BIOGEOGRAPHICAL RELATIONSHIPS BETWEEN LANDSCAPE PATTERNS, SOME LOCAL ABIOTIC FACTORS AND VEGETATION OF FOREST EDGES (CZECH REPUBLIC)

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Abstract

Forest edges consist of specific ecotone plant associations. Their species composition reflects conditions within the local environment and the character of the surrounding landscape, as well as the history of the given area. This article aims to ascertain the importance of local conditions and the characteristics of the surrounding landscape on the species composition. The results show that the species composition of forest edges is adversely influenced by agricultural use of the surrounding landscape and differs according to the north-south gradient of aspect. In terms of their species composition, forest edges represent important refuges of certain plant species that have already disappeared from the surrounding landscape.

Shrnutí

Biogeografické vztahy mezi charakterem zemědělské krajiny, lokálními abiotickými podmínkami a vegetací lesních okrajů (Česká republika)

Lesní okraje představují specifická ekotonová společenstva rostlin. Jejich druhové složení odráží lokální podmínky prostředí, charakter okolní krajiny i historii daného území. V tomto příspěvku jsme se zabývali významem lokálních podmínek a charakteristik okolní krajiny na jejich druhové složení. Zjistili jsme, že druhové složení lesních okrajů je negativně ovlivňováno zemědělským využíváním okolí a liší se podle severojižního gradientu expozice. Lesní okraje svým druhovým složením představují významná refugia některých druhů rostlin, které z okolní krajiny již zmizely.

Keywords: *patch isolation, patch area, agricultural landscape, forest edges, plant diversity, land cover, Bohemian-Moravian Upland, Czech Republic*

1. Introduction

The species composition of isolated forest edge fragments is influenced by the size of the biotope, the degree of its isolation and the character of the surrounding environment, as well as by the characteristics of the species occurring in the given biotope. Fragmentation of natural biotopes due to human activity is considered the main cause of diminishing plant biodiversity worldwide (Eriksson, Ehrlén, 2001; Hobbs, Yates, 2003; Honnay et al., 2005; Cousins, 2009). The consequences of biotope fragmentation may severely affect ecosystems, populations, and individual species (Young et al,. 1996). Fragmentation involves interrelated processes of landscape change, such as shrinking biotopes leading to the physical reduction of population sizes (Endels et al., 2002a, 2002b; Leimu et al., 2006) and to the splitting-up of biotopes giving rise to size reduction

of populations and exacerbating isolation (Saunders et al., 1991; Wiens, 1997; Dupré, Ehrlén, 2002). The increasing fragmentation makes patches draw apart, with lower probability of their re-colonisation as a result (Opdam, 1988). Splitting-up of the populations due to fragmentation leads to the formation of mutually isolated species-specific populations in the landscape; these populations communicate through migration and are characterised by local population extinction and colonisation of available free spaces (Hanski, Gilpin, 1997).

With the growing biotope fragmentation, the influence of the edge effect increases, a process related to the greater inhospitality of the biotope area, and manifests itself through the reduced fitness (reproductive success) of the surviving species, resulting from the penetration of adverse impacts from the landscape

matrix (Jules, 1998; Endels et al., 2002a, 2002b; Lienert, Fischer, 2003; Brys et al., 2004). In small woodland patches, the impacts of the edge effect are more profound (Forman, Godron, 1986; Pauchard, Alaback, 2004). The structure of the landscape and the environmental demands of the individual species also significantly influence the mobility of organisms (Hanski, Ovasakinen, 2000). The research reported here investigates which groups of forest edge species are more prone to limitation by the increasing fragmentation and how they are influenced by the structure of the surrounding landscape. Six species groups were categorised according to their modes of dissemination and pollination. These were individually analysed by canonical correspondence analysis (CCA) with special attention to detecting the importance of relevant local landform variables, size of the biotope, and landscape characteristics. Concrete plant species were identified in terms of their preference for northern or southern edges and their relation to the heterogeneity of the closest (100 m) surroundings. A significant relationship between species composition and land use was established; it is modified by landform conditions, position of the phytocoenological area and the size of the biotope.

2. Materials and methods

2.1 Study area

The study areas are situated on the south-western and eastern edge of the Bohemian-Moravian Upland in the Czech Republic (Fig. 1). The landscape is mostly a mosaic of farmland and forests. Deciduous forests represent 1.6%–72.0% (average 18.2%) of land cover. Forest margins surround small woodland edges with near-natural species composition. The species composition of the woodland patches corresponds approximately to the potential natural vegetation of the *Luzulo albidae-Quercetum*, *Dentario enneaphylli-Fagetum* and M*elampyro nemorosi-Carpinetum* (Neuhäuslová et al., 1997) associations. The most common trees are *Fagus sylvatica*, *Carpinus betulus*, while admixed species include *Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *Fraxinus excelsior*, *Sorbus aucuparia*, *Tilia cordata*, and *Abies alba*. Herbaceous undergrowth is often enriched by the presence of mesophilous woodland species such as *Convallaria majalis*, *Hepatica nobilis*, *Lathyrus vernus*, *Melampyrum nemorosum*, *Mercurialis perennis*, *Polygonatum odoratum*, *P. multiflorum*, *Pulmonaria obscura* and *P. officinalis*. Evergreen forests, consisting of spruce monocultures, take up 0.0%–52.0% (average 20.0%). The key component of the landscape structure is arable land (average 30.8%) and meadows (average 27.7%). The bedrock is granitic

(south-western part) and metamorphic, such as gneiss and mica schist (eastern part). Elevations range from 470 to 658 m a.s.l. Average annual precipitation is 610.3 mm and average annual air temperature is 7.0 °C (Tolasz et al., 2007).

The total lengths of the forest edges studied ranged between 85.0 and 726.3 m (average 229.8 m).

2.2 Species data

The total number of woodland edges studied was 38. Two 2 m × 2 m phytosociological quadrats was laid in each forest edge, always on the southern and northern borders. The size of phytosociological quadrats based on the minimum width of forest edges. All species of higher vascular plants within them were recorded. The occurrence of vascular plant species was quantified by means of the nine-degree Braun-Blanquet abundance and dominance scale (Westhoff, van der Maarel, 1978). A total of 157 species were recorded in the quadrats, then categorised into groups by their mode of dissemination and pollination for separate analysis.

According to the Biolflor database (Klotz et al., 2003), the following categories of species were defined: endozoochoric species (e.g. *Actaea spicata*, *Convallaria majalis*, *Polygonatum multiflorum*, *Vaccinium myrtillus*), ectozoochoric species (e.g. *Ballota nigra*, *Galeopsis pubescens*, *Hieracium pillosela*, *Medicago falcata*), myrmecochoric + autochoric species (e.g. *Convallaria majalis*, *Corydalis intermedia*, *Genista tinctoria*, *Maianthemum bifolium*), anemochoric species (e.g. *Betula pendula*, *Hieracium murorum*, *Poa nemoralis*, *Silene nutans*), entomogamic species (e.g. *Securigera varia*, *Campanula persicifolia*, *C. rotundifolia*, *Thymus pulegioides*), and anemogamic species (e.g. *Betula pendula*, *Poa nemoralis*, *P. pratensis agg.*, *Rumex acetosa*). Nomenclature and taxonomic approaches are after Kubát et al. (2002). The number of species in each category was understood as a proportion
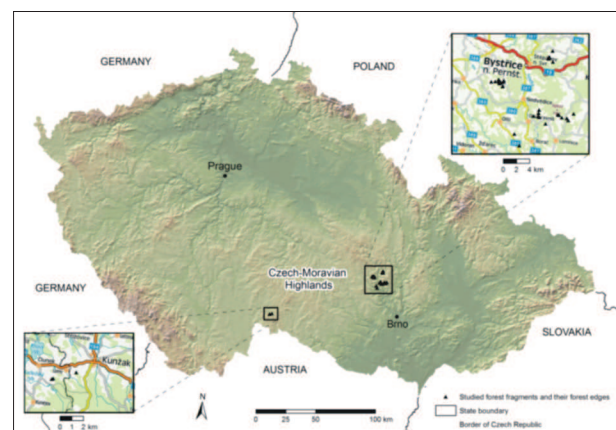

Fig. 1: Location of study areas within the Czech Republic

of their classification in the given category, i.e. a species belonging to two categories (e.g. anemochoric and ectozoochoric at the same time) was rated at 0.5.

2.3 Patch and land cover characteristics

All the woodland edges were vectorized, including 700 m of their surroundings, using ArcGIS 9.1. Seven types of land cover were differentiated: acidophilous grassland, deciduous woodland, coniferous woodland, wetland, arable land and ruderal vegetation, meadow, and settlement. Calculations were performed for all segments in terms of their share and length of boundaries in the buffer zones surrounding each of the forest edges at distances of 50 m, 100 m, 400 m, and 700 m.

2.4 Data analysis

Species data for multivariate analyses were adjusted by merging all the plants into a single vertical layer (merging of trees covering more than one vegetation layer) and the surface-cover ratio of the species was logarithmically transformed using Hill's scaling and underweighting of rare species significance. Due to the long gradient (over 3.0 SDU) detected upon detrended correspondence analysis (DCA) in most of the species groups, unimodal techniques (CCA canonical correspondence analyses) were used in accordance with the recommendations of ter Braak, Šmilauer (2005). Statistical significance was determined by means of the Monte Carlo permutation test (999 permutations). In several cases of the defined groups, species were missing in some quadrats; they were excluded from the analysis of the forest-edge quadrat pairs. The number of the quadrat pairs analysed is listed in Tab. 1.

Variables entered into gradient analyses included geographical (elevation, average annual precipitation, average annual air temperature), exchangeable soil pH, length of the forest edge, position of the quadrat (north/south) and selected landscape characteristics – shares and relative lengths of forest-free area boundaries (fields + meadows) within 50 m, 100 m, 400 m, and 700 m of the perimeter. The lengths of the boundaries were expressed as length per unit area (m^2/ ha). An explanation of some of the abbreviated variable terms and symbols used in the charts is presented in Tab. 2.

The shares and lengths of forest-free area boundaries within 100 m and 700 m of the perimeters were then selected along with the length of the forest edge and the position of the quadrat, which were analysed using partial canonical correspondence analysis (pCCA). Selected variables were analysed independently with the key variables (geographical, length of the forest edge and quadrat position) included as covariates.

Species group	Number of analysed relevé pairs
All species	38
Anemochores	38
Anemogam	38
Ectozoochores	38
Endozoochores	37
Entomogam	38
Autochores and Myrmecochores	35

Tab. 1: The number of quadrat pairs in the defined species groups processed by multivariate analyses

Temperature	average annual air temperature
Precipitation	average annual precipitation
Soil pH	exchangeable soil pH
MF (%) 50 m	shares of forest free areas within 50 m buffer zone
aMF (b) 50 m	absolute length of forest-free area boundaries within 50 m buffer zone
rMF (b) 50 m	relative length of forest-free area boundaries within 50 m buffer zone (m^3/ha)

Tab. 2: Expansion of abbreviated terms and symbols used for the variables

The relation of the actual plant species to selected environment variables (position of the quadrat and length of the forest-free boundaries within 100 m) was expressed through ranking the species by their score on the first canonical axis of the pCCA after selection of 20 species with the highest fit values. Only species with a frequency of at least six occurrences were shown. The presence-absence species data were used to express the relation of the actual species to the selected variable. Ellenberg´s indicator values (Ellenberg et al., 1992) calculated for each phytosociological quadrat in JUICE (Tichý, 2002) was also used to compare environmental factors on the northern and southern forest edges.

The normality of the data was analysed by STATISTICA 8.0 (Statsoft Inc., 2000), using the Shapiro-Wilks W test. In view of the abnormal distribution of some of the data, non-parametric methods were used. Numbers/shares of species in all of the relevés were used in correlation analyses.

3. Results

3.1 Influence of variables on species composition

The most important of the analysed variables are the geographical variables, especially elevation, some of the applied landscape characteristics, especially the share of forest-free areas within 700 m, the length of forest edge, and the position of the quadrat (Tab. 3).

	All species			Endozoochores			Ectozoochores			Autochores and Myrmecochores		
	var. (%)	F	P	var. (%)	F	P	var. (%)	F	P	var. (%)	F	P
All variables	26.6	1.581	≤ 0.001	26.9	1.495	≤ 0.001	24.8	1.350	≤ 0.001	27.0	1.450	≤ 0.001
Altitude	3.1	2.400	≤ 0.001	2.9	2.168	≤ 0.001	2.3	1.833	0.004	3.1	2.201	≤ 0.001
Temperature	1.8	1.476	0.012	-	-	n.s.	-	-	n.s.	2.2	1.651	0.007
Precipitation	2.3	1.857	0.002	-	-	n.s.	-	-	n.s.	-	-	n.s.
Soil pH	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
MF (%) 50 m	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
MF (%) 100 m	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
MF (%) 400 m	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
MF (%) 700 m	2.9	2.280	≤ 0.001	3.6	2.672	≤ 0.001	3.3	2.505	≤ 0.001	3.0	2.122	≤ 0.001
rMF (b) 50 m	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
rMF (b) 100 m	-	-	n.s.	2.4	1.807	0.008	-	-	n.s.	1.9	1.418	0.040
rMF (b) 400 m	1.9	1.545	0.006	-	-	n.s.	-	-	n.s.	2.4	1.780	≤ 0.001
rMF (b) 700 m	-	-	n.s.	-	-	n.s.	-	-	n.s.	-	-	n.s.
Length of forest edge	2.0	1.603	0.003	-	-	n.s.	2.8	2.163	0.005	-	-	n.s.
Phytosociological qadrat position	2.6	2.055	≤ 0.001	2.4	1.857	0.002	1.8	1.444	0.043	2.5	1.778	0.002
Sum of var. (%)	16.7	-	-	11.2	-	-	10.2	-	-	15.2	-	-

Tab. 3: Results of canonical correspondence analysis. Selected species groups as analysed by forward selection method Var. (%) – explained variability, F – test strength, p – statistical significance, n.s. – not significant

	Anemochores			Anemogames			Entomogames		
	var. (%)	F	P	var. (%)	F	P	var. (%)	F	P
All variables	36.9	1.656	≤ 0.001	29.8	1.851	≤ 0.001	23.7	1.350	≤ 0.001
Altitude	4.1	2.359	≤ 0.001	5.1	3.971	≤ 0.001	2.3	1.748	0.002
Temperature	-	-	n.s.	-	-	n.s.	-	-	n.s.
Precipitation	4.6	2.627	≤ 0.001	3.3	2.678	≤ 0.001	-	-	n.s.
Soil pH	-	-	n.s.	-	-	n.s.	-	-	n.s.
MF (%) 50 m	2.9	1.758	0.006	2.2	1.828	0.015	-	-	n.s.
MF (%) 100 m	4.0	2.389	≤ 0.001	2.0	1.727	0.024	-	-	n.s.
MF (%) 400 m	-	-	n.s.	-	-	n.s.	-	-	n.s.
MF (%) 700 m	-	-	n.s.	3.7	2.967	≤ 0.001	2.2	1.668	≤ 0.001
rMF (b) 50 m	-	-	n.s.	-	-	n.s.	-	-	n.s.
rMF (b) 100 m	-	-	n.s.	-	-	n.s.	2.0	1.569	0.003
rMF (b) 400 m	-	-	n.s.	-	-	n.s.	-	-	n.s.
rMF (b) 700 m	-	-	n.s.	-	-	n.s.	-	-	n.s.
Length of forest edge	2.6	1.579	0.029	2.1	1.742	0.029	1.9	1.450	0.037
Phytosociological qadrat position	3.4	2.056	≤ 0.001	2.3	1.933	0.010	2.4	1.802	≤ 0.001
Sum of var. (%)	21.5	-	-	20.6	-	-	10.7	-	-

Tab. 3 – Continuation

Partial canonical analyses also demonstrated a high significance for landscape variables in the variability of species composition (Tab. 4). In terms of landscape characteristics, the greatest part of species data variability was explained by the shares of forest-free areas within 700 m for most of the species groups defined. Heterogeneity of the forest edge surroundings expressed by the relative length of forest-free area boundaries had a significant and more prominent influence on the quadrat species composition within the nearer 100 m surroundings than within 700 m. The length of the forest edge significantly influenced the species variability in most of the species groups analysed, largely the anemochoric (2.8% F = 1.655, p = 0.012) and ectozoochoric species (2.7% F = 2.147, p = 0.003). The position of the quadrat explained most of the species data variability in the anemochoric species (3.3% F = 1.992, p ≤ 0.001); on the other hand, it had no significant influence on the variability of ectozoochoric species.

3.2 Isolation and fragmentation

The results of the partial canonical analyses of the individual species groups (Tab. 4) show that the share of forest-free areas within 100 m or 700 m was among the most important of the environmental variables analysed in all the groups. Forest-free area shares explained the greatest part of the species data variability in those species groups with diasporas that disperse easily in open landscapes, i.e. the anemochoric and anemogamic species (Tab. 4).

Heterogeneity of the forest edge surroundings expressed by relative lengths of borders influenced the species composition of all species groups only within 100 m of perimeters. Further, the position of the quadrat (north/south) and the length of forest edge were important variables for the species composition variability in all the species groups (Tab. 4).

Tables 5–8 clearly show a marked difference between the correlations of numbers and shares of species with the length of the forest edge and lengths of forest-free borders within 100 m and 700 m, while the species diversity and species composition of the southern borders better reflect the use of the surrounding landscape and the size of the biotope than the northern quadrats.

	All species			Endozoochores			Ectozoochores			Autochores and Myrmecochores		
	var. (%)	F	P	var. (%)	F	P	var. (%)	F	P	var. (%)	F	P
MF (%) 100 m	2.6	2.133	≤ 0.001	2.7	2.111	≤ 0.001	3.1	2.476	≤ 0.001	2.3	1.656	0.008
MF (%) 700 m	2.8	2.229	≤ 0.001	3.1	2.383	≤ 0.001	2.6	2.090	0.003	2.7	1.984	≤ 0.001
rMF (b) 100 m	2.6	2.052	≤ 0.001	3.0	2.331	≤ 0.001	2.9	2.325	0.002	2.6	1.899	≤ 0.001
rMF (b) 700 m	1.7	1.350	0.040	-	-	n.s.	-	-	n.s.	-	-	n.s.
Length of forest edge	1.9	1.541	0.007	-	-	n.s.	2.7	2.147	0.003	1.8	1.289	0.143
Phytosociological qadrat position	2.6	1.087	≤ 0.001	2.3	1.760	0.006	-	-	n.s.	2.4	1.753	≤ 0.001

Tab. 4: Results of partial canonical correspondence analysis
Selected species groups were analysed by forward selection with the inclusion of selected variables as covariate.
Var. (%) – explained variability, F – test strength, p – statistical significance, n.s. – not significant

	Anemochores			Anemogames			Entomogames		
	var. (%)	F	P	var. (%)	F	P	var. (%)	F	P
MF (%) 100 m	3.9	2.355	≤ 0.001	3.4	2.841	≤ 0.001	2.0	1.591	0.003
MF (%) 700 m	3.6	2.168	≤ 0.001	3.4	2.896	≤ 0.001	2.1	1.671	≤ 0.001
rMF (b) 100 m	3.3	1.985	0.003	3.0	2.548	0.002	2.2	1.711	≤ 0.001
rMF (b) 700 m	-	-	n.s.	-	-	n.s.	-	-	n.s.
Length of forest edge	2.8	1.655	0.012	2.0	1.623	0.037	1.8	1.413	0.041
Phytosociological qadrat position	3.3	1.992	≤ 0.001	2.3	1.921	0.009	2.4	1.841	≤ 0.001

Tab. 4 – Continuation

	Length of forest edge	MF (%) 100 m	MF (%) 700 m	aMF (b) 100 m	aMF (b) 700 m	rMF (b) 100 m	rMF (b) 700 m
All species	0.46**	−0.58***	−0.49**	0.47**	n.s.	n.s.	n.s.
Endozoochores	n.s.	−0.48**	−0.47**	n.s.	n.s.	n.s.	n.s.
Ectozoochores	0.72***	n.s.	−0.39*	0.46**	n.s.	n.s.	n.s.
Anemochores	0.52***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Myrmecochores + autochores	n.s.	−0.61***	−0.46**	0.50**	n.s.	0.32*	n.s.
Anemogames	0.50**	n.s.	n.s.	0.44**	n.s.	n.s.	n.s.
Entomogames	0.37*	−0.56***	−0.48**	0.42**	n.s.	n.s.	n.s.

Tab. 5: Spearman's correlation of environmental variables with the number of species within the defined groups in the quadrats from the **southern** parts of the forest edges
Significance levels: *p < 0.05, **p < 0.01, ***p < 0.001; n.s. – not significant

	Length of forest edge	MF (%) 100 m	MF (%) 700 m	aMF (b) 100 m	aMF (b) 700 m	rMF (b) 100 m	rMF (b) 700 m
All species	0.42**	n.s.	−0.56***	n.s.	n.s.	n.s.	n.s.
Endozoochores	n.s.	n.s.	−0.51**	n.s.	n.s.	n.s.	n.s.
Ectozoochores	n.s.	n.s.	−0.36*	n.s.	n.s.	n.s.	n.s.
Anemochores	0.42**	n.s.	−0.47**	n.s.	n.s.	n.s.	n.s.
Myrmecochores + autochores	0.36*	n.s.	−0.43**	n.s.	n.s.	n.s.	n.s.
Anemogames	0.33*	−0.33*	−0.39*	n.s.	n.s.	n.s.	n.s.
Entomogames	0.40*	n.s.	−0.59***	n.s.	n.s.	n.s.	n.s.

Tab. 6: Spearman's correlation of environmental variables with the number of species within the defined groups in the quadrats from the **northern** parts of the forest edges
Significance levels: *p < 0.05, **p < 0.01, ***p < 0.001; n.s. – not significant

	Length of forest edge	MF (%) 100 m	MF (%) 700 m	aMF (b) 100 m	aMF (b) 700 m	rMF (b) 100 m	rMF (b) 700 m
Endozoochores	−0.43**	n.s.	n.s.	n.s.	−0.33*	n.s.	n.s.
Ectozoochores	0.39*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Anemochores	n.s.	0.37*	0.33*	n.s.	n.s.	n.s.	n.s.
Myrmecochores + autochores	n.s.	−0.43**	n.s.	0.34*	n.s.	n.s.	n.s.
Anemogames	n.s.	0.33*	n.s.	n.s.	n.s.	n.s.	n.s.
Entomogames	n.s.	−0.33*	−0.37*	n.s.	n.s.	n.s.	n.s.

Tab. 7: Spearman's correlation of environmental variables with the share of species within the defined groups in the quadrats from the **southern** parts of the forest edges
Significance levels: *p < 0.05, **p < 0.01, ***p < 0.001; n.s. – not significant

	Length of forest edge	MF (%) 100 m	MF (%) 700 m	aMF (b) 100 m	aMF (b) 700 m	rMF (b) 100 m	rMF (b) 700 m
Endozoochores	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ectozoochores	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Anemochores	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Myrmecochores + autochores	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Anemogames	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Entomogames	n.s.	n.s.	−0.39*	n.s.	n.s.	n.s.	n.s.

Tab. 8: Spearman's correlation of environmental variables with the share of species within the defined groups in the quadrats from the **northern** parts of the forest edges
Significance levels: *p < 0.05, **p < 0.01, ***p < 0.001; n.s. – not significant

4. Discussion

The results obtained were considered in the light of the of partial canonical correspondence analysis (pCCA), which was also used to analyse the relationships of individual plant species to the boundary length (heterogeneity) of the forest-free areas within 100 m of the perimeter and the position of the quadrat at the forest edge. The position of the quadrat, together with the use of presence-absence data, explained 3.1% (F = 2.184, p ≤ 0.001) and length of boundaries within the 100 m surroundings explained 2.6% (F = 1.813, p ≤ 0.001) of species data variability. The 20 plant species selected by their fit values constitute a relatively heterogeneous collection (see Tab. 9). This includes the typical forest species such as *Viola reichenbachiana*, *Fagus sylvatica*, *Quercus petraea agg.* and *Acer campestre* as well as the species of forest-free areas: *Genista tinctoria*, *Hypericum perforatum*, *Securigera varia*, and *Veronica chamaedrys*. The species bound to forest edges within the higher heterogeneity of the 100 m surroundings, in particular, include several species that do not disseminate easily – their dispersion is facilitated by the higher connectivity of suitable biotopes. These include *Viola reichenbachiana*, which is relatively closely bound to the forest environment; its seeds are spread by ants carrying them only over short distances (Grime et al., 1988; Oberdorfer, 1994; Hermy et al., 1999; Honnay et al., 2005; Digiovinazzo et al., 2009). Similar difficulties in spreading are faced by species with large seeds and autochoric means of dissemination – *Genista tinctoria* and *Securigera varia*, growing mainly in various types of grassland (Chytrý et al., 2001). In contrast, species more closely associated with forest edges with less

heterogenic surroundings also included anemochoric plant species such as *Knautia arvensis agg.*, *Holcus mollis*, and *Elytrigia repens*.

The survival of various plant species in isolated forest edges is also influenced by the orientation of the edge in which they grow. Ellenberg's indicative values express significant differences in the species composition of northern and southern forest edges. Northern edges tend to be more humid (Fig. 2), thanks to which they offer better access to nutrients in comparable soil conditions (Fig. 3). Northern edges are favoured by ruderal species with high competition success rates, such as *Anthriscus sylvestris*, *Dactylis glomerata subsp. glomerata* and *Urtica dioica*, as well as some sciophilous forest species, e.g. *Asarum europaeum* or *Geranium robertianum* (Tab. 10).

Southern edges, in contrast, facilitate the survival of many types of grassland that are more light-demanding and less capable of competing with larger ruderal species. Grassland species growing in southern parts of the forest edges include e.g. *Achillea millefolium agg.*, *Genista tinctoria*, *Knautia arvensis agg.*, *Pimpinella saxifraga* and *Securigera varia* (Tab. 10).

Separately calculated correlations of the numbers and shares of species belonging to the defined groups from relevés laid in the northern and southern parts of the forest edges disclosed significantly different results. In most cases, the correlations with selected variables were more marked in the southern parts of the forest edges. The species composition in the southern quadrats thus better reflects the relation to the surrounding land cover and size of the biotope. The northern parts of the forest edges tend to be more
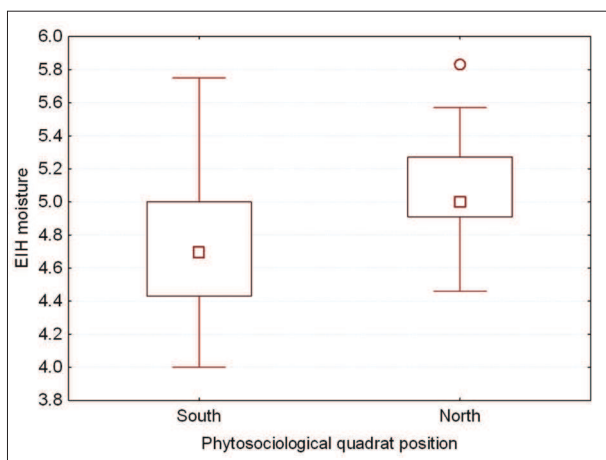
□ = *Median;* ▢ = *25–75% Inter-quartile Range;* ⊥ = *Whiskers;* ○ = *Outliers*

KW-H (1;76) = 15.28; P < 0.001
Fig. 2: Comparison of Ellenberg's indicative values for humidity between quadrats from southern and northern parts of forest edges
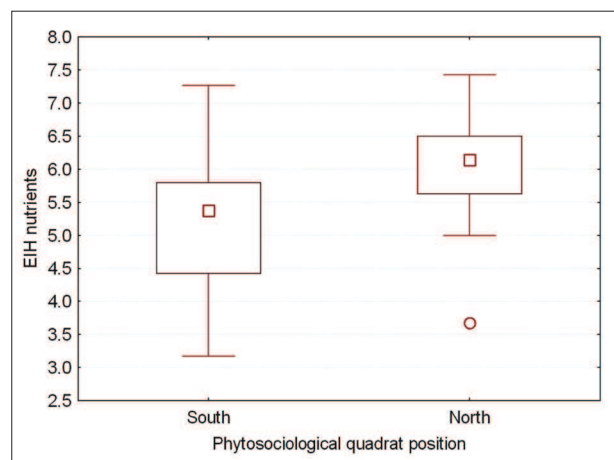
KW-H (1;76) = 14.43; P < 0.001
Fig. 3: Comparison of Ellenberg's indicative values for nutrients between quadrats from southern and northern parts of forest edges

Gradient	Plant species	Frequency	Score pCCA 1	Fit
↓	*Fagus sylvatica*	15	0.6218	0.0818
	Galium album	15	0.4517	0.0500
↓	*Knautia arvensis agg.*	6	0.4230	0.0178
	Galium aparine	23	0.4051	0.0565
	Prunus spinosa	9	0.3765	0.0195
	Holcus mollis	18	0.3708	0.0394
	Elytrigia repens	39	0.3599	0.0965
	Quercus petraea agg.	13	0.2981	0.0190
	Hypericum perforatum	20	0.2544	0.0247
Length of forest free area margins	*Fragaria vesca*	12	−0.2869	0.0221
	Veronica chamaedrys	14	−0.3113	0.0238
	Prunus avium	19	−0.3176	0.0322
	Geum urbanum	13	−0.3241	0.0249
	Taraxacum sect. Ruderalia	18	−0.3773	0.0528
	Acer campestre	12	−0.4222	0.0397
	Securigera varia	7	−0.4565	0.0259
	Dactylis glomerata subsp. glomerata	26	−0.4847	0.1385
↓	*Genista tinctoria*	9	−0.5413	0.0420
	Aegopodium podagraria	6	−0.6207	0.0426
↓	*Viola reichenbachiana*	6	−0.8722	0.0789

Tab. 9: Occurrence of species in forest edges on the gradient of relative forest-free area boundary length (heterogeneity of surroundings) up to a 100 m distance; the species are ranked according to their score on the 1st canonical axis of the pCCA; only the species occurring in more than six quadrats within the area are shown.

Phytosociological quadrat position	Plant species	Frequency	Score pCCA 1	Fit
	Asarum europaeum	8	0.9500	0.1196
	Urtica dioica	15	0.6996	0.1198
	Campanula rapunculoides	7	0.4041	0.0198
	Geum urbanum	13	0.3777	0.0339
North	*Fraxinus excelsior*	14	0.3642	0.0322
	Acer campestre	12	0.3580	0.0286
	Sorbus aucuparia subsp. aucuparia	10	0.3476	0.0180
	Geranium robertianum	29	0.3471	0.0673
	Dactylis glomerata subsp. glomerata	26	0.2829	0.0472
	Anthriscus sylvestris	28	0.1964	0.0290
	Prunus spinosa	9	−0.3488	0.0168
	Rubus fruticosus agg.	18	−0.4586	0.0628
	Achillea millefolium agg.	15	−0.5990	0.0974
	Hypericum perforatum	20	−0.7014	0.1878
South	*Securigera varia*	7	−0.7605	0.0720
	Genista tinctoria	9	−0.9909	0.1407
	Pimpinella saxifraga	6	−1.0084	0.1008
	Knautia arvensis agg.	6	−1.0212	0.1035
	Fallopia convolvulus	6	−1.0548	0.0698
	Corylus avellana	26	−1.1036	0.0228

Tab. 10: Occurrence of species in the forest edges according to their position within the forest edge; the species are ranked according to their score on the 1st canonical axis of the pCCA; only the species occurring in more than six quadrats within the area are shown

humid and nutritive. Such conditions attract highly competitive species such as eutrophic and ruderal species and the pCCA showed that this masks the significance of the variables analysed (Tab. 10). The key importance of competition in the more nutritive sites was confirmed also by the work of Foster et al. (2004). As the phytosociological data from the southern parts of the forest edges provide better evidence of species composition, only these results will be further commented upon here.

The species diversity of most of the defined species groups expanded with the increasing length of the forest edge, with the exception of endozoochoric and myrmecochoric + autochoric species (Tab. 5). The most marked relationship between the number of species and the size of the biotope (length of forest edge) was recorded for the ectozoochoric species. Forest edges (ecotones) are characterised by a relatively high ground cover factor of both herbaceous and shrub layers; in a fragmented landscape, they are important refuges and sources of food for wildlife (Fitzgibbon, 1997). That the most marked relationship between the species diversity and the length of the forest edge was recorded in the ectozoochoric species indirectly confirms the importance of the increasing length of the forest edge for the presence or frequency of wildlife occurrence. The attractiveness of the forest edge for wildlife lies mainly in its function as a refuge from predators and an environment containing sources of food (Fitzgibbon, 1997; Wolf, Batzli, 2002). The closest relationship between the species composition (Tab. 4) and diversity (Tab. 5) and the size of the biotope in ectozoochoric species may be explained by their relatively close relationship (in terms of available biotopes within farmland) with forest edges and similar habitats. Saunders et al. (1991) confirmed that diversity of specialist species tends to be most severely impacted by the reduction of biotope size. In farmland, forest edges represent space-restricted types of biotope in which both ectozoochoric and anemochoric species may thrive. For anemochoric species, forest edges may function as "nets" stretched across the landscape that capture their diasporas in numbers proportional to their extent. The greatest influence of forest edge length on the variability of species composition was recorded (again through pCCA) in ectozoochoric and anemochoric species.

On the other hand, endozoochoric species are limited by being spread by birds or mammals that have closer relationships to the particular biotopes, predominantly forests, in which they live, a situation similar to the myrmecochoric species disseminated by ants (van Dorp, 1987; van Dorp, Kalkhoven, 1998).

The myrmecochoric species (together with the autochoric) stood out because, of all the species groups, the increasing heterogeneity of the nearest surroundings (length of boundaries within 100 m) was of the highest importance for their higher abundance. However, an increasing isolation factor (share of forest-free areas within 100 m and 700 m) reduces the diversity of both myrmecochoric and anemochoric species (Tab. 5). Dzwonko and Loster (1992) and van Dorp (1987) also recorded higher sensitivity to isolation for myrmecochoric and autochoric species compared to the easily spreading anemochoric species. For example, Tremlová and Münzbergová (2007) categorise ectozoochoric and anemochoric species as space-dominating, with the highest dissemination capacity.

5. Conclusion

The share of forest-free areas had a significant influence on the diversity of some species groups in both the closer surroundings up to 100 m and over larger distances up to 700 m, but the closer surroundings had a more marked influence on the species diversity (Tab. 7). The structure of the surrounding landscape (absolute length of forest-free boundaries) influenced the species diversity only within the distance of up to 100 m, while relative boundary lengths were of practically no significance (Tab. 5). Diversity and species composition of forest edges are influenced by the parts of the landscape immediately surrounding the forest edges, but also by the relatively distant surroundings. Likewise, Rogers et al. (2002) demonstrated that the species composition of isolated forest fragments was most influenced by the impacts of landscape changes rather than by local variables.

The diversity and species composition of isolated forest edges are defined by the size of the biotope, by the degree of its isolation and by local environmental conditions, all of which substantially influence the competitive relations between plants. Land use in the proximity of forest edges significantly influences the degree of isolation that in turn affects the representation of various species types in terms of the dissemination of their diasporas. The results of this research report suggest the major importance of land-use approaches for the species composition and for the diversity of plant societies in small-scale, isolated fragments of vegetation.

Acknowledgments

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