J	0.7856	0.8929	0.8810	0.7955	0.9242	0.7235	0.9426	0.8753	0.8572	0.8195	0.8454	0.7256
	V	0.7778	0.8880	0.8756	0.7878	0.9207	0.7125	0.9406	0.8708	0.8523	0.8130	0.8398	0.7157
1.5 m	H	0.3855	0.3442	0.2710	0.4495	0.5494	0.3560	0.8044	0.5668	0.5703	0.2229	0.7314	0.4755
	J	0.8080	0.7214	0.4501	0.6431	0.9125	0.5913	0.8907	0.9414	0.9472	0.3702	0.8099	0.9966
	V	0.7964	0.7045	0.4222	0.6269	0.9080	0.5705	0.8866	0.9384	0.9445	0.3382	0.8027	0.9964
2.0 m	H	0.3010	0.4713		0.1478	0.1681	0.2364	0.6285	0.2950	0.3980		0.2764	0.2774
	J	1.0000	0.9878		0.4910	0.5585	0.4955	0.8076	0.9801	0.8342		0.9183	0.7555
	V	1.0000	0.9871		0.4463	0.5197	0.4649	0.7997	0.9783	0.8241		0.9111	0.7340

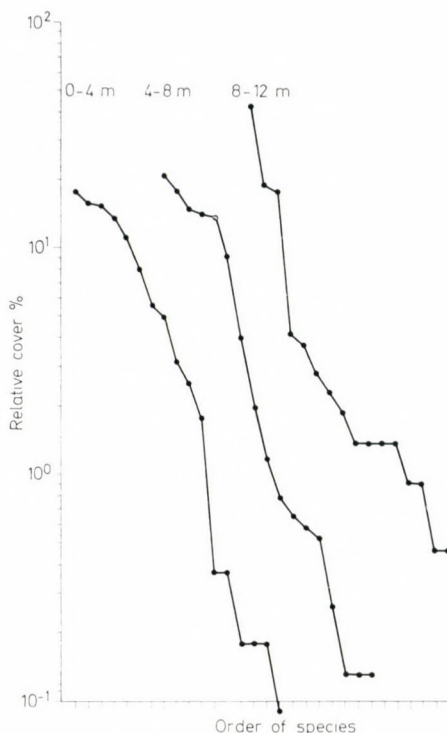


Fig. 2. Dominance-diversity curves

Proceeding vertically upwards, the diversity is generally decreasing. The high diversity values are most often shown in the level of 0.3 to 1 m, and the low ones, in the level of 2 meters. In some instances the change of the equitability and evenness is similar to that of the diversity. In instances (e.g.  $a_1$  and  $a_2$ ) where 2–3 species can be found in the examined level having approximately the same cover, the equitability and evenness will be high. At the same time the diversity will be lower than in levels containing.

#### *Dominance-diversity curves*

The dominance-diversity curves were constructed on the basis of the relative cover values as values of importance (WHITAKER 1965). In the equidistant plots of the transects the cover values of the species were averaged, the averages were summed, and the relative cover of the species were expressed in the percentage of the sum (Fig. 2).

In semi-logarithmic plotting the dominance-diversity curve relating to the zone of 0 to 4 meters approaches to a sigmoid shape. On the upper part of the curve four or five species are in the vicinity of each other (*Acer tatar-*



Table 8

Community matrix for the outer

$\alpha_{ih}$	$\alpha_{hi}$	<i>Cornus sanguinea</i>	<i>Rosa canina</i>	<i>Euonymus europaeus</i>	<i>Acer tataricum</i>	<i>Euonymus verrucosus</i>	<i>Ligustrum vulgare</i>
<i>Cornus sanguinea</i>		2.3200	0.8182	0.9466	0.5973	0.8886	0.5349
<i>Rosa canina</i>		0.7864	2.4799	0.7692	0.7109	0.6602	0.6511
<i>Euonymus europaeus</i>		0.8676	0.7187	2.0382	0.5014	0.8091	0.7170
<i>Acer tataricum</i>		0.7422	0.7389	0.6911	3.1144	0.7416	0.6882
<i>Euonymus verrucosus</i>		0.7942	0.6361	0.8443	0.5473	2.0167	1.0979
<i>Ligustrum vulgare</i>		0.6696	0.6435	0.7749	0.5880	0.9266	2.0759
<i>Cornus mas</i>		0.9572	1.0940	2.7696	1.2309	2.1541	1.6416
<i>Prunus avium</i>		0.6380	0.3870	0.6548	0.3309	0.6700	0.5445
<i>Prunus spinosa</i>		0.8515	0.6241	0.8484	0.5014	0.8380	0.7595
<i>Crataegus monogyna</i>		0.8437	0.6556	0.7315	0.8949	0.6610	0.5703
<i>Crataegus oxyacantha</i>		0.3646	0.5332	0.4168	0.4640	0.3967	0.6300
<i>Viburnum lantana</i>		0.9980	0.6827	0.9814	0.5889	0.7731	0.7125
<i>Pyrus pyraeaster</i>		1.0000	0.3244	1.0000	0.2708	1.0000	0.8772
Species effect		0.7928	0.6547	0.9524	0.6022	0.8766	0.7854

Values  $B_1$  in the main diagonal

*cum*, *Ligustrum vulgare*, *Rosa canina*, *Cornus sanguinea*, *Prunus spinosa*). It shows partly that there is no species which would have a considerable competitive advantage over the other species and take up the greater part of the nichespace, and partly that the environmental conditions are favourable for more species. The latter remark is supported by the fact, too, that the average of species-relative cover diversity, equitability and evenness is highest also in this zone.

The curve relating to the zone of 4 to 8 meters is also approaching to the sigmoid shape but the species found in the preceding one only partly can be found on its top (*Cornus sanguinea*, *Acer tataricum*, *Ligustrum vulgare*; new species: *Euonymus verrucosus*, *Crataegus oxyacantha*) and the order of the species is also different. There is no species either in this zone which would take up the greatest part of the nichespace by oneself. The average diversity, equitability and evenness values are lower than in the zone of 0 to 4 meters.

The shape of the curve relating to the innermost zone (8 to 12 meters) is different from that of the preceding two curves. The first section of this curve shows a great similarity with the curve of the geometric series (WHITTAKER 1965). In this section three species (*Cornus mas*, *Acer tataricum* and *Ligustrum vulgare*) can be found, which take up the great part of the nichespace. According to this the average diversity is lowest in this zone.



*(0 to 4 m) zone*

<i>Cornus mas</i>	<i>Prunus avium</i>	<i>Prunus spinosa</i>	<i>Crataegus monogyna</i>	<i>Crataegus oxyacantha</i>	<i>Viburnum lantana</i>	<i>Pyrus pyraister</i>	Community effect
0.5727	0.8636	0.8542	0.5411	0.5168	0.6888	0.5499	0.6977
0.7200	0.4973	0.6689	0.3821	0.6415	0.6882	0.4198	0.6330
1.0587	0.8614	0.8189	0.4480	0.5556	0.8153	0.8000	0.7476
0.7500	0.7089	0.6039	0.6947	0.5286	0.6454	0.4250	0.6632
0.8235	0.8633	0.8588	0.3898	0.5870	0.6529	1.0000	0.7579
0.4616	0.7658	0.8036	0.2921	0.6784	0.7309	1.0564	0.6993
4.9237	3.6928	1.2309	—	1.2309	—	—	1.7780
0.7500	1.4649	0.5196	0.3077	0.3362	0.5770	0.6623	0.5315
0.2500	0.7656	2.1230	0.5409	0.7667	0.9421	0.8118	0.7083
—	0.7027	0.8149	4.0387	0.1496	—	—	0.6694
0.2500	0.3978	0.6259	0.0426	2.0289	0.5219	0.1347	0.3982
—	0.8550	1.0443	—	0.5859	2.6863	0.8993	0.8121
—	1.0000	1.0000	—	0.0831	1.0000	2.0000	0.7556
0.6263	0.9979	0.8203	0.4043	0.5550	0.7263	0.6759	

### Niche-width and overlap

A niche-axis was formed on the basis of the cover estimated from species to species in various heights. This axis corresponds to the "light conditions".

On the basis of the niche-width (community matrix Tables 8, 9 and 10) the species can be divided into the following groups: 1. There is species of which the niche-width is unchanged proceeding inwards from the edge of the margin: *Pyrus pyraister*; 2. Species of which the niche-width is narrow in the second zone (4 to 8 meters) and wide in the first (0 to 4 meters) and third (8 to 12 meters) zones: *Cornus mas* and *Viburnum lantana*; 3. Species of which the niche-width is narrow in the first and third zones and wide in the second zone: *Euonymus verrucosus* and *Crataegus oxyacantha*; 4. The niche-width of the following species is narrowing from the outer zone towards the inside of the forest: *Acer tataricum*, *Rosa canina*, *Cornus sanguinea*, *Prunus spinosa*, *Ligustrum vulgare*.

The average of the niche-width of these 10 species is also decreasing from the outer edge of the margin towards the inside of the forest.

The conclusion can be drawn from the community matrix that in the outer zone the overlap is great between *Prunus avium* and *Cornus mas*, *Cor-*

**Table 9**  
Community matrix for the

$a_{ih}$ \ $a_{hi}$	<i>Cornus sanguinea</i>	<i>Rosa canina</i>	<i>Euonymus europaeus</i>	<i>Acer tataricum</i>	<i>Euonymus verrucosus</i>	<i>Ligustrum vulgare</i>
<i>Cornus sanguinea</i>	2.0435	0.7118	0.5716	0.5822	0.7130	0.8666
<i>Rosa canina</i>	0.5205	1.6348	0.6113	0.4403	0.6014	0.6268
<i>Euonymus europaeus</i>	0.2986	0.5689	1.1500	0.1236	0.4064	0.7477
<i>Acer tataricum</i>	0.7021	0.6354	0.2863	2.5240	0.7685	0.5671
<i>Euonymus verrucosus</i>	0.7816	0.8904	0.8687	0.7323	2.3856	0.7477
<i>Ligustrum vulgare</i>	0.7844	0.5474	0.9865	0.4621	0.6343	1.8446
<i>Cornus mas</i>	0.0903	1.0000	1.0000	0.0779	0.3160	0.1618
<i>Prunus spinosa</i>	0.6595	0.4945	0.6877	0.5010	0.6651	0.7944
<i>Crataegus monogyna</i>	0.3525	0.4617	0.4697	0.3946	0.4076	0.5662
<i>Crataegus oxyacantha</i>	0.5754	0.8095	0.1237	0.8237	0.6819	0.4757
<i>Viburnum lantana</i>	1.0000	—	—	1.0000	1.0000	0.9616
<i>Pyrus pyraster</i>	1.0000	1.0000	1.0000	0.3462	0.6970	1.0000
Species effect	0.6150	0.7120	0.6606	0.4985	0.6265	0.6833

Values  $B_1$  in the main diagonal

**Table 10**  
Community matrix for the

$a_{ih}$ \ $a_{hi}$	<i>Cornus sanguinea</i>	<i>Rosa canina</i>	<i>Acer tataricum</i>	<i>Euonymus verrucosus</i>	<i>Ligustrum vulgare</i>
<i>Cornus sanguinea</i>	1.8822	1.1764	0.5097	0.7058	0.7969
<i>Rosa canina</i>	0.6250	1.4000	0.2886	0.3750	0.5419
<i>Acer tataricum</i>	0.6963	0.5786	2.3939	0.2923	0.4927
<i>Euonymus verrucosus</i>	0.3750	0.3334	0.1397	1.3000	0.7613
<i>Ligustrum vulgare</i>	1.1590	0.8290	0.5032	0.8166	1.8688
<i>Cornus mas</i>	0.6635	0.9231	1.0386	0.2310	0.7744
<i>Prunus avium</i>	—	1.0000	0.2188	1.0000	1.0000
<i>Prunus spinosa</i>	1.0000	0.6667	0.2657	0.8750	0.9033
<i>Crataegus oxyacantha</i>	—	0.3333	0.0313	0.7000	1.0000
<i>Viburnum lantana</i>	—	1.0000	0.4688	1.1785	1.2857
<i>Pyrus pyraster</i>	0.5750	1.2000	0.5000	0.5999	0.7741
Species effect	0.7848	0.8041	0.3964	0.6774	0.8280

Values  $B_1$  in the main diagonal

## middle (4 to 8 m) zone

<i>Cornus mas</i>	<i>Prunus spinosa</i>	<i>Crataegus monogyna</i>	<i>Crataegus oxyacantha</i>	<i>Viburnum lantana</i>	<i>Pyrus pyraeaster</i>	Community effect
0.1513	0.7547	0.7679	0.3406	0.5664	0.9978	0.6385
1.0000	0.5014	0.7335	0.4901	—	0.8999	0.6425
1.0000	0.6633	0.1661	0.1237	—	0.8000	0.4898
0.2124	0.6237	0.7375	0.6653	0.9730	0.5271	0.6089
0.5748	0.7800	0.7072	0.5976	0.7353	0.9758	0.7629
0.3988	0.8813	0.9602	0.4281	0.9970	0.8449	0.7097
1.5834	0.2793	0.0000	0.0000	0.0000	—	0.2973
0.5071	1.7453	0.8003	0.2190	0.6667	0.5000	0.5905
0.0000	0.6893	1.1082	0.4542	0.5000	0.5000	0.4360
0.0000	0.3878	0.6355	2.9052	0.5000	0.3424	0.4869
0.0441	0.5714	1.0000	1.0000	2.0000	—	0.8221
—	1.0000	1.0000	0.1910	—	2.0000	0.8038
0.3889	0.6484	0.6826	0.4100	0.6233	0.7098	

## inner (8 to 12 m) zone

<i>Cornus mas</i>	<i>Prunus avium</i>	<i>Prunus spinosa</i>	<i>Crataegus oxyacantha</i>	<i>Viburnum lantana</i>	<i>Pyrus pyraeaster</i>	Community effect
0.3006	—	0.9411	—	—	1.0195	0.7786
0.2222	0.8999	0.5500	0.5999	0.6999	0.6667	0.5469
0.6428	0.2425	0.3561	0.0694	0.4041	0.3125	0.4087
0.0556	0.8000	0.8500	1.2000	0.7333	0.3333	0.5582
0.5103	0.5000	1.0520	1.0000	0.5000	1.2072	0.8077
4.1545	—	0.5771	—	—	0.6924	0.7000
—	2.0000	1.0000	1.0000	0.8333	—	0.8646
0.2778	0.5000	1.5000	1.0000	0.5000	1.0000	0.6989
—	0.5000	1.0000	1.0000	0.5000	—	0.5807
—	1.0715	1.2857	1.2857	2.5714	—	1.0823
0.3000	—	0.8999	—	—	1.7999	0.7498
0.3299	0.6448	0.8512	0.8793	0.5958	0.7474	



*mas* and *Euonymus europaeus* and *Cornus mas* and *Euonymus verrucosus*, respectively. Great overlap values, like the preceding ones, cannot be found in the middle zone. In the inner zone *Viburnum lantana* has a considerable overlap with *Ligustrum vulgare* and *Crataegus oxyacantha* further on there is a great overlap between *Crataegus oxyacantha* and *Euonymus verrucosus*, *Ligustrum vulgare* and *Pyrus pyraeaster*.

In the outer zone the highest community effect can be found at *Cornus mas* while the lowest one, at *Crataegus oxyacantha* (Table 8). The species effect is highest at *Prunus avium*, *Euonymus europaeus* is close to it. The species effect is lowest at *Crataegus monogyna*.

In the middle zone the community effect is approximately of the same greatness at *Viburnum lantana* and *Pyrus pyraeaster* and is lowest at *Cornus mas* (Table 9). The species effect is high in case of 9 species, and comparing to the preceding ones, it is low in case of 3 species.

In the inner zone the species have the greatest effect on *Viburnum lantana* and the smallest one on *Acer tataricum* (Table 10). The species effect of *Crataegus oxyacantha*, *Prunus spinosa*, *Ligustrum vulgare* and *Rosa canina* is approximately of the same greatness. *Acer tataricum* and *Cornus mas* have similarity effect on the other species.

In case of *Viburnum lantana* a great community effect can be generally found in each zone while in case of *Rosa canina*, *Acer tataricum* and *Crataegus oxyacantha* a very small one can be found. *Prunus spinosa* and *Ligustrum vulgare* have great effect on the other species. *Acer tataricum* and *Cornus mas* exert a small effect on the other species.

### Conclusions

The species-relative cover diversity of the shrubs is decreasing from the edge of the forest margin towards the inside of the forest. This means an increase in the "ordering" of the shrub layer from this point of view.

In the outer zones of the forest margin the microclimatic and soil factors render the existence of many species possible so that none of the species has a competitive advantage over the other species. Proceeding inwards the forest the environmental factors are modified and the competitive relations are changing due to the closing of the foliage of the trees. The species which most adapted to the modified conditions take up the greater part of the niche-space. Most of the shrub species response for the shading intensifying inwards the forest with narrowing their niche-width.

The community and species effects are variable, in the various zones different species show high and low values. The community effect is generally high in case of *Viburnum lantana* and low in case of *Rosa canina*, *Acer tataricum*



*cum* and *Crataegus oxyacantha*. *Prunus spinosa* and *Ligustrum vulgare* have great effect on the other species, *Acer tataricum* and *Cornus mas* have a small one.

On the basis of floristic similarity, species-relative cover diversity, evenness and dominance-diversity curves it can be stated that the greatest width of the margin of the turkey-oak forest is appr. 8 meters. Inner from this distance shrub-structure characterizing the inside of the forest can be found.

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