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Changes in the vegetation of the Žofínský Prales nature reserve in the period 1975–2008

Pavel Unar

The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Department of Forest Ecology, Lidická 25/27, CZ-60200 Brno, Czech Republic
pavel.unar@vukoz.cz

Abstract
A primary research in the Žofínský Prales nature reserve was conducted by E. Průša and J. Vokoun in 1975. They established a network of 44 phytocoenological plots covering site diversity of the locality. In 1997 and 2008 a repeated sampling was carried out, resulting in a set of three phytocoenological observations depicting forest structure development and species composition changes over 30 years. Site conditions and time were detected as the two main factors explaining species variability. Ecologically similar relevé groups were found by TWINSPAN analysis. The development of a number of observed species, values of Shannon-Wiener diversity index and changes in Ellenberg indicator values (EIV) over time were assessed for these groups. A decreasing average EIV for soil reaction and nutrients were registered for the beech forests relevé group. The wet sites of spring areas and peat bogs were characterized by an increasing number of observed species, an increase in the Shannon-Wiener diversity index and a rise in EIV for light and temperature. Shifts in species composition in the herb layer over time and structural development of woody synusia were also analysed over the whole set of relevés. A statistically significant shift in these targets was shown.

Key words: old-growth forest, plant community, Ellenberg indicator values, woody synusia, herb layer

Introduction

Although the Žofínský Prales nature reserve (hereinafter Žofín) is a continuous complex of forest, several ecologically very different sites exist there (Průša & Vokoun 1984, Průša 1985, Lepší et al. 2007). Dissimilarity in these parts is conditioned especially by the water table. This factor determines not only the character of vegetation but also its developmental dynamics. The site diversity of the studied area is covered by a preferential network of permanent plots. This primarily reflects ecological conditions.

The development dynamic of forest communities is recorded by three repeated observations with an interval longer than 10 years. The frequency of observations is an important factor. The desired interval between measurements can be determined by comparing an estimate of the rarity of changes (Koop 1989). The applied interval corresponds with stems map updating. Whereas a long interval between observations seems to be appropriate for the woody synusia, the herb layer is much more sensitive to many factors that change annually. The herb layer reflects canopy species development naturally. On the other hand the climatic course of the vegetation season or the previous winter plays an important role too. From this point of view results of repeated observations from permanent research plots are very interesting. It makes possible to separate development trends or cyclic changes and deviations caused by accidental factors.

The objectives of this study were (1) a description of vegetation variability on observed plots, (2) to find out the development trends of the main vegetation types, and (3) to assess the shifts of forest communities composition registered by the whole set of relevés during the observed period.

Materials and methods

Study area

The Žofínský Prales nature reserve (primeval forest) is situated in the Žofínská Hornatina highlands in the Novohradské Hory Mts. territory (Demek 1987). It lies in South Bohemia near the border with Austria (Fig. 1). The forest reserve occupies north, north-west and north-east oriented hillsides in the range of altitudes from 740 to 820 m and covers 97.72 ha. The core area, since 1838 under strict protection, is 74.5 ha. From the aspect of phytocoenological zoning of the Czech Republic Žofín belongs to the Czech oreophytic district (Skalický in Hejný & Slavík 1997).

In terms of phytocoenological classification the plant communities mostly belong to the sub-alliance *Eu-Fagenion* Oberdofer 1957 em. Tüxen in Oberdofer et Tüxen 1958, the association *Dentario enneaphylli-Fagetum* Oberdofer ex W. et A. Matuszkiewicz 1960, sub-association *Dentario enneaphylli-Fagetum impatientetosum* (Hartmann et Jahn 1967) Moravec 1974 (Moravec et al. 2000). The differential species occurring are *Picea abies* (as a natural admixture), *Circaea alpina*, *Petasites albus*, *Phegopteris connectilis*, *Ranunculus lanuginosus*, and *Stellaria nemorum*. Mostly wet acidophilous spruce parts are qualified as the associations *Equiseto-Piceetum* Šmarda 1950, *Calamagrostio villosae-Piceetum* Hartmann in Hartmann at Jahn 1967 and *Sphagno-Piceetum* (Tüxen 1937) Hartmann 1953 of the alliance *Piceion excelsae* Pawłowski in Pawłowski, Sokołowski et Wallisch 1928 (Husová et al. 2002). From diagnostic species *Picea abies*, *Sorbus aucuparia*, *Calamagrostis villosa*,

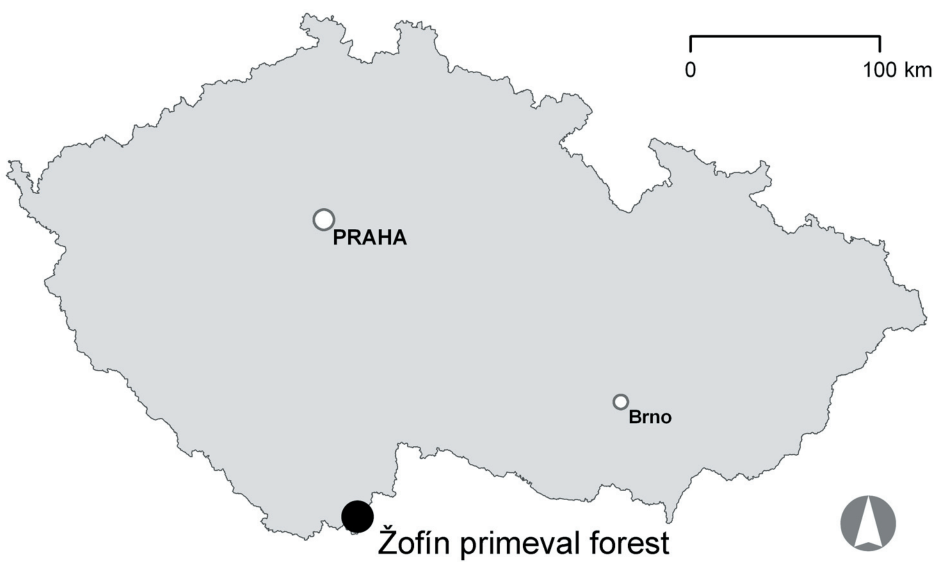


Fig. 1. Position of the Žofín primeval forest in the the Czech Republic.

Luzula sylvatica, *Lycopodium annotinum*, and *Soldanella montana* were observed. The association *Veronico montantanae-Caricetum remotae* Sýkora in Hadač 1983 of the alliance *Cardaminion amarae* Maas 1959 was found at open spring areas (Moravec 1983).
Altogether 136 species of vascular plants were recorded during repeated observations in 1975, 1997 and 2008. The floristic research carried out in 2004 and 2005 included 209 species (Lepší et al. 2007).

Data acquisition

During the primary research carried out by J. Vokoun and E. Průša in 1975, the positions of all live and dead stems with a diameter at breast height (DBH) ≥ 10 cm were registered on an area of 74.5 ha, recording species and DBH (Průša & Vokoun 1984; Průša 1985, 1990). The research included the basic pedological survey, forest types mapping and vegetative characteristics of typological units. The system of forest typology by the Forest management institute (Melichar & Maršík 2000) was used in this case. An overview and characterization of phytocoenological vegetation units are included in Lepší et al. (2007) and Albrecht et al. (2003).

Phytocoenological data were collected in a network of 44 permanent plots established with the aim of covering site diversity of the studied area. Distribution of permanent plots is in relation with Průša's and Vokoun's vegetation mapping. Midpoints of relevés have been fixed in the stem positions map (Průša 1985), which enable their repeated identification with approximately 2 m accuracy. The plots are circular with diameter of 25 m. Relevés were resampled in 1997 and 2008.

Vegetation records were made using the Braun-Blanquet 7-point combined scale (Braun--Blanquet 1964) of abundance and dominance adjusted by Zlatník to the gentler 11-point scale (Randuška et al. 1986). The vertical structure of phytocoenoses was classified as follows (Randuška et al. 1986, Hennekens & Schaminée 2001): 1 Tree layer – high (main- and overstorey); 2 Tree layer – middle (understorey, higher than a half-height of trees in the main level); 3 Tree layer – low (tree height ranging from 1.30 m to a half-height of co-dominant trees); 4 Shrub layer – high (woody species of the height ranging from 0.20–1.30 m); 5 Shrub layer – low (woody species up to a height of 0.20 m, individual conifers with at least one lateral shoot, individual broadleaves without cotyledons); 6 Herb layer; 8 Seedling layer. This numerical marking of vegetation layers is used further in the paper. Plant taxonomy is harmonised by Kubát (2002). Mosses and lichens were not included. The term 'woody synusia' (used further in the text) includes the layers 1–5 and 8.

Data analysis

Relevés from 42 permanent plots were used for analyses. First information about species and sample distribution in ordination space was given by principal components analysis (PCA). The whole set of relevés was analysed (Table 1). Woody synusia and herb layer were used as the species data in analysis 1 because general overview of collected data was intended. Layers of woody synusia were not merged in any case. The year of sampling was used as a supplementary environmental variable. Focus scaling on inter-sample distances, centering by species and samples, and no data transformation was used (Fig. 2). The relationship between the first two ordination axes and the years of relevé acquisition is expressed by correlation coefficient. Dependence between sample scores on ordination axes and average EIV for environmental factors of the herb layer was calculated by regression analysis (Table 2). Because the site conditions are reflected significantly in the species data variability, three main site types were defined. The groups of relevés representing different sites were identified by TWINSPAN analysis. TWINSPAN was set for 3 clusters, 5 pseudospecies cut level and values of cut level 0, 2, 5, 10, 20. Such setting respects the dominance of species (Fig. 3). Only the herb layer of relevés was used in this case. As an indicator of β diversity the Sörrensen dissimilarity index was computed for relevé groups. Characteristic species of the separated groups of relevés were identified according to taxon fidelity, using phi coefficient (Chytrý et al. 2002). The phi coefficient, computed from presence/absence data as $\Phi = (N \times n_p - n \times N_p / \sqrt{[n \times N_p (N-n) \times (N-N_p)]}$, was chosen as the fidelity measure, where N is the number of relevés in the data set, N_p is number of relevés in the target vegetation unit (in this case determined relevé groups), n is the number of occurrences of the species in the data set and n_p is number of occurrences of the species in the target vegetation unit. An advantage of the phi coefficient is its independence of data set size but on the other hand the phi coefficient contains no information about statistical significance (Tichý & Holt 2006).

The distribution of samples marked by identified relevé groups in ordination space (Fig. 4) is created as a species and samples biplot with herb layers used as species data. Logarithmic transformation, focus scaling on interspecies correlations and centring by species were used.

Plant community development was assessed separately for the relevé groups representing main vegetation types. Number of observed species, Shannon-Wiener diversiry index and average EIV (Ellenberg et al. 1992) were the variables determined for each year of the research (Fig. 5). For this purpose only species of the herb layer were included. The Shannon-Wiener index was calculated from the equation: $H' = -\Sigma p_i ln p_i$ where p_i is the relative proportion of ith species (e.g. Moravec 1994). Turboveg for Windows 2.0 (Hennekens & Schaminée 2001) and Juice 6.5 software (Tichý 2002) were used for data storage and processing. Statistical significance of variables was tested by ANOVA analysis using Statistica 6.0 software (Statsoft 2003).

Table 1. Settings of ordination analysis; 126 relevés in all analyses, PCA – Principal Component Analysis, RDA – Redundancy Analysis, Woody synusia: 1 Tree layer – high, 2 Tree layer – middle, 3 Tree layer – low, 4 Shrub layer – high, 5 Shrub layer – low, 8 Seedlings layer.

Analysis	Analysed data	Number of species	Analysis type	Transformation	Enviromental data	Covariable data	Supplementary data
1	Woody synusia and herb layer	160	PCA	None	None	None	Year of research
2	Herb layer	119	PCA	Logarithmic	None	None	None
3	Herb layer	119	RDA	Logarithmic	Year of research	Plot number	None
4	Woody synusia	41	RDA	Logarithmic	Year of research	Plot number	None

Table 2. Correlation coefficients of years of research, average Ellenberg indicator values (EIV) and first two ordination axes in PCA. Because the years of research were used as supplementary variables, statistical significance of this dependent was not assessed. Statistical significance of the relationship between average EIV and scores of samples on first two ordination axes is expressed by symbol in exponent: * 0.049 > p > 0.01, ** 0.009 > p > 0.001, *** p < 0.001.

	Axis I	Axis II
1975	0.05	–0.7
1997	0.00	0.22
2008	–0.06	0.47
Light	0.70***	0.00
Temperature	–0.53***	–0.24**
Moisture	0.67***	0.04
Soil reaction	–0.70***	–0.26**
Nutrients	–0.69***	–0.21*

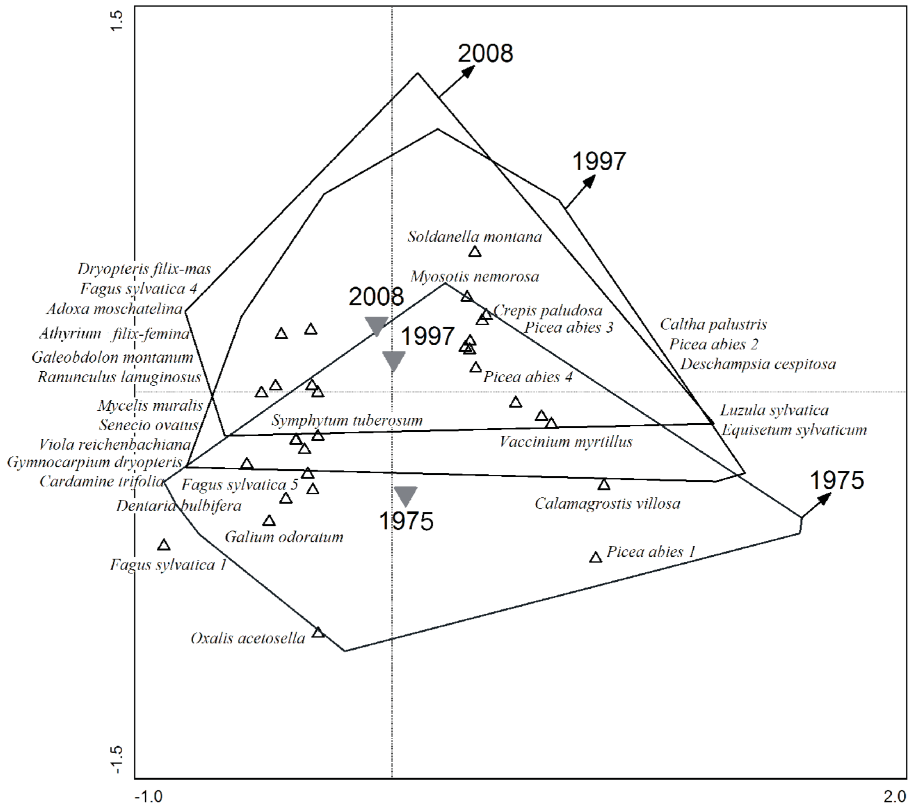


Fig. 2. Analysis 1, PCA – Principal Component Analysis. Herb layer and woody synusia are used as species data. Years of relevés logging are used as supplementary variables. The first ordination axis explains 47.5% of species variability. The second axis explains 15.9% of species variability. Polygons represent perimeters of samples made in the appropriate year. Species with a fit ≥ 8% are illustrated. Species are displayed as symbols even in the linear ordination method.

Projection of trends detected in ecologically distinct parts to the whole study area is shown by redundancy analysis (RDA). Species composition changes of the herb layer were assessed using the whole set of relevés (Fig. 6). The shifts in structure of vegetation layers in the woody synusia were evaluated by the same way (Fig. 7). The time was used as a continuous environmental variable. The year of acquisition of particular relevé was the time determinant. The plot mark was used as a covariable. This setting of ordination analyses preserved variability within relevés in time and removed variability between plots. Logarithmic transformation, focus scaling on interspecies correlations and centering by species were used.

The types of ordination analyses were selected on the basis of data sets homogeneity expressed by length of the first variability gradients in detrended correspondence analysis (DCA) (Lepš & Šmilauer 2003).

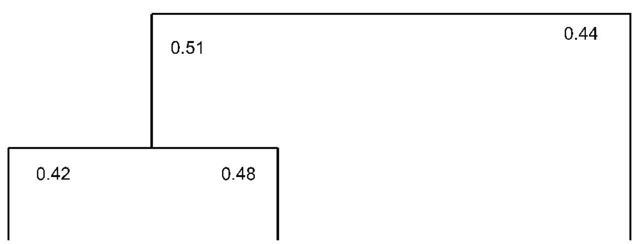
Ordination analyses were processed in Canoco for Windows 4.5 and CanoDraw for Windows 4.0 (ter Braak & Šmilauer 2002, Lepš & Šmilauer 2003). Significance of variables in CCA was tested using the Monte Carlo test with 4999 permutations. Only the species with the highest weight are displayed in graphic outputs.

The critical level of significance in all analyses was set at α = 0.05.

Results

The first (horizontal) axis in PCA (Fig. 2) separates species and samples by site conditions regardless of time. It explains 47.5% of species data variability. Vegetation changes over time are illustrated by the second (vertical) axis that explains 15.9% of data variability. The correlation coefficients between years of sampling used as supplementary variables and the 1st ordination axis are negligible in comparison with the same ones and the 2nd axis (Table 2). Since the site conditions explain the biggest part of species-data variability, three groups of relevés were identified by TWINSPAN to separate main vegetation types as follows: relevé group 1 – spring areas and peat bogs (5 permanent plots), relevé group 2 – wet acidophilous spruce communities (10 permanent plots), relevé group 3 – beech forests (27 permanent plots) (Fig. 3). The distribution of samples marked by relevé groups and significant herb species in ordination space is illustrated by PCA (Fig. 4).

The changes in herb species composition in time were different for separated vegetation types. These changes were studied by shifts in average EIV as well as by shifts in species diversity in the years under study. On spring areas and peat bogs (relevé group 1) a significant increase in both the number of observed species and the value of Shannon-Wiener diversity index in 2008 was detected. The trend of growing EIV for light and temperature over time is discernible too. Wet acidophilous spruce communities (relevé group 2) appear to be stable in the observed period – there is no significant shift in studied values except for a small increase in Shannon-Wiener diversity index. As against relevé group 1, number of observed species has dropped in the beech forest (relevé group 3). EIV for light and moisture are growing up but the indicator values for soil reaction and nutrients are significantly decreasing (Fig. 5, Table 3).



Chaerophyllum hirsutum	79.5	---	---
Crepis paludosa	70.6	---	---
Carex remota	69.6	---	---
Myosotis nemorosa	70.6	---	---
Tephroseris crispa	68.4	---	---
Calamagrostis villosa	13.1	47.6	---
Vaccinium myrtillus	26	35.4	---
Soldanella montana	---	40.6	---
Maianthemum bifolium	---	28.2	---
Lycopodium annotinum	---	27.6	---
Avenella flexuosa	---	23.2	---
Galeobdolon montanum	---	---	93.8
Galium odoratum	---	---	69.3
Dentaria bulbifera	---	---	64.6
Gymnocarpium dryopteris	---	---	46.1
Dentaria enneaphyllos	---	---	37.5

Fig. 3. TWINSPAN dendrogram. Species which are characteristic for the relevé groups are identified by species fidelity. As an indicator of β diversity the Sörrensen dissimilarity index was computed for relevé groups.

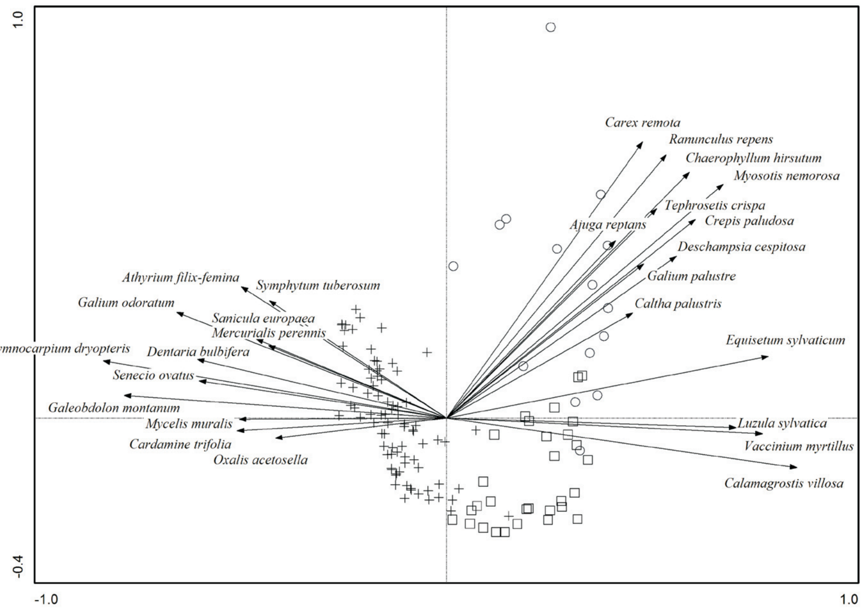


Fig. 4. Analysis 2, PCA – Principal Component Analysis. Herb layers were used as species data. Samples are marked by relevé group: circle – relevé group 1 – spring areas and peat bogs, square – relevé group 2 – wet acidophilous spruce communities, cross – relevé group 3 – beech forests. Species with a fit ≥ 15% are shown.

Table 3. Comparison of number of observed species, Shannon-Wiener index of diversity, average Ellenberg indicator values for light, temperature, moisture, soil reaction and nutrients for the years under study. Statistical significance of differences between values for years of observation was assessed by ANOVA, a post hoc Tukey test. The level of statistical significance was set at 0.05.

	Observed species		**Shannon-Wiener index**		**Light**		**Temperature**		**Moisture**		**Soil reaction**		**Nutrients**	
Relevé group 1 - spring areas and peat bogs														
Year	1975	1997	1975	1997	1975	1997	1975	1997	1975	1997	1975	1997	1975	1997
1997	0.98	–	0.84	–	0.89	–	0.26	–	0.54	–	0.57	–	0.66	–
2008	0.001	0.001	0.003	0.007	0.01	0.03	0.003	0.06	0.40	0.08	0.92	0.79	1.00	0.66
Relevé group 2 - wet acidophilous spruce communities														
Year	1975	1997	1975	1997	1975	1997	1975	1997	1975	1997	1975	1997	1975	1997
1997	0.26	–	0.57	–	0.84	–	0.16	–	0.81	–	0.32	–	0.68	–
2008	0.90	0.12	0.29	0.04	0.93	0.98	0.64	0.59	0.83	0.47	0.35	1.00	0.19	0.61
Relevé group 3 - beech forests														
Year	1975	1997	1975	1997	1975	1997	1975	1997	1975	1997	1975	1997	1975	1997
1997	0.000	–	0.87	–	0.99	–	0.004	–	0.01	–	0.19	–	0.97	–
2008	0.014	0.158	0.98	0.95	0.06	0.04	0.168	0.29	0.04	0.89	0.008	0.39	0.007	0.01

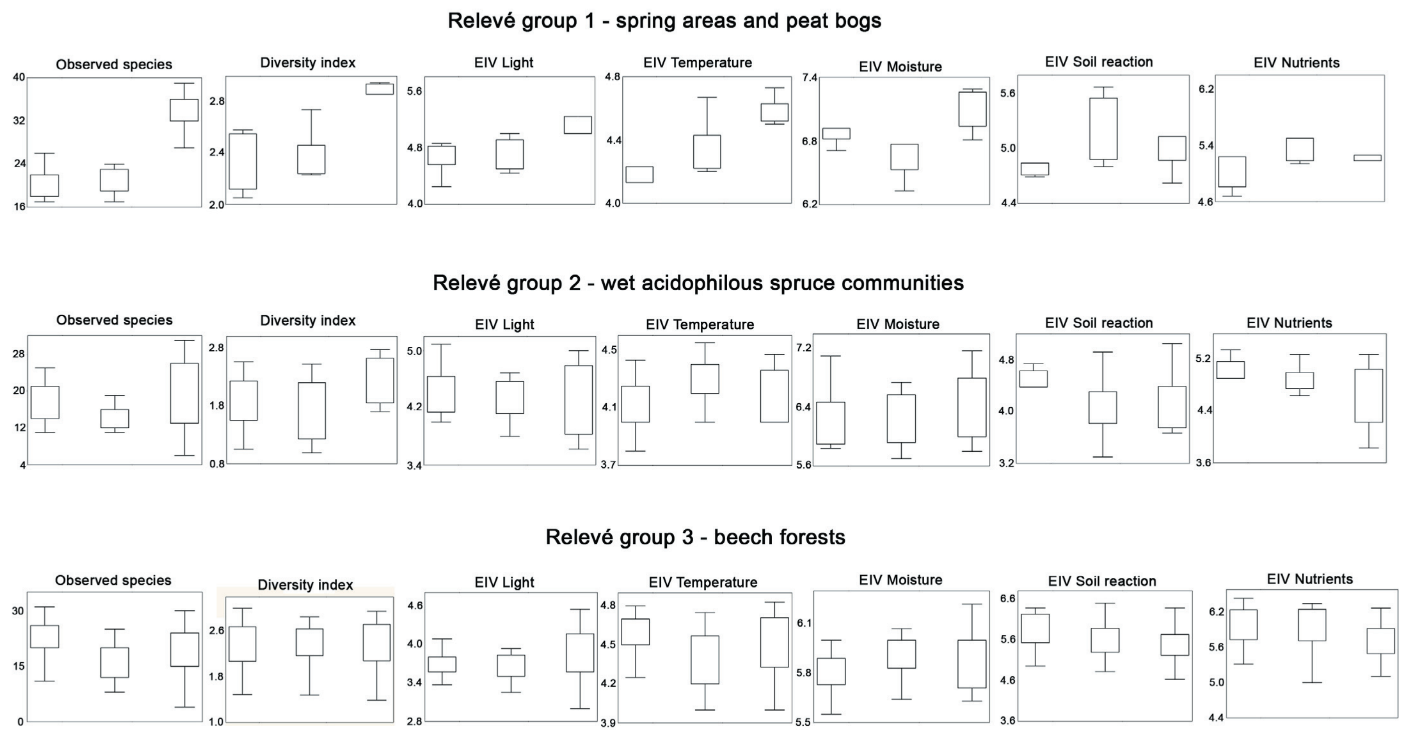


Fig. 5. Values of number of observed species, Shannon-Wiener diversity index and average Ellenberg indicator values for years of research. Left, middle, and right boxes in every plot show respective values from observation in 1975, 1997, and 2008.

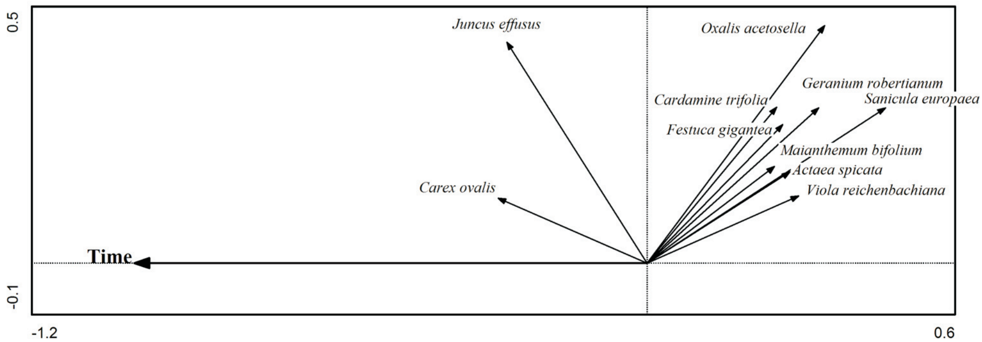


Fig. 6. Analysis 3, RDA – Redundancy Analysis. The herb layer is used as species data. Time is used as a continuous environmental variable. Statistically significant canonical axis (p = 0.002) explains 4% of species variability. Species with a fit ≥ 6 % are shown.

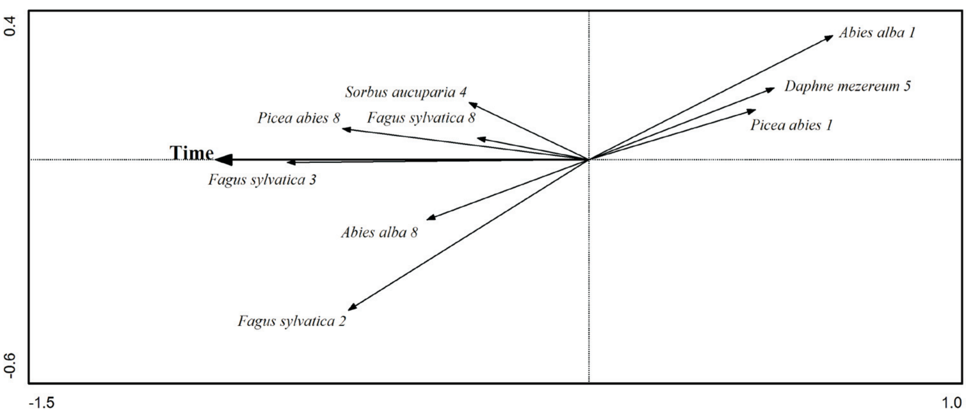


Fig. 7. Analysis 4, RDA – Redundancy Analysis. Woody synusia are used as species data. Time is used as a continuous environmental variable. Statistically significant canonical axis (p = 0.002) explains 23% of species variability. Species with a fit ≥ 8 % are shown.

The biggest proportion of permanent plots (27) is situated in beech forest communities. Therefore, reduced EIV for soil reaction and nutrients shown through analyses of the whole set of relevés are given by the changes of species composition in the 3rd relevé group (Fig. 6). Increasing occurrence over time were revealed for *Carex ovalis* and *Juncus effusus*. The occurrence of species that are more sensitive to soil reaction or nutrients (*Cardamine trifolia*, *Festuca gigantea*, *Oxalis acetosella*, *Geranium robertianum*, *Sanicula europaea*, *Actaea spicata*) is decreasing. The statistical significant canonical axis – time (*p* value = 0.002) explains 4% of species variability. The frequency and modified fidelity index of occurring herbal species with relation to relevé group and year of sampling is shown by Table 4.

The shift of woody synusia in the measured area is shown by the declining occurrence of *Picea abies* and *Abies alba* in the mid and overstorey. The abundance of *Fagus sylvatica* in layer 1 (tree layer high) is slowly decreasing too (Fig. 5, Fig. 7). In lower layers *Fagus sylvatica* is becoming the absolutely dominant species as it regenerates everywhere except wet sites. The growing abundance of *Picea abies* and *Abies alba* seedlings has not been reflected in higher woody layers. Twenty three percent of species variability is explained by the canonical ordination axis (time). The statistical significance of this axis was tested (*p* = 0.002).

Table 4. Synoptic table with percentage frequency and modified fidelity index (phi coefficient).

	Relevé group 1						Relevé group 2						Relevé group 3					
Year of sampling	**1975**		**1997**		**2008**		**1975**		**1997**		**2008**		**1975**		**1997**		**2008**	
No. of relevés	**5**		**4**		**6**		**8**		**11**		**11**		**29**		**27**		**25**	
Galeobdolon montanum	.	–	.	–	.	–	.	–	9	–	.	–	97	48.1	89	42.3	100	50.7
Oxalis acetosella	100	9.2	75	–	83	–	88	–	100	9.2	100	9.2	97	4.3	100	9.2	100	9.2
Senecio ovatus	.	–	50	–	33	–	62	1.1	73	8.5	45	–	93	23.2	96	25.6	96	25.3
Gymnocarpium dryopteris	60	–	50	–	67	–	62	–	27	–	55	–	100	23.9	100	23.9	96	20.9
Athyrium filix-femina	100	18.5	75	–	83	4.1	62	–	36	–	73	–	100	18.5	85	5.7	92	11.6
Dryopteris carthusiana	.	–	.	–	67	31.9	.	–	.	–	82	44	.	–	.	–	92	52.2
Cardamine trifolia	.	–	25	–	67	10.9	25	–	36	–	55	2.3	100	34.5	78	18.8	76	17.5
Impatiens noli-tangere	40	–	75	14.9	100	32.6	12	–	27	–	18	–	90	25.3	52	–	72	12.7
Circaea alpina	80	4.7	100	20.9	100	20.9	75	–	64	–	55	–	48	–	74	–	72	–
Urtica dioica	60	1.8	75	12.5	100	30.4	38	–	27	–	36	–	66	5.7	52	–	64	4.6
Dryopteris filix-mas	.	–	.	–	.	–	12	–	.	–	.	–	41	27.3	11	–	64	50.1
Galium odoratum	.	–	.	–	.	–	.	–	.	–	.	–	69	44.6	44	22.6	60	36.5
Dentaria bulbifera	.	–	.	–	.	–	.	–	.	–	.	–	62	41.9	33	15	60	40
Deschampsia cespitosa	80	8.4	75	4.6	100	23.7	100	23.7	55	–	45	–	66	–	41	–	60	–
Mycelis muralis	.	–	25	–	.	–	25	–	9	–	.	–	79	42.3	44	14.3	56	23.6
Maianthemum bifolium	80	10.1	25	–	50	–	62	–	100	25.1	91	18.3	83	12.2	56	–	52	–
Dryopteris dilatata	80	1.4	75	–	67	–	100	18.6	100	18.6	64	–	83	3.8	85	5.9	52	–
Phegopteris connectilis	60	10.5	.	–	67	15.2	38	–	36	–	55	6.6	48	2.2	52	4.7	52	4.8
Stellaria nemorum	40	–	75	12.8	50	–	75	12.8	45	–	45	–	79	15.9	59	1.6	44	–
Moehringia trinervia	.	–	.	–	.	–	.	–	.	–	.	–	21	19.7	.	–	40	46.9
Carex ovalis	.	–	.	–	17	12.3	.	–	.	–	.	–	.	–	15	9.8	36	38.3
Paris quadrifolia	.	–	25	–	33	7.3	25	–	9	–	.	–	59	28.1	37	10.4	32	6.2

Table 4. Continued.

	Relevé group 1						Relevé group 2						Relevé group 3					
Year of sampling	**1975**		**1997**		**2008**		**1975**		**1997**		**2008**		**1975**		**1997**		**2008**	
No. of relevés	**5**		**4**		**6**		**8**		**11**		**11**		**29**		**27**		**25**	
Symphytum tuberosum	.	–	.	–	.	–	.	–	.	–	.	–	41	38.8	11	2.1	32	27.4
Adoxa moschatellina	.	–	.	–	.	–	.	–	.	–	.	–	24	21.3	15	9.1	32	31.6
Sanicula europaea	.	–	.	–	.	–	12	–	.	–	.	–	72	56.9	26	10.8	24	8.9
Prenanthes purpurea	.	–	.	–	.	–	25	7.6	18	1.2	18	1.2	45	26.3	22	5	24	6.7
Digitalis purpurea	.	–	.	–	.	–	.	–	9	8.5	9	8.5	.	–	.	–	20	27.6
Carex remota	80	25.6	100	39.9	100	39.9	12	–	36	–	36	–	3	–	7	–	20	–
Viola reichenbachiana	.	–	.	–	.	–	.	–	.	–	.	–	48	42.5	30	21.3	20	10.4
Dentaria enneaphyllos	.	–	.	–	.	–	.	–	.	–	.	–	17	15.1	22	22.2	20	19.1
Mercurialis perennis	.	–	.	–	.	–	.	–	.	–	.	–	38	34.9	30	24.8	16	8.2
Milium effusum	.	–	.	–	33	26.6	12	2.4	.	–	.	–	21	11.9	11	–	16	6.5
Calamagrostis villosa	80	12	50	–	83	14.4	100	26.7	91	20	100	26.7	31	–	22	–	16	–
Cardamine flexuosa	.	–	50	18.5	100	58.4	.	–	9	–	27	–	21	–	19	–	16	–
Rubus idaeus	.	–	.	–	33	25.1	12	1.6	18	8	9	–	3	–	11	–	12	1
Galeopsis tetrahit	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	12	32.9
Juncus effusus	.	–	25	7.1	83	61.5	.	–	27	9.2	9	–	.	–	.	–	12	–
Festuca gigantea	60	38.5	.	–	33	14	.	–	.	–	9	–	45	24.5	4	–	12	–
Carex tomentosa	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	12	32.9
Carex murica agg.	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	12	32.9
Ranunculus lanuginosus	.	–	.	–	.	–	.	–	.	–	.	–	28	33.7	11	8.4	12	9.8
Taraxacum sect. *Ruderalia*	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	8	26.8
Veronica officinalis	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	8	26.8
Geranium robertianum	.	–	.	–	.	–	.	–	.	–	.	–	41	55.7	.	–	8	3.9

Table 4. Continued.

	Relevé group 1						Relevé group 2						Relevé group 3					
Year of sampling	**1975**		**1997**		**2008**		**1975**		**1997**		**2008**		**1975**		**1997**		**2008**	
No. of relevés	**5**		**4**		**6**		**8**		**11**		**11**		**29**		**27**		**25**	
Hieracium murorum	.	–	.	–	.	–	50	38	27	14.4	.	–	24	11.2	11	–	8	–
Poa nemoralis	.	–	25	24	.	–	.	–	18	14.7	.	–	.	–	15	10.1	8	–
Luzula sylvatica	100	28.5	75	10.4	67	4.3	100	28.5	82	15.3	73	8.7	34	–	7	–	8	–
Actaea spicata	.	–	.	–	.	–	.	–	.	–	.	–	45	48.3	19	13.9	8	–
Mercurialis perennis	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	4	18.9
Cirsium palustre	.	–	.	–	17	26.4	.	–	.	–	9	11.4	.	–	.	–	4	1.4
Carex pallescens	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	4	18.9
Crepis paludosa	100	43.6	100	43.6	67	19.5	50	7.5	27	–	9	–	.	–	.	–	4	–
Aegopodium podagraria	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	4	18.9
Luzula pallescens	.	–	.	–	17	33.9	.	–	.	–	.	–	.	–	.	–	4	4
Neottia nidus-avis	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	4	18.9
Carex elongata	.	–	.	–	50	65.5	.	–	.	–	.	–	.	–	.	–	4	–
Avenella flexuosa	.	–	25	9.4	17	1.2	38	21.6	9	–	36	20.5	10	–	.	–	4	–
Festuca altissima	.	–	.	–	.	–	.	–	.	–	.	–	3	10.2	.	–	4	12.4
Calamagrostis epigejos	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	4	18.9
Petasites albus	.	–	.	–	.	–	.	–	.	–	.	–	10	24.7	.	–	4	6.8
Pulmonaria officinalis	.	–	.	–	.	–	.	–	.	–	.	–	3	10.2	.	–	4	12.4
Soldanella montana	20	–	50	12.2	17	–	62	21.6	45	8.8	73	29.2	21	–	11	–	4	–
Carex brizoides	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	4	18.9
Euphorbia dulcis	.	–	.	–	.	–	.	–	.	–	.	–	7	12.2	7	13.5	4	4.9
Myosotis nemorosa	80	25	100	39.2	100	39.2	38	–	36	–	45	–	.	–	.	–	4	–
Stellaria longifolia	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–	4	18.9

Table 4. Continued.

	Relevé group 1						Relevé group 2						Relevé group 3					
Year of sampling	**1975**		**1997**		**2008**		**1975**		**1997**		**2008**		**1975**		**1997**		**2008**	
No. of relevés	**5**		**4**		**6**		**8**		**11**		**11**		**29**		**27**		**25**	
Rubus fruticosus agg.	.	–	.	–	17	26.4	.	–	.	–	9	11.4	.	–	.	–	4	1.4
Chrysosplenium alternifolium	40	10.9	100	59.1	67	32.3	.	–	9	–	18	–	3	–	.	–	.	–
Stellaria media	.	–	.	–	.	–	.	–	.	–	.	–	.	–	7	25.8	.	–
Anemone nemorosa	.	–	.	–	.	–	.	–	.	–	.	–	17	39.5	.	–	.	–
Poa palustris	.	–	.	–	17	38.9	.	–	.	–	.	–	.	–	.	–	.	–
Lysimachia nemorum	20	8.5	25	13.9	50	41	.	–	.	–	.	–	7	–	7	–	.	–
Agrostis stolonifera	.	–	.	–	17	38.9	.	–	.	–	.	–	.	–	.	–	.	–
Agrostis capillaris	.	–	.	–	.	–	.	–	.	–	.	–	7	24.9	.	–	.	–
Myosotis sylvatica	.	–	.	–	.	–	12	16.5	.	–	.	–	21	31.9	.	–	.	–
Epipactis helleborine	.	–	.	–	.	–	.	–	.	–	.	–	.	–	4	18.2	.	–
Circaea lutetiana	.	–	.	–	.	–	.	–	.	–	.	–	.	–	4	18.2	.	–
Cardamine impatiens	.	–	.	–	.	–	.	–	.	–	.	–	.	–	4	18.2	.	–
Fragaria vesca	.	–	.	–	17	24	.	–	.	–	.	–	17	25	.	–	.	–
Carex nigra	.	–	.	–	17	38.9	.	–	.	–	.	–	.	–	.	–	.	–
Veronica montana	.	–	.	–	50	47.3	.	–	.	–	18	9.7	10	–	11	1.4	.	–
Pseudorchis albida	.	–	.	–	.	–	.	–	9	28.6	.	–	.	–	.	–	.	–
Epilobium ciliatum	.	–	.	–	50	68.6	.	–	.	–	.	–	.	–	.	–	.	–
Bromus benekenii	.	–	25	33.2	.	–	.	–	.	–	.	–	.	–	19	22.6	.	–
Scirpus sylvaticus	.	–	.	–	50	68.6	.	–	.	–	.	–	.	–	.	–	.	–
Stellaria alsine	.	–	.	–	67	80	.	–	.	–	.	–	.	–	.	–	.	–
Vaccinium myrtillus	80	22.7	50	1.5	67	13.3	75	19.2	91	30.4	55	4.7	7	–	7	–	.	–
Veronica anagallis-aquatica	.	–	.	–	17	38.9	.	–	.	–	.	–	.	–	.	–	.	–

Table 4. Continued.

	Relevé group 1						Relevé group 2						Relevé group 3					
Year of sampling	**1975**		**1997**		**2008**		**1975**		**1997**		**2008**		**1975**		**1997**		**2008**	
No. of relevés	**5**		**4**		**6**		**8**		**11**		**11**		**29**		**27**		**25**	
Dactylorhiza fuchsii	.	–	.	–	33	47.7	.	–	9	7.3	.	–	.	–	.	–	.	–
Cardamine amara	20	42.6	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–
Lychnis flos-cuculi	.	–	.	–	50	68.6	.	–	.	–	.	–	.	–	.	–	.	–
Lycopodium annotinum	20	14.3	.	–	.	–	12	4.8	.	–	45	46.2	.	–	.	–	.	–
Juncus articulatus	.	–	.	–	33	55.5	.	–	.	–	.	–	.	–	.	–	.	–
Poa trivialis	.	–	.	–	33	47.7	.	–	.	–	9	7.3	.	–	.	–	.	–
Potentilla erecta	20	42.6	.	–	.	–	.	–	.	–	.	–	.	–	.	–	.	–
Galium palustre	40	21.8	.	–	67	46.9	.	–	27	9.8	18	1.2	.	–	.	–	.	–
Carex echinata	.	–	.	–	50	68.6	.	–	.	–	.	–	.	–	.	–	.	–
Stellaria holostea	.	–	25	47.8	.	–	.	–	.	–	.	–	.	–	.	–	.	–
Polygonatum verticillatum	.	–	.	–	.	–	.	–	9	28.6	.	–	.	–	.	–	.	–
Glechoma hederacea	.	–	25	47.8	.	–	.	–	.	–	.	–	.	–	.	–	.	–
Equisetum sylvaticum	80	25.9	75	22.3	67	16.4	62	13.4	64	14.2	45	1.3	.	–	.	–	.	–
Ficaria verna ssp. *bulbifera*	.	–	.	–	.	–	.	–	45	65.2	.	–	.	–	.	–	.	–
Ajuga reptans	60	32.4	50	23.9	67	38.1	12	–	.	–	9	–	.	–	.	–	.	–
Epilobium angustifolium	.	–	.	–	.	–	.	–	.	–	9	28.6	.	–	.	–	.	–
Valeriana dioica	.	–	.	–	17	38.9	.	–	.	–	.	–	.	–	.	–	.	–
Glyceria fluitans	40	30.6	25	14.2	33	23.3	.	–	.	–	9	–	.	–	.	–	.	–
Epilobium montanum	.	–	25	47.8	.	–	.	–	.	–	.	–	.	–	.	–	.	–
Doronicum austriacum	.	–	.	–	.	–	38	49.3	.	–	9	5.4	3	–	.	–	.	–
Chaerophyllum hirsutum	100	39.3	100	39.3	100	39.3	50	3.7	18	–	27	–	3	–	4	–	.	–
Luzula pilosa	.	–	.	–	.	–	.	–	.	–	.	–	7	24.9	.	–	.	–

Table 4. Continued.

	Relevé group 1						Relevé group 2						Relevé group 3					
Year of sampling	**1975**		**1997**		**2008**		**1975**		**1997**		**2008**		**1975**		**1997**		**2008**	
No. of relevés	**5**		**4**		**6**		**8**		**11**		**11**		**29**		**27**		**25**	
Tephroseris crispa	80	46.8	25	1.1	83	49.6	12	–	.	–	9	–	3	–	.	–	.	–
Asarum europaeum	.	–	.	–	.	–	12	28.7	.	–	.	–	3	4.5	.	–	.	–
Ranunculus repens	60	19.5	75	30.7	100	49.3	12	–	18	–	36	1.8	3	–	.	–	.	–
Viola palustris	20	14.2	.	–	33	30.9	25	20.4	.	–	.	–	.	–	.	–	.	–
Prunella vulgaris	60	57.6	.	–	33	26.6	.	–	.	–	.	–	.	–	.	–	.	–
Lythrum salicaria	.	–	.	–	33	55.5	.	–	.	–	.	–	.	–	.	–	.	–
Caltha palustris	40	22.2	.	–	67	47.5	25	7.9	.	–	18	1.5	.	–	.	–	.	–
Luzula luzuloides	.	–	.	–	.	–	12	16.1	18	26.6	.	–	3	–	.	–	.	–
Pulmonaria obscura	.	–	.	–	.	–	.	–	.	–	.	–	3	17.5	.	–	.	–
Equisetum arvense	.	–	.	–	17	29.3	.	–	9	13.2	.	–	.	–	.	–	.	–

Discussion

The authors have recorded the relevés during repeating observations. Even though they used the same methodology, it is not possible to remove their subjectivity that is reflected in the number of observed/overlooked species or abundance and dominance estimations (Lepš & Hadincová 1992, Vittoz & Guisan 2007). This fact may influence the analyses and it may explain the increase in the number of observed species and the value of Shannon-Wiener diversity index for relevé group 1 (spring areas and peat bogs) in 2008. But the trend of growing EIV for light and temperature suggests the impact of site conditions changes. The tree layers in several plots of this relevé group were completely disturbed by the Kyrill and Emma windstorms. Open canopy and mild winter seasons might enable expansion of more light and temperature demanding species.

Also the increase in EIV for light in the beech forests (relevé group 3) could be explained by the dropping dominancy of layer 1 conditioned by windfalls. The probability of occurrence of light-demanding herb species under reduced canopy increases. An unambiguous explanation of decreasing average EIV for soil reaction and nutrients of herb layer is not yet available. Phenomena connected with the dynamics of forest development, especially with the change of generation, is one of the possibilities. Statistically significant changes in soil reaction and soil nitrogen depending on stages of forest development are described from the Carpathians (Šamonil & Vrška 2007). In their study the decrease in EIV for soil reaction detected between repeated observations relates to the withdrawing of *Dentaria enneaphyllos*, *Galeobdolon montanum* and *Galium odoratum* together with the expansion of *Vaccinium myrtillus* and *Luzula luzuloides*. It corresponds with decreasing occurence of *Dentaria enneaphyllos* published by Hédl (2004) as well as with the positive correlation between soil reaction and the occurrence of *Galium odoratum*, *Dentaria bulbifera*, and *Lamium galeobdolon* observed by Falkengren-Grerup & Tyler (1991) and Falkengren-Grerup (1995). Although the above-named species are common in relevés of the relevé group 3 (beech forests) there is not any trend in the frequency of their occurrence. Declining average EIV for soil reaction and nutrients are linked with decreasing frequency of *Actaea spicata*, *Paris quadrifolia*, *Sanicula europaea*, *Stellaria nemorum*, *Viola reichenbachiana*, and *Mercurialis perennis*. The population of *Dentaria enneaphyllos* seems to be stable over time.

The relationship between changes in the herb layer and soil acidification by imissions in the past seems to be likely; on the other hand, the impact of changes in stand structure and portion of windfalls should not be excluded. This causality can be supported by small (statistically insignificant) differences in EIV for soil reaction and nutrients between the years 1975 and 1997. Statistically significant shifts are revealed only by comparison with values from 2008 – that is after the windstorms when the number of windfalls markedly increased and the vertical structure of woody layers was often changed. The example of the influence of windstorms on the components of the herb layer gives *Juncus effusus* (Fig. 6). It was repeatedly recorded in the hollows made by roots of fallen stems. Although the locality often looked unsuitable for this species, water concentrated in the depression enabled its successful development. The positive effect of forest management on the presence of *Juncus effusus* was described for example by Brunet et al. (1996). Also the occurrence of *Digitalis purpurea* – an alien species expanding into the ecosystems of primeval forest (Lepší et al. 2007) – presumably relates to a specific stand structure. It is interesting that it occupies similar sites as *Carex ovalis*, whose presence is increasing over time (Fig. 6). Both species were recorded on the plots with the dominance of the upper tree layer in the woody synusia that covered 40–60% of the plot area. The cover of lower woody layers ranged from 0 to 25%. Localities with partly disturbed layer 1, but without fully developed regeneration, were also occupied.

The stability of assessed factors over time is characteristic for relevé group 2 (wet acidophilous spruce forests). It is a question whether the relatively low portion of wind disturbances on studied plots affected the results of analyses.

Time, as the statistically significant environmental variable used as the first canonical axis in the analysis of woody synusia changes (Fig. 7), shows the shifts in species composition and structure of woody species on permanent plots over time. However, a study of the gap dynamic of Žofín in the period 1971–2004 (Kenderes et al. 2009) did not find any major changes in overall gap characteristics of the locality (number of gaps per hectare, gap size, etc.). Also differences in numbers of recorded living trees by stem mapping among the years of surveys are lower than 1%. There are oscillations of cover and dominancy of species and layers in woody synusia. Some changes are observable also in the herb layer (Unar & Šamonil 2008). But the share of living and dead woody biomass (except for large scale disturbances) in beech dominated forests remains relatively stable over time (Vrška et al. 2001 a,b). It is in agreement with shifting mosaic steady state defined by Borman & Likens (1979).

Ecosystem development shown by the presented observations and analyses is going from mixed forest built by layer 1 towards stands of the richer stand structure with dominance of *Fagus sylvatica*. Growing dominance of *Fagus sylvatica* can be expected also in the future. The further development of the herb layer is hard to anticipate. Cycling of forest developmental stages (Leibundgut 1959, Korpel 1995) is difficult to handle by phytocoenological relevés due to the impact of the wider neighbourhood. The relationship between changes of woody synusia structure and quality of herb layer (cover, species composition, or dominant species) was described for instance by Koop (1989). From this point of view the connection of stem mapping and phytocoenological surveys is promising.

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