ENVIRONMENTAL FACTORS INFLUENCING THE SPECIES COMPOSITION OF ACIDOPHILOUS GRASSLAND PATCHES IN AGRICULTURAL LANDSCAPES

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Abstract

The acidophilous grasslands of the south-western part of the Czech-Moravian Highlands in the Czech Republic were substantially reduced in the 20th century. These patches are addressed in this paper, in terms of the impacts of their size, isolation, and the quality of the surrounding land cover. Species recorded in the acidophilous grasslands are categorized by hemeroby and life form. Multivariate gradient analysis revealed that the greatest proportions of the variability of species data were explained by two local variables (soil pH and the shape of the patch). Some species groups were also substantially influenced by microrelief. The importance of the surrounding land cover for the species composition was studied by means of regression trees. An assumption that, aside from local factors (soil pH and micro-relief), the species composition is significantly influenced by the heterogeneity of the surrounding landscape, was confirmed.

Shrnutí

Faktory ovlivňující druhové složení ostrůvků acidofilních trávníků v zemědělské krajině

Acidofilní trávníky jihozápadní části Českomoravské vrchoviny byly ve 20. století výrazně redukovány. V této práci byly zjišťovány důsledky izolace, velikosti plochy ostrůvku a kvality okolního krajinného pokryvu na jejich druhové složení. Byly rozlišeny druhy zaznamenané v acidofilních trávnících podle hemerobie a životní formy. S pomocí mnohorozměrné gradientové analýzy bylo zjištěno, že z použitých lokálních proměnných vysvětlilo největší část variability druhových dat pH půdy, ale rovněž tvar ostrůvku, některé skupiny druhů jsou také výrazně ovlivněny mikroreliéfem. Význam okolního land cover na druhové složení byl analyzován s pomocí regresních stromů. Byl potvrzen předpoklad, že druhové složení je vedle lokálních faktorů jako jsou pH půdy nebo mikroreliéf významně ovlivňováno heterogenitou okolní krajiny.

Keywords: *acidophilous grasslands, hemeroby, patch isolation, patch area, regression trees, Bohemian-Moravian Highland, Czech Republic*

1. Introduction

The study of processes influencing the species composition in fragmented biotopes stems from the presumption of the validity of the island biogeography theory (MacArthur, Wilson, 1967). The application of this theory to fragmented biotopes in an anthropogenically altered landscape requires an approach including basic parameters such as size, shape, landform heterogeneity and isolation of the islands, as well as characteristics of the surrounding land cover. This article therefore summarises the biogeographical regularities of the appearance of certain plant species in the context of human influence on the landscape.

In the south-western part of the Bohemian-Moravian Highland, the landscape consisting of farmland and pure spruce woods of varying sizes, still contains fragments of acidophilous grassland in the form of very small patches enclosed within arable land. The fragmentation of the previously common acidophilous grasslands in the 20th century was associated with more intensive use of agricultural land and eutrophication of their surroundings; moreover, cattle grazing in the open, once widespread, ceased almost everywhere. In a regional context, the conservation value of these patches is not usually very high, although some of them still harbour rare plant species. The minute size of these acidophilous grassland patches led to their being somewhat neglected by scientists in the past. However, interest in acidophilous grassland patches has been recently revived in the light of a number of surprising findings of animal species, especially of relatively thermophilous insects (Křivan et al., 2009).

The disappearance of acidophilous vegetation habitats and heathlands, together with the widespread extension of meadowlands as part of the intensification of agriculture is evident in much of Europe (Pott, 1996; Mac Donald et al., 2000; Odé et al., 2001). More intensive agriculture leads to fragmentation and also to a larger degree of isolation of biotopes (Meffe, Caroll, 1997). The processes of fragmentation and isolation impair partial populations (Pimm et al., 1988). The species diversity of acidophilous grasslands is influenced by many factors: apart from the size and isolation of the island, which affect the rate of extinction and immigration (MacArthur, Wilson, 1967), these include namely local conditions and landscape context (Cousins et al., 2007).

2. Material and methods

2.1 Study area

The study was conducted in the south-western part of the Bohemian-Moravian Highland in the Czech Republic (Fig. 1). Total area containing the studied patches takes up approximately 4 km^2 and it is situated in the cadastral area of Matějovec (Jindřichův Hradec district). The area lies within the territory built of granite bedrock. In the past, acidophilous grasslands occurred here most frequently as linear vegetation along paths and roads, on balks, at forest margins, and still around bedrock outcrops. The elevation of the gently undulating study area ranges between 650 and 680 m a.s.l. Average total precipitation amount is 715 mm, average annual air temperature is 6.7 °C (Tolasz et al., 2007).

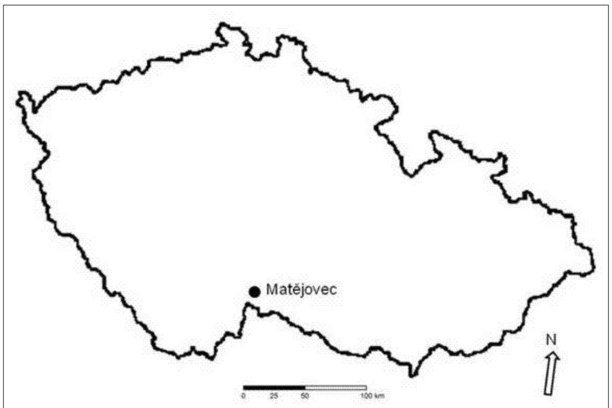

Fig. 1: Location of study area in the Czech Republic

2.2 Floristic and species data

The species composition of the vegetation studied may be categorized as that of acidophilous grasslands on shallow soils, submontane and montane Nardus grasslands, and secondary submontane and montane heaths (Chytrý et al., 2001). Acidophilous grasslands on shallow soils are low and open growths with dominating *Festuca ovina* or *Scleranthus perennis*, rarely also *Agrostis capillaris* or *A. vienalis* and *Hieracium pilosella*. Besides the dominant species, there are also some species of dry and poor soils such as *Hypericum perforatum*, *Jasione montana*, and *Lychnis viscaria*. The community occurs on acidic silicate rocks in uplands and mountain areas. Submontane and montane Nardus grasslands and secondary submontane and montane heaths are represented by growths of Nardus stricta and other grass species, e.g. *Agrostis capillaris*, *Danthonia decumbens*, *Festuca filiformis*, *F. ovina* and *F. rubra agg.*, accompanied by herbs such as *Galium pumilum*, *G. saxatile*, *Polygala vulgaris*, and *Viola canina*. The habitat includes mixed herbaceous and grass stands of both rich and poor species varieties differentiated by the soil nutrient content (Chytrý et al., 2001).

The individual patches often create mosaic or transition patterns, which are simplified as acidophilous grasslands for the purposes of this paper. A total of 35 patches were addressed, of which only 21 were selected for this paper, all of them isolated from the surrounding area either by arable land or wetland. A total of 54 phytosociological relevés were included. The non-included patches were situated within degraded areas of acidophilous grassland or had a higher share of woody plants. On each patch, three relevés were made sized 2 × 2 m, located where possible at the southern and northern edges and in the central part. All higher plant species within the patch were recorded, while the same was done for deliberately-laced phytosociological plots. The occurrence of vascular plants was quantified using the nine-degree Braun-Blanquet abundance and dominance scale (Westhoff, van der Maarel, 1978). In total, 89 species of vascular plants were recorded on 21 patches, and were divided into groups by hemeroby, life form, and origin; these groups were analysed separately.

In terms of hemeroby, the species groups were defined by means of the Biolflor database (Klotz et al., 2003). The selection was simplified to three groups

1. oligohemerobic plant species, which also covered some ahemerobic plant species,
2. mesohemerobic plant species, and
3. b-euhemerobic plant species, also covering some c-euhemerobic and polyhemerobic plant species.

Oligohemerobic plant species occur in habitats that are less influenced by human activity, e.g. in occasionally used woodlands, semi-natural moorlands and dry grasslands; examples of oligohemerobic plant species in the acidophilous grasslands studied are *Calluna vulgaris*, *Festuca filiformis*, *Jasione montana* or *Scleranthus perennis*. Mesohemerobic plant species occur in woodlands with native species composition and on more species-diverse meadows with more intensive use; examples of mesohemerobic plant species on the patches studied include the previous oligohemerobic plant species accompanied by a number of species that can withstand higher anthropogenic pressure, e.g. *Ranunculus acris*, *Rumex acetosa* or T*rifolium aureum*. The b-euhemerobic plant species group, which also included the c-euhemerobic and polyhemerobic species, consists of those species that occur in habitats substantially altered by humans, such as ruderal habitats or forest monocultures (Klotz et al., 2003). Species of the most impacted habitats include e.g. *Arrhenatherum elatius*, *Holcus mollis*, *Galeopsis pubescen*. All the recorded species, including hemeroby and life form categories, are listed in Supplement 1.

In terms of life forms, only oligohemerobic chamaephytes and nanophanerophytes were recognised in accordance with Kubát et al. (2002). The number of species in the relevant categories was understood as the proportion of their classification in the given category, i.e. a species belonging in two categories (e.g. ahemerobic and oligohemerobic at the same time) was rated as 0.5.

2.3 Patch and land cover characteristics

All acidophilous grassland patches were vectorized, including 600 m of their surroundings, using ArcGIS8.3 (www.esri.com). Seven types of land cover were differentiated: acidophilous grassland, broadleaved woods, coniferous woods, wetlands, fields and ruderal vegetation, meadows and settlements. Land area was defined for all segments, followed by the calculation of their shares, lengths of boundary, number of segments, numbers of land cover type in the buffer zones surrounding each of the patches at a distance of 25 m, 50 m, 75 m, 100 m, 200 m, 300 m, and 600 m. One of the methods used for expressing landscape heterogeneity was the Shannon-Wiewer index (Pielou, 1966) calculated from the land cover quotient in the buffer zones:

$$H' = -\sum [(n_i/n)\ ln(n_i/n)]$$

where "n_i" is the share of land cover types, "n" is the number of land cover types.

The shape of the patch was defined using the *P*/*A* ratio (where *P* is circumference, *A* total area) and two indexes:

$$S = P\ /\ (2\sqrt{A\ \pi}),$$ (Faeth, Kane, 1978)

where *P* is the circumference and *A* the total area, the index reaches higher values with the increasing divergence of the woodland patch from the circular shape;

$$Frac = 2 \times lnP\ /\ lnA,$$ (De Sanctis et al., 2010)

where *P* is the circumference and *A* the total area, the index value oscillates between 1 (regular shape) and 2 (irregular shape).

The ratios of land cover units at selected distances were weighted by three coefficient alternatives (Tab. 1) and added up to produce a variable expression of the meaning of differently distant land cover categories. The size of acidophilous patches ranged between 41 m^2 and 503 m^2 (mean 225 m^2). The irregularity of patches represented by indexes *P*/*A*, *S* and *Frac* ranged between 0.18 and 0.58 (P/A, mean 0.33), betwen 0.12 and 0.21 (S, mean 0.16) and between 1.31 and 1.45 (Frac, mean 1.38).

In addition to the variables produced by ArcGIS – area, circumference, *S*, *Frac*, and *P*/*A* – active soil pH, rock cover, inclination, index radiation and head (McCune, Keon, 2002), elevation above the surrounding terrain, and position of the phytosociological relevé within the patch were incorporated for the analysis.

2.4 Data analysis

Normality of the data was examined by means of STATISTICA 8.0 software (Statsoft Inc., 2000) and the Shapiro-Wilk W test. The abnormal

Distances (m)	0–25	26–50	51–75	76–100	101–200	201–300	301–600
w1	1.07	1.03	1.00	0.90	0.80	0.70	0.60
w2	1.14	1.07	1.00	0.80	0.60	0.40	0.20
w3	1.20	1.10	1.00	0.70	0.40	0.10	0.00

Tab. 1: Coefficients for weighting the ratio of land cover units at various distances

distribution of most data dictated the use of non-parametric methods. The species composition for multi-component analyses were logarithmically transformed using Hill scaling and considering the long gradient (over 3.0 SDU). In most of the species groups, the canonical correspondence analysis (CCA) was used in line with the recommendations of ter Braak and Šmilauer, 2005. Statistical significance was determined by the Monte Carlo permutation test (999 permutations).

To investigate the relation between the ratio of selected species groups in the phytosociological relevés and all recorded variables including landscape characteristics, we used the method of creating regression trees (Breiman et al., 1984; De'ath, Fabricius, 2000) in Statistica 8.0 software (Statsoft Inc., 2000).

In the graphic representation of the trees, each node is characterised by a value explaining the variables used for the relevant division, average share of species in the node with a standard deviation and the number of relevés falling into that node. The optimal tree was selected using 10-fold cross-validation, with the analysis being repeated on 10 randomly selected sub-files, and one tree with a minimum value of explained variability of the validation data was selected from the resulting trees with the adjustment of Standard Error rule = 0. Four surrogates were calculated for each of the trees, which provide divisions as close as possible to the primarily selected factor. In the results, they are shown under the values of the explanatory variable and only if their associative value was > 0.50. The shares of species processed in regression trees were derived only from the numbers of herbaceous plants.

3. Results

3.1 Multivariate analyses

The analysis of phytosociological relevés taken within the fragment of a biotope of the known size may be used to determine whether the influence of the size and shape of that fragment reflects in the species composition even over the area of a constant size.

The variable that proved most important for the diversity of the species composition of phytosociological relevés was soil pH the significance of which is the highest in the species bound to acidophilous grasslands and lower in the groups of species bound to other biotopes (Tab. 2). Size and circumference did not play a significant role in any of the defined groups, while the shape characteristics of the patch significantly showed in all groups of the species at a level of the phytosociological relevés. In the oligohemerobic group, the variability of the species composition was affected also by the position of the phytosociological relevé within the patch.

	Oligohemerobic			**Mesohemerobic**			**B-euhemerobic**			**Oligohemerobic chamaephytes and nanophanerophytes**		
	var. (%)	F	P	var. (%)	F	P	var. (%)	F	P	var. (%)	F	P
Soil pH	8,6	4,772	≤0.001	7,1	3,982	≤0.001	4,2	2,282	≤0.001	14,7	8,109	≤0.001
Slope	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
Radiation	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
Heat	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
Shell	2,8	1,645	0,042	-	-	n.s.	-	-	n.s.	5,6	3,627	0,006
Area	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
Circumference	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
P/A	4,0	2,320	0,003	3,7	2,109	0,004	2,9	1,605	0,038	3,8	2,502	0,034
S	-	-	n.s.	-	-	n.s.	-	-	n.s.	6,3	3,621	0,008
Frac	-	-	n.s.	2,7	1,537	0,046	-	-	n.s.	4,6	2,840	0,014
South	3,1	1,812	0,022	-	-	n.s.	-	-	n.s.	5,4	3,082	0,020
Middle	1,6	-	-	-	-	n.s.	-	-	n.s.	1,6	-	-
North	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
Elevation	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
Σ	**20,1**	**-**	**-**	**13,5**	**-**	**-**	**7,1**	**-**	**-**	**42,0**	**-**	**-**

Tab. 2: Results of canonical correspondence analysis. Selected species groups were analysed using the forward selection method; Var. (%) – explained variability, F – value of test, P – statistical significance level, n.s. – not significant

The number of b-euhemerobic species and non-indigenous species positively correlates with soil pH values while the number of chamaephytes and nanophanerophytes negatively correlates with the soil pH (Tab. 3). The higher pH also eliminates the share of species characteristic of acidophilous grasslands – oligohemerobic, chamaephytes, and nanophanerophytes (Tab. 4).

The share of skeleton on the phytosociological relevé area reduces the diversity of oligohemerobic and mesohemerobic species and in contrast increases the proportion of non-indigenous species (Tabs. 3, 4). Patch area was the most important factor for the number of mesohemerobic and oligohemerobic species and on the other hand, it had no significant influence on the number of b-euhemerobic and non-indigenous species (Tab. 3, Figs. 2, 3). Patch shape significantly influenced the groups of species typical for acidophilous grasslands and was positively correlated with the number of oligohemerobic and mesohemerobic species, chamaephytes, and nanophanerophytes, i.e. the more irregular and elongated the patch, the lower the diversity of these species (Tab. 3, Figs. 4, 5, 6). A similar situation was also seen in the proportions of these species where the irregular shape correlated positively with the share of the b-euhemerobic species (Tab. 4).

The position of the phytosociological relevé significantly influenced only chamaephytes and nanophanerophytes, with their numbers and shares correlating positively with the position in the patch centre (Tabs. 3, 4).

Difference in elevation positively correlated with the numbers and shares of oligohemerobic and mesohemerobic species, as well as chamaephytes and nanophanerophytes (Tab. 4). The numbers and share of b-euhemerobic species decreased significantly with the increasing difference in elevation (Tabs. 3, 4).

3.2 Regression trees

The regression tree demonstrating the share of oligohemerobic species formed six end nodes and explained 26.4% of data variability (Fig. 7). The first

	Oligohemerobic	Mesohemerobic	B-euhemerobic	Oligohemerobic and chamaephytes and nanophanerophytes
Soil pH	n.s.	n.s.	0.54***	–0.29*
Slope	n.s.	n.s.	n.s.	n.s.
Radiation	n.s.	n.s.	n.s.	n.s.
Heat	n.s.	n.s.	n.s.	n.s.
Shell	n.s.	n.s.	n.s.	n.s.
Area	0.32*	0.45***	n.s.	n.s.
Circumference	n.s.	0.36**	n.s.	n.s.
P/A	–0.32*	–0.43**	n.s.	n.s.
S	–0.32*	–0.43**	n.s.	n.s.
Frac	n.s.	n.s.	n.s.	–0.27*
South	n.s.	n.s.	n.s.	n.s.
Middle	n.s.	n.s.	n.s.	n.s.
North	n.s.	n.s.	n.s.	–0.29*
Elevation	0.35**	n.s.	–0.51***	n.s.

*Tab. 3: Spearman's correlation of environmental variables with the numbers of species of the defined groups Significance levels: *P < 0.05, **P < 0.01, ***P < 0.001; n.s. not significant*

	Oligohemerobic	Mesohemerobic	B-euhemerobic	Oligohemerobic and chamaephytes and nanophanerophytes
Soil pH	–0.48***	–0.35	0.45***	–0.48***
Slope	n.s.	n.s.	n.s.	n.s.
Radiation	n.s.	n.s.	n.s.	n.s.
Heat	n.s.	n.s.	n.s.	n.s.
Shell	n.s.	-0.30*	n.s.	n.s.
Area	n.s.	0.29*	n.s.	n.s.
Circumference	n.s.	n.s.	n.s.	n.s.
P/A	n.s.	–0.30*	0.28*	n.s.
S	n.s.	–0.30*	0.28*	n.s.
Frac	–0.27*	n.s.	n.s.	–0.33*
South	n.s.	n.s.	n.s.	n.s.
Middle	n.s.	n.s.	n.s.	0.33*
North	n.s.	n.s.	n.s.	n.s.
Elevation	0.55***	0.41**	–0.54***	0.30*

*Tab. 4: Spearman's correlation of environmental variables with the share of species of the defined groups Significance levels: *P < 0.05, **P < 0.01, ***P < 0.001; n.s. not significant*

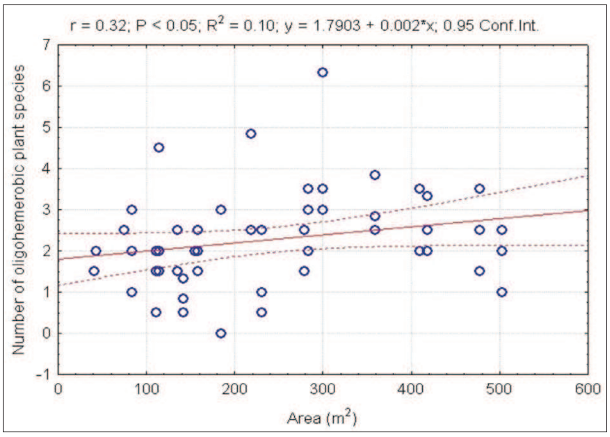

Fig. 2: Relation between the number of oligohemerobic plant species in the phytosociological relevé and the patch area

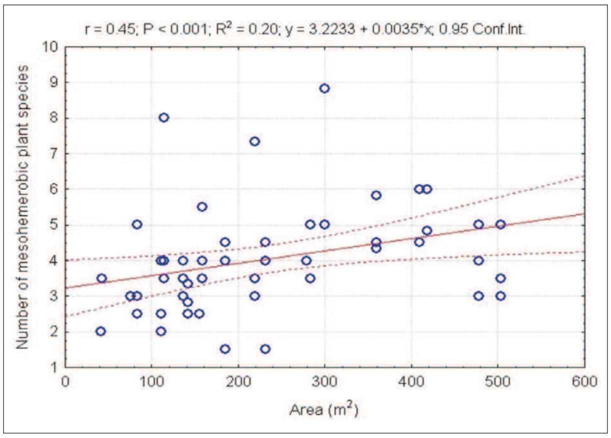

Fig. 3: Relation between the number of mesohemerobic plant species in the phytosociological relevé and the patch area

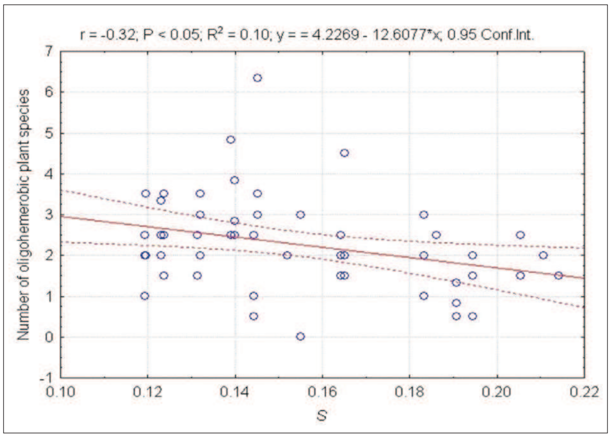

Fig. 4: Relation between the number of oligohemerobic plant species in the phytosociological relevé and the patch shape index

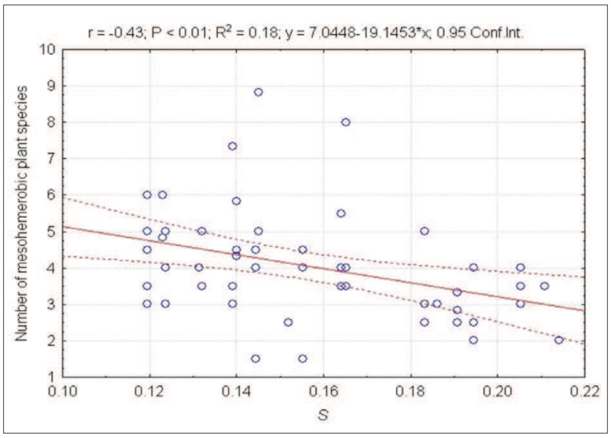

Fig. 5: Relation between the number of mesohemerobic plant species in the phytosociological relevé and the patch shape index

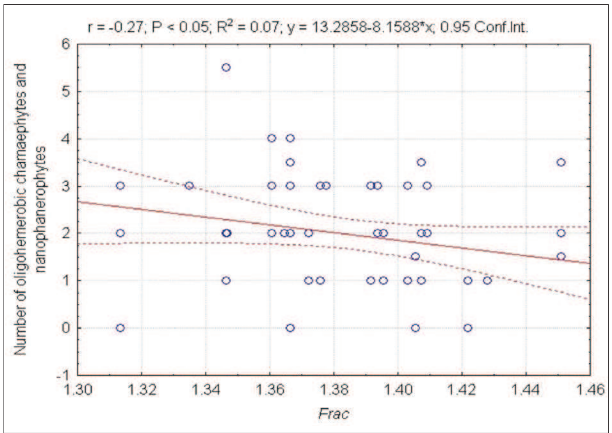

Fig. 6: Relation between the number of oligohemerobic chamaephytes and nanophanerophytes in the phytosociological relevé and the patch shape index

branching of the regression tree (1) is made according to the variable of phytosociological relevé elevation above the surrounding terrain; the higher share of oligohemerobic species is in the phytosociological relevés located higher above the surrounding terrain.

The group of phytosociological relevés with the lower ratio of oligohemerobic species was further divided into categories according to the extent of forest-free area boundaries (combined meadow and field segments) within a radius of 200 m where a higher ratio of oligohemerobic species was found in the group with higher heterogeneity of the forest-free area (5). The higher heterogeneity of the forest-free area also corresponded with generally higher heterogeneity given by the total length of all boundaries; moreover, the surroundings of these phytosociological relevés contained fewer forest-free areas (meadows, fields, acidophilous grasslands) than the other group (4). The group of phytosociological relevés with the higher ratio of oligohemerobic species (5) was further categorized by the proportion of meadows within a radius of 600 m. Higher shares of oligohemerobic species were found in the group (9) with more meadows in the surroundings and with higher heterogeneity of meadows and forest-free areas (meadows and fields) within a radius of 100 m and 200 m. The group of phytosociological relevés

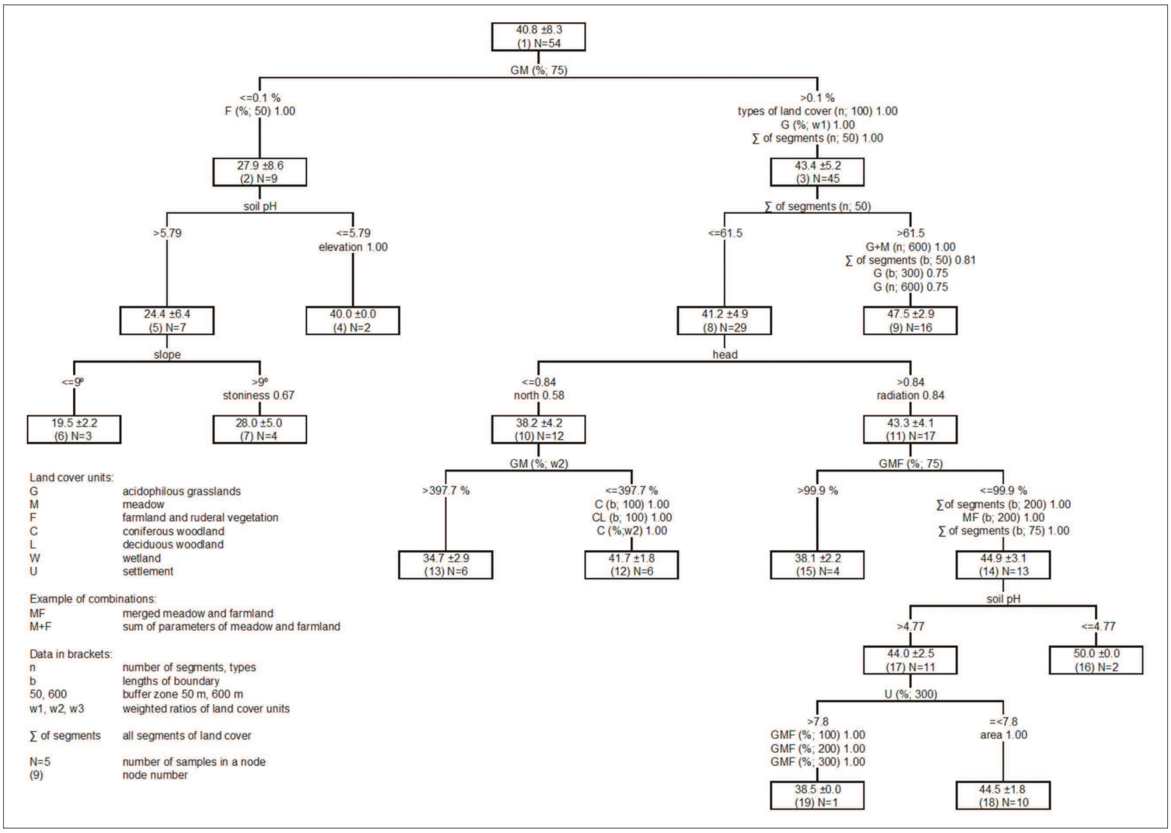

Fig. 7: Regression tree explaining the proportion of oligohemerobic plants in the phytosociological relevés. Each dichotomic division is characterised by a variable separating two homogeneous groups of phytosociological relevés, i.e. two nodes. Each node (its number stated in brackets) is accompanied by the value of the variable that has lead to its separation and is characterised by the average ± standard deviation of the share of oligohemerobic species therein and the number of phytosociological relevés belonging thereto. Under the variable values are marked the so-called surrogates providing the division of the most similar variable used in the particular branching. Surrogates are situated on that side of the dichotomic branching on which they gain higher values with their associative value being stated at the end.

(3) with the higher representation of oligohemerobic species in the relatively highest parts of the patches was further divided according to the share of acidophilous grasslands within a radius of 600m; higher proportions of oligohemerobic species were found in phytosociological relevés with a greater share of acidophilous grasslands within a radius of 600 m. The group of phytosociological relevés in the node (22) was further divided according to the radiation index; a higher proportion of oligohemerobic species was found in the relatively more irradiated relevés.

The regression tree demonstrating the representation of mesohemerobic species revealed 11 end nodes and explained 11.3% of data variability (Fig. 8). The first division was made according to the share of acidophilous grasslands and meadows within a boundary radius of 75 m. The proportion of mesohemerobic species was higher in phytosociological relevés that had a higher share of acidophilous grasslands and meadows in their surroundings; apparently, mere tenths of the per cent of these habitats make a difference. At the same time, the surroundings of these relevés showed a higher heterogeneity within a boundary radius of 50 m, expressed by the number of land cover segments, and a more diverse land cover within a 100 m radius.

The group of relevés with a lower share of mesohemerobic species (2) was subsequently divided according to soil pH values; relevés with higher soil pH values had a smaller proportion of mesohemerobic species. This group was divided once more according to the slope gradient; the group of relevés with a greater slope gradient (> 9°) exhibited a greater share of mesohemerobic species. The group of relevés with a higher proportion of mesohemerobic species (3) generated during the first division was further split according to the number of land cover segments within a boundary radius of 50 m; phytosociological relevés (9) with the higher heterogeneity of surroundings expressed by a larger number of land cover segments had a greater share of mesohemerobic species. The group of relevés (8) with less heterogeneous surroundings was divided according to the head index. Less insolated relevés exhibited a lower share of the mesohemerobic

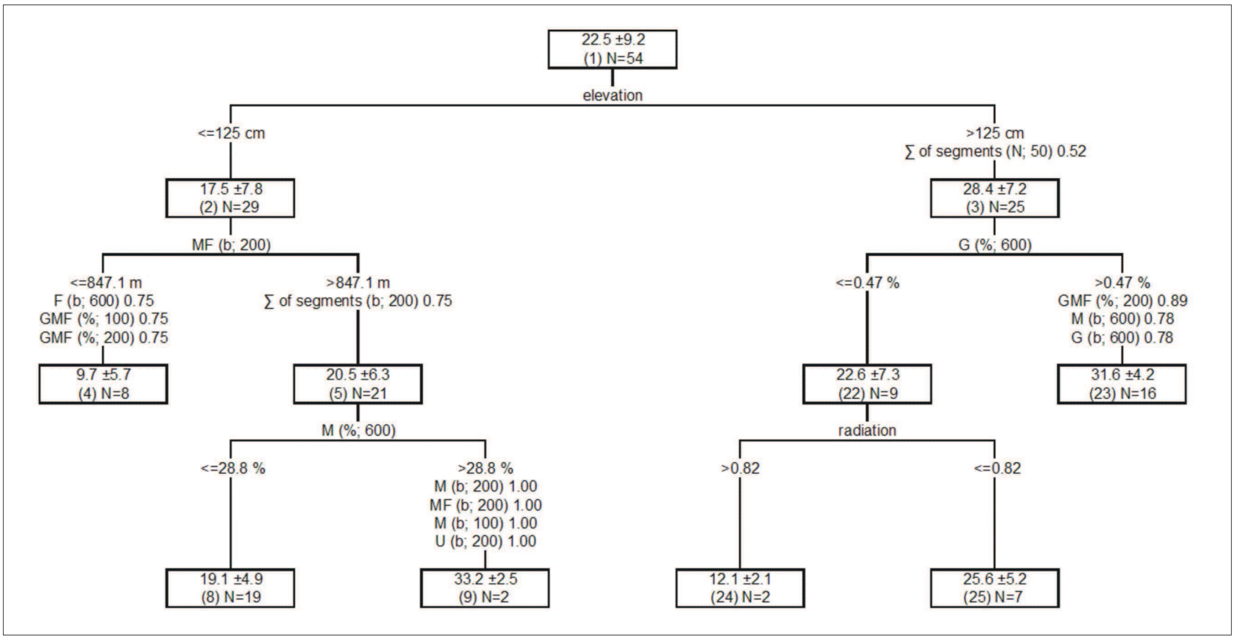

Fig. 8: Regression tree explaining the proportion of mesohemerobic plants in the phytosociological relevé. For explanatory description and legend see Fig. 7

species. The subsequent division split this group (10) according to the weighted values of forest-free areas (meadows and fields), i.e. the phytosociological relevés with closer and larger forest-free areas in their surroundings showed a lower share of mesohemerobic species. Relevés with higher head values (node 11) were divided according to the proportion of forest-free areas (acidophilous grasslands, meadows, fields) within a radius of 75 m. Patches entirely isolated within forest-free areas had a lower proportion of the mesohemerobic species. The group with more abundant mesohemerobic species (14) was further divided according to soil pH values; higher shares of mesohemerobic species were found in relevés with pH values > 4.76. The group of relevés (17) was further divided according to the area of settlements within a radius of 300 m; higher proportions of mesohemerobic species were detected in relevés with lower shares of settlements in their surroundings.

The regression tree demonstrating the ratio of b-euhemerobic species revealed three end nodes, explaining 43.8% of data variability (Fig. 9). In the first step, the regression tree was divided according to the proportion of fields within a radius of 50 m; phytosociological relevés almost entirely isolated in arable land had a higher share of b-euhemerobic species. The group of phytosociological relevés with

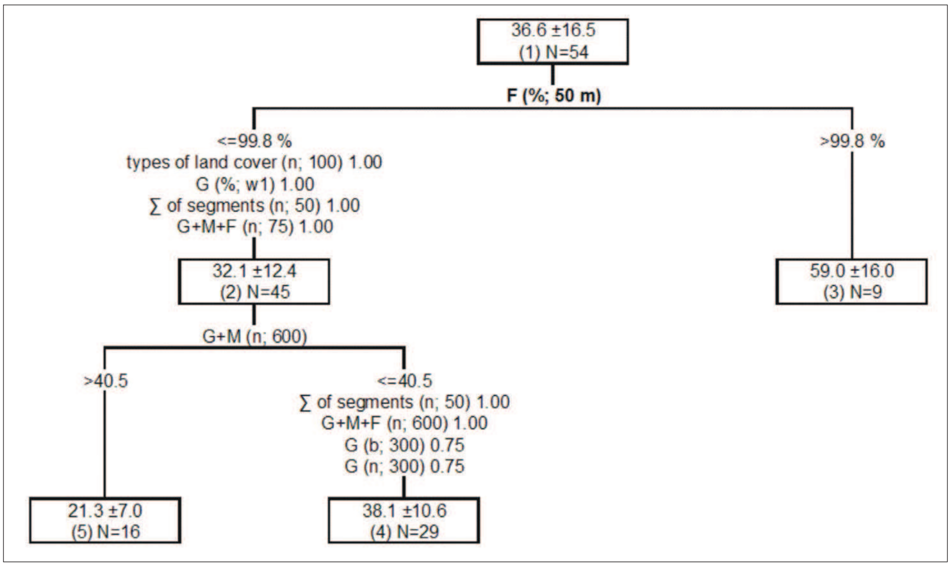

Fig. 9: Regression tree explaining the proportion of b-euhemerobic plants in the phytosociological relevé. For explanatory description and legend see Fig. 7

the lower share of b-euhemerobic species was divided once more, this time by the number of acidophilous grassland and meadow segments within a radius of 600 m. This group (5) showed a higher proportion of these permanent crops within a surrounding radius of 600 m and at the same time a substantially lower share of b-euhemerobic species.

4. Discussion

The size of the patch has a positive influence on the number of species within the patch; similar conclusions were also drawn by Kohn and Walsh (1994), who studied maritime islands in Great Britain, and Pärtel and Zobel (1999), Krauss et al. (2004), Öster et al. (2007), who worked on fragmented grasslands. In relation to the island biogeography theory (MacArthur and Wilson, 1967), this phenomenon may be explained by the higher number of habitats on larger islands. The significant relation between the number of species within one phytosociological relevé and the size of the island may have two causes that act simultaneously.

In the analysed species groups, there was a significant relation between the size of the patch and the number of species only in the oligohemerobic and mesohemerobic species groups, i.e. the groups that are most characteristic of acidophilous grasslands and heathlands. This could be explained by the saturation of the habitat as well as by the differences between generalist and specialist species. Foster et al. (2004) maintain that the species diversity of poor communities is limited by the number of available diasporas, whereas on more productive sites competition plays a much more important role. The stronger relation between the oligohemerobic and mesohemerobic species may also be explained by the characteristics of specialists, which are more limited by the size of the patch, while generalists also find their diaspora sources in the surrounding landscape (Krauss et al., 2004).

The division of species in the phytosociological relevés into three groups by hemeroby was important for distinguishing the species characteristic of acidophilous grasslands and heathlands (oligohemerobic), and less specialised (mesohemerobic) species from the species entirely allochthonous for these habitats (b-euhemerobic).

These three groups of species may also be used as indicator tools for investigating the relation of species composition with the character of the surrounding landscape. As the canonical correspondence analysis shows (Tab. 2), of all analyzed groups, the variability of oligohemerobic species composition is most influenced by the soil pH and by the patch shape, immediately after the specific group of oligohemerobic chamaephytes and nanophanerophytes, whereas in b-euhemerobic species this situation is reversed. We may assume that most of the recorded oligohemerobic species, oligohemerobic chamaephytes and nanophanerophytes within the studied area are currently bound to the remnants of the acidophilous grasslands and largely include specialized species with a competitive advantage on acidic and poor soils. B-euhemerobic species include a number of ruderal species that are quite common on arable land or on abandoned agricultural areas. Their occurrence in acidophilous grasslands may be limited by the low soil pH or by the low availability of nutrients while their broad distribution in the contemporary landscape clearly indicates that they are not limited by the patch size. Mesohemerobic species have a transient position according to the values of explained variability of species composition with the soil pH and patch shape. Differences between the above characterized species groups may therefore be explained by the "specialist and generalist concept" (Kraus et al., 2004).

The results of multivariate analysis are further complemented by correlations between the species number and abundance. The number of oligohemerobic and mesohemerobic species positively correlates with the area size of the patch, and for mesohemerobic species this relation is even more significant ($r = 0.45$; $p < 0.001$) compared to oligohemerobic species ($r = 0.32$; $p < 0.05$). Mesohemerobic species constitute the most abundant group of species present in all the patches studied while oligohemerobic species were not recorded in the phytosociological plots from some patches. Apart from the area size, there are other factors that significantly influence the occurrence of oligohemerobic species, e.g. the degree of influence expressed by a positive correlation of species numbers with the increasing elevation above the surrounding terrain. Both the numbers and the proportions of oligohemerobic chamaephytes, nanophanerophytes, as well as mesohemerobic species, correlate with the shape of the patch. With the increasing irregularity of the patch shape, the number and proportion of these species would decrease. B-euhemerobis species significantly positively correlate with the tortuousness of the patch shape. The patches of acidophilous grasslands are more influenced by the supply of b-euhemerobic species diasporas the greater is their contact area with their surroundings. B-euhemerobic species are thus more limited in patches of circular shape and with relatively high super-elevation; the opposite holds for oligohemerobic species.

The results of the regression trees demonstrate that the most important predictor for the diversity of oligohemerobic species in the set of the phytosociological relevés used is the elevation of the image area above the surrounding terrain. Higher situated parts of acidophilous grasslands are better protected from impacts threatening the oligohemerobic species. Other important predictors for a higher proportion of oligohemerobic species include the higher heterogeneity of the surrounding landscape and the higher share of meadows which, unlike other land cover types, may host more species common with the acidophilous grasslands. The most important predictor of the higher occurrence of mesohemerobic

Species	Life form	Hemeroby			Species	Life form	Hemeroby	
Quercus robur	MFf	o	m	-	*Cerastium arvense*	Chf	m	b
Holcus lanatus	Hkf	o	m	-	*Lathyrus pratensis*	Hkf	m	b
Prunus avium	MFf	o	m	-	*Rubus idaeus*	NFf	m	b
Fragaria vesca	Hkf	o	m	-	*Hieracium pilosella*	Hkf	m	b
Hieracium laevigatum	Hkf	o	m	-	*Stellaria graminea*	Hkf	m	b
Lychnis viscaria	Hkf	o	m	-	*Agrostis capillaris*	Hkf	m	b
Potentilla tabernaemontani	Hkf	o	m	-	*Holcus mollis*	Gf	m	b
Frangula alnus	NFf	o	m	-	*Arrhenatherum elatius*	Hkf	m	b
Dianthus deltoides	Tf	o	m	-	*Carex ovalis*	Hkf	m	
Scleranthus perennis	Hkf	o	m	-	*Apera spica-venti*	Tf	-	b
Carex caryophyllea	Hkf	o	m	-	*Cirsium vulgare*	Tf	-	b
Veronica officinalis	Chf	o	m	-	*Rubus caesius*	Chf	-	b
Pteridium aquilinum	Gf	o	m	-	*Scleranthus annuus*	Tf	-	b
Hieracium lachenalii	Hkf	o	m	-	*Taraxacum sect. Ruderalia*	Hkf	-	b
Solidago virgaurea	Hkf	o	m	-	*Epilobium angustifolium*	Hkf	-	b
Campanula rotundifolia	Hkf	o	m	-	*Galeopsis tetrahit agg.*	Tf	-	b
Festuca filiformis	Hkf	o	m	-	*Sonchus arvensis*	Hkf	-	b
Potentilla erecta	Hkf	o	m	-	*Vicia hirsuta*	Tf	-	b
Polygonatum odoratum	Gf	o	m	-	*Poa supina*	Hkf	-	b
Thymus pulegioides	Chf	o	m	-	*Senecio viscosus*	Tf	-	b
Galium pumilum	Hkf	o	m	-	*Arabidopsis thaliana*	Tf	-	b
Genista tinctoria	NFf	o	m	-	*Myosotis arvensis*	Tf	-	b
Calluna vulgaris	Chf	o	m	-	*Veronica arvensis*	Tf	-	b
Vaccinium myrtillus	Chf	o	m	-	*Vicia angustifolia*	Tf	-	b
Avenella flexuosa	Hkf	o	m	-	*Cirsium arvense*	Hkf	-	b
Sorbus aucuparia	MFf, NFf	o	m	b	*Acer pseudoplatanus*	MFf	-	b
Geranium pusillum	Tf	-	m	b	*Galium aparine*	Tf	-	b
Nardus stricta	Hkf	-	m	b	*Viola arvensis*	Tf	-	b
Ranunculus acris	Hkf	-	m	b	*Urtica dioica*	Hkf	-	b
Hieracium murorum	Hkf	-	m	b	*Linaria vulgaris*	Hkf	-	b
Vicia cracca	Hkf	-	m	b	*Galeopsis pubescens*	Tf	-	b
Rumex acetosa	Hkf	-	m	b	*Galium album*	Hkf	-	b
Lathyrus sylvestris	Hkf	-	m	b	*Hypericum perforatum*	Hkf	-	b
Hylotelephium maximum	Hkf	-	m	b	*Picea abies*	MFf	-	b
Phleum pratense	Hkf	-	m	b	*Brassica napus*	Tf	-	b
Trifolium aureum	Hkf	-	m	b	*Fallopia convolvulus*	Tf	-	b
Veronica chamaedrys	Hkf	-	m	b	*Anthemis cotula*	Tf	-	b

Supplement 1: The List of all recorded vascular plant species with categories of hemeroby and life form. Life forms: MFf – macrophanerophyte, NFf – nanophanerophyte, Hkf – hemicryptophyte, Tf – therophyte, Chf – chamaephyte, Gf – geophyte,; hemeroby: o – oligohemerobic, ahemerobic, m –mesohemerobic, b – b-euhemerobic, c-euhemerobic and polyhemerobic

species is a greater share of acidophilous grasslands and meadows. Similarly as in the oligohemerobic species, the occurrence of mesohemerobic species would increase with higher heterogeneity of the ambient environment but also with higher extremity of the habitat expressed for example by greater slope gradient or values of radiation and head index.

The most significant predictor of the occurrence of b-euhemerobic species is the share of arable land in the immediate surroundings. The results of the regression trees suggest how essentially important are characteristics of the surrounding landscape in addition to local variables. The results providing regression trees support a stronger relation of the species composition of narrower species groups to local conditions, illustrating also the key importance of the landscape context. Cousins et al. (2007) studied the effect of the landscape context on the species composition, too and found out that species diversity correlated with the percentage share of the same habitat within a radius of 1,000 m. Rogers et al. (2009) also came to similar conclusions when they studied the extinction of species in the undergrowth of fragmented woodlands, highlighting a greater importance for the landscape context compared to the conventionally-used local environment variables. In the regression analysis, characteristics from the 600-m surroundings were applied; we therefore assume that the influence on the species composition of the studied patches does not cease at this distance.

5. Conclusion

The results of this work show that the species composition of fragmented vegetation complies with the principles of the island biogeography theory (MacArthur and Wilson, 1967), and depends on the surrounding land cover in both local and greater landscape contexts. The context of the surrounding landscape on the species composition may have a greater influence for some groups of species than the variable environment that is conventionally used in vegetation studies. The size and shape of the patch is more important for the characteristic species of the acidophilous grasslands, while the number of species typical for habitats under strong anthropogenic influence depends more on the quality of the surrounding landscape. The protection of the acidophilous grassland patches studied should therefore include at least partial re-establishment of historic farming methods – grazing and cutting as well as a more considerate use of their close surroundings.

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