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The influence of *Picea abies* on herb vegetation in forest plant communities of the Veporské vrchy Mts.

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ABSTRACT: Natural mixed beech-fir forests were quite widely replaced by spruce dominated stands in Slovakia. Given the demands on the assessment of the forest status as well as on stopping the biodiversity loss it is required to evaluate the influence of *Picea abies* (L.) Karst. on the species composition. In a case study from the Veporské vrchy Mts. natural beech dominated forests were compared to stands with different spruce proportion. Within three groups of relevés with no, less and more than a half proportion of *Picea abies* the species diversity and Ellenberg indicator values were compared. The response of particular species to the proportion of *Picea abies* was evaluated by partial relation in direct gradient analysis. The increasing spruce proportion causes particularly higher occurrence of acidophytes and a decrease in nitrophytes. Species with the highest positive response to spruce are mostly shallow-rooted or characteristic of natural spruce forests. Greater richness along with the highest diversity was found in mixed stands with less than a half proportion of *Picea abies*. The most significant difference in species composition was between natural and spruce dominated stands. However the proportion of *Picea abies* does not reduce the species diversity in general, it causes significant changes in the species composition. As the results show, to avoid the negative effect and loss of phytodiversity it is required not to grow spruce dominated stands out of the natural occurrence of *Picea abies*.

Keywords: beech forest; biodiversity; herb vegetation; *Picea abies* (L.) Karst.; species composition

A very common form of the anthropic influence on biodiversity is the growing of *Picea abies* (L.) Karst. instead of natural forest stands. The knowledge how the growing of spruce affects biodiversity is needed according to the European states target of stopping the loss of biodiversity and for the purpose of assessment of the forest ecosystem status.

The species composition is an important indicator of the forest status assessment. Its changes caused by the growing of *Picea abies* were the objective of investigation in several papers. Hadač and Sofron (1980) proposed the classification of spruce stands relative to the intensity of changes in the herb layer composition. They reported that the changes differ in dependence on the generation of *Picea abies*. The generation as a main reason for change intensity was mentioned also in Fajmonová (1974). In these papers and also in the others (Kontriš, Jurko 1982; Ambros 1990; Poleno 2001; Šimurdová 2001; Šomšák, Balkovič 2002; Šomšák 2003; Vladovič et al. 2008) the species composition of natural and secondary coniferous stands in Slovakia and in the Czech Republic is compared. Some of them also evaluated the effect of secondary spruce forests on the phytoenvironment. Ewald (2000a) stated that several authors reported the inhibition of vascular plants (Teuscher 1985; Simmons, Buckley 1992), especially lower species richness under coniferous canopies and, on the other hand, others (Bürger 1991; Lücke, Schmidt 1997) found spruce plantations to be richer than deciduous stands.

The first aim of this paper is to investigate the influence of *Picea abies* on the herb layer composition in natural forests with *Fagus sylvatica* dominance. The second aim is to evaluate the extent of difference in the herb species composition within natural beech dominated and non-natural spruce dominated stands. The investigation is carried out on the basis of a case study from the Veporské vrchy Mts.

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MATERIALS AND METHODS

Study area

The Veporské vrchy Mts. are situated in the central part of Slovakia and belong to the central West Carpathians. The studied area covers approximately 800 km^2. The most spread parent rock material is granodiorite (Bezák et al. 1999). The soils are mostly classified as Dystric Cambisols, less frequently as Skeletic Cambisols (IUSS Working Group WRB 2006). The soil conditions of selected vegetation units including secondary spruce and larch (*Larix decidua* Mill.) plantations in the study area are characterized in Máliš et al. (2005). Mean annual temperatures vary between 3.5 and 7.5°C (Šťastný et al. 2002), mean annual precipitation between 650 and 950 mm (Faško, Šťastný 2002). The elevation of relevés ranges between minimum 490 m and maximum 1,195 m. In this altitudinal zone the beech (*Fagus sylvatica* [L.]) forests dominate. In the higher zone beech forests are mainly mixed with *Abies alba*, *Fraxinus excelsior*, *Acer pseudoplatanus*, very rarely with *Picea abies*. In the lower zone with *Quercus petraea*, on the rocky slopes mainly with *Fraxinus excelsior*, *Acer pseudoplatanus*, *Ulmus glabra*, *Acer platanoides*, *Tilia* sp., though the oak dominated and scree and ravine forests are excluded from analysis. All considered stands are classifiable as syntaxa of *Eu-Fagenion* (Mucina, Maglocký 1985) excluding those bounded to carbonate rocks.

Data acquisition and analysis

Phytosociological sampling of the area was carried out in order to survey the vegetation variability of the Veporské vrchy Mts. in 2005–2009. The plots were distributed over the whole area of the Veporské vrchy Mts. and located only in stands older than 80 years. Stands for sampling were selected subjectively with the purpose to cover the whole vegetation variability of the study area. Each stand, which was homogeneous from the aspect of species composition and environmental conditions, was sampled only with one subjectively located plot. The area of square-shaped plots was 400 m^2. For the recording of relevés the Braun-Blanquet 7-point scale of abundance and dominance adjusted by Barkman et al. (1964) was used. The vertical structure of phytocoenoses was classified following the layers in TURBOVEG software for Windows 2.0 (Hennekens, Schaminée 2001). According to the objectives of this paper 110 phytosociological relevés were considered. The plant species names follow the checklist of non-vascular and vascular plants of Slovakia (Marhold, Hindák 1998).

Our data analysis is based on comparing the composition of herb species within three groups of relevés. The groups are created with reference to the proportion of *Picea abies* in tree layers on the sampling plot. The first group represents natural and near-natural beech dominated stands without *Picea abies*. The second group involves mixed stands with the spruce proportion under 50%. The relevés with the proportion of spruce exceeding 50% are classified into the third group. The proportion is estimated by summation of the abundance values of tree species in tree layers which involve the trees higher than a half-height of the trees in the main level. The floristic comparison of groups was done in JUICE 6.5 programme (Tichý 2002). The fidelity using phi coefficient and presence/absence data was calculated for each species. The size of all relevé groups was standardized to equal size and Fisher's exact test was carried out using a significance level $P < 0.05$. Fidelity as a tool for comparison of the species composition between spruce forests and other forests was applied also in Chytrý et al. (2002). The measuring of fidelity statistically determines the diagnostic species and they play a key role in characterization and differentiation of the vegetation units. In this case they provide the comparison of units within the proportion of spruce. Bryophytes, shrubs and trees were excluded. The calculation of Ellenberg indicator values (EIV), Shannon-Wiener index and evenness (Shannon's equitability proposed by Pielou 1975) was also done in JUICE programme. The mean EIV were weighted by the average non-zero cover.

In order to evaluate the extent of difference in the herb species composition the distance between relevé groups was calculated. The calculation was done in JUICE programme using the Mann-Whitney *U* test for similarity of relevé groups. Results are twofold, as a similarity measure the Sorensen similarity index and the Euclidean distance were used according to the recommendation of index selection in Moravec et al. (1994). All available combinations of relevé pairs were selected. The analysis was carried out with and also without presence/absence data transformation in order to observe the influence of species abundance on differences between the groups.

None of all these analyses based on species groups evaluates the direct partial relation between each species and the proportion of spruce. For this purpose, the direct ordinance unimodal method CCA (Canonical Correspondence Analysis) was used with the proportion of spruce as the only environmental

Table 1. Synoptic table of relevé groups within different proportions of *Picea abies* with constancy and fidelity (phi coefficient; presence/absence data; Fisher's test with standardization of groups to equal size; $P < 0.05$). Species response to the proportion of *Picea abies* (CCA score on the horizontal axis equal to the only one environmental variable – proportion of *Picea abies*; covariables – altitude, slope; logarithmic data transformation)

Relevé group	1		2		3		Species response to spruce (CCA score)
Proportion of *Picea abies* (%)	0		1–50		50–100		
Number of relevés	57		31		22		
Constancy (%) – con; Fidelity – fid	con	fid	con	fid	con	fid	
Species with significant fidelity in the 1st group							
Alliaria petiolata	25	42.2	0	–	0	–	–0.4520
Tithymalus amygdaloides	26	33.3	3	–	5	–	–0.3130
Campanula rapunculoides	12	29.2	0	–	0	–	–0.4981
Polygonatum multiflorum	26	27.8	13	–	0	–	–0.4201
Galium odoratum	91	21.9	81	–	64	–	–0.2300
Monotropa sp.	19	23.1	10	–	0	–	–0.5311
Chelidonium majus	23	18.3	10	–	9	–	–0.2727
Species with significant fidelity in the 2nd group							
Galeopsis pubescens	4	–	26	27.5	9	–	–0.1966
Viola reichenbachiana	61	–	81	22.5	55	–	–0.1048
Anemone nemorosa	5	–	26	21.7	14	–	–0.1845
Petasites albus	5	–	19	23.0	5	–	–0.0872
Senecio nemorensis agg.	54	–	81	13.2	82	–	0.0813
Species with significant fidelity in the 3rd group							
Hieracium murorum	9	–	32	–	59	38.6	0.7047
Maianthemum bifolium	4	–	23	–	45	35.9	0.7178
Luzula luzuloides	26	–	45	–	68	30.7	0.4395
Soldanella montana	0	–	6	–	23	31.0	1.0981
Prenanthes purpurea	30	–	52	–	73	30.2	0.1187
Milium effusum	16	–	39	–	55	26.8	0.3845
Avenella flexuosa	4	–	3	–	18	25.3	0.6124
Vaccinium myrtillus	2	–	10	–	23	25.2	0.7230
Festuca altissima	7	–	13	–	27	22.4	0.5079
Polygonatum verticillatum	14	–	26	–	41	22.3	–0.4714
Species with significant fidelity in the 2nd and the 3rd group							
Oxalis acetosella	60	–	94	20.0	95	23.6	0.3058
Dryopteris carthusiana agg.	32	–	74	19.1	77	23.6	0.1713
Athyrium filix-femina	61	–	90	12.3	100	31.0	0.1113
Rubus idaeus	32	–	68	12.8	77	26.5	0.1163
Veronica officinalis	2	–	29	11.3	36	23.7	0.6504
Species without significant fidelity with constancy in the 1st group ≥ 10%							
Glechoma hirsuta	12	–	6	–	9	–	–0.1146

Table 1 to be continued

Relevé group	1		2		3		Species response to spruce (CCA score)
Proportion of *Picea abies* (%)	0		1–50		50–100		
Number of relevés	57		31		22		
Constancy (%) – con; Fidelity – fid	con	fid	con	fid	con	fid	
Festuca drymeia	14	–	3	–	5	–	–0.3788
Polystichum aculeatum	11	–	6	–	0	–	–0.5527
Polypodium vulgare	11	–	3	–	0	–	0.2002
Species without significant fidelity with constancy in the 2nd group ≥ 10%							
Veronica montana	5	–	16	–	5	–	–0.1044
Circaea lutetiana	7	–	16	–	0	–	–0.2315
Moehringia trinervia	5	–	10	–	0	–	–0.2217
Epilobium angustifolium	4	–	13	–	5	–	–0.1594
Phegopteris connectilis	2	–	10	–	5	–	–0.0573
Circaea alpina	0	–	10	–	5	–	0.5861
Luzula sylvatica	2	–	10	–	9	–	0.4000
Adoxa moschatellina	7	–	10	–	5	–	–0.3111
Cicerbita alpina	9	–	10	–	5	–	–0.6294
Bromus benekenii	7	–	10	–	0	–	–0.7376
Species without significant fidelity with constancy in the 3rd group ≥ 10%							
Carex muricata agg.	5	–	3	–	14	–	0.2856
Hypericum maculatum	2	–	3	–	14	–	0.3406
Galeopsis sp.	0	–	6	–	14	–	1.0740
Species without significant fidelity with constancy in the 1st and the 2nd group ≥ 10%							
Poa nemoralis	25	–	19	–	0	–	–0.4511
Stachys sylvatica	30	–	29	–	9	–	–0.4533
Myosotis sylvatica agg.	21	–	16	–	5	–	0.0465
Pulmonaria obscura	32	–	39	–	5	–	–0.2914
Galeobdolon montanum	12	–	23	–	5	–	–0.0888
Aegopodium podagraria	11	–	10	–	0	–	–0.6616
Species without significant fidelity with constancy in the 2nd and the 3rd group ≥ 10%							
Calamagrostis arundinacea	9	–	13	–	23	–	0.0789
Chrysosplenium alternifolium	4	–	16	–	14	–	0.6153
Species without significant fidelity with constancy in the 1st, the 2nd and the 3rd group ≥ 10%							
Stellaria nemorum	37	–	42	–	55	–	–0.0323
Mycelis muralis	72	–	81	–	73	–	0.0641
Epilobium montanum	11	–	23	–	18	–	0.2586
Scrophularia nodosa	9	–	19	–	14	–	0.2656
Salvia glutinosa	60	–	68	–	41	–	–0.0576
Geranium robertianum	68	–	74	–	50	–	–0.1163
Actaea spicata	32	–	42	–	23	–	–0.0905
Asarum europaeum	47	–	42	–	32	–	–0.1417

Table 1 to be continued

Relevé group	1		2		3		Species response to spruce (CCA score)
Proportion of *Picea abies* (%)	0		1–50		50–100		
Number of relevés	57		31		22		
Constancy (%) – con; Fidelity – fid	con	fid	con	fid	con	fid	
Urtica dioica	60	–	58	–	50	–	–0.0234
Galeobdolon luteum	67	–	71	–	50	–	–0.5054
Mercurialis perennis	63	–	65	–	45	–	–0.1736
Dryopteris filix-mas	93	–	94	–	95	–	–0.0100
Festuca gigantea	11	–	23	–	14	–	0.1527
Fragaria vesca	19	–	26	–	23	–	0.1395
Paris quadrifolia	32	–	48	–	36	–	–0.0885
Rubus hirtus	32	–	52	–	41	–	–0.1780
Impatiens noli-tangere	21	–	39	–	32	–	0.0759
Gymnocarpium dryopteris	21	–	45	–	45	–	0.0614
Ajuga reptans	19	–	29	–	36	–	0.1422
Sanicula europaea	19	–	26	–	23	–	–0.0111
Dentaria bulbifera	65	–	71	–	41	–	–0.2354

Other species (name; constancy in the 1st; 2nd; 3rd group; CCA score)
Aconitum sp.; 0; 3; 0; 0.4798; *Adenostyles alliariae*; 0; 6; 5; 0.6573; *Agrostis capillaris*; 0; 0; 5; 1.2107; *Anthriscus nitidus*; 2; 3; 0; –0.9551; *Asplenium trichomanes*; 4; 0; 0; –0.4735; *Athyrium distentifolium*; 0; 6; 0; 0.1314; *Brachypodium* sp.; 0; 0; 5; 1.0288; *Brachypodium sylvaticum*; 5; 0; 0; –0.4971; *Calamagrostis epigejos*; 0; 3; 0; 0.8996; *Campanula patula*; 0; 6; 0; 0.9207; *Campanula persicifolia*; 4; 0; 0; –0.4928; *Campanula trachelium*; 4; 3; 0; –0.5366; *Cardamine amara* ssp. *amara*; 0; 0; 5; 1.8662; *Cardamine impatiens*; 2; 6; 5; –0.2612; *Cardaminopsis arenosa*; 2; 0; 0; –0.1545; *Carex digitata*; 2; 3; 0; 0.4124; *Carex michelii*; 0; 3; 0; 0.9124; *Carex sylvatica*; 4; 3; 0; –0.4584; *Cephalanthera longifolia*; 2; 3; 0; –0.4661; *Chaerophyllum aromaticum*; 2; 0; 0; –0.9296; *Chaerophyllum hirsutum*; 0; 6; 0; 0.7631; *Chaerophyllum* sp.; 0; 3; 0; –0.2072; *Chaerophyllum temulum*; 9; 0; 5; –0.2121; *Corydalis cava*; 2; 0; 0; –0.5505; *Crepis paludosa*; 0; 3; 0; –0,6478; *Cystopteris fragilis*; 5; 6; 0; –0.6375; *Dactylis glomerata* agg.; 5; 0; 0; –0.3965; *Dentaria enneaphyllos*; 9; 6; 5; –0.609; *Dentaria glandulosa*; 2; 0; 0; –0.2612; *Deschampsia caespitosa*; 0; 3; 5; 1.3221; *Digitalis grandiflora*; 2; 0; 0; –0.3901; *Doronicum austriacum*; 0; 3; 5; 1.0765; *Epipactis pontica*; 2; 0; 0; –0.4032; *Eupatorium cannabinum*; 0; 3; 0; 0.4067; *Fallopia convolvulus*; 2; 0; 0; –0.5955; *Festuca rubra*; 0; 3; 0; –0.8765; *Galeopsis bifida*; 2; 0; 0; –0.691; *Galeopsis tetrahit*; 4; 0; 0; –0.5376; *Galium schultesii*; 2; 0; 0; –0.3901; *Gentiana asclepiadea*; 0; 3; 0; 0.6917; *Geum urbanum*; 4; 3; 0; –0.701; *Glechoma hederacea*; 5; 3; 5; 0.3489; *Gymnocarpium robertianum*; 2; 3; 0; –0.8332; *Hedera helix*; 5; 0; 0; –0.3256; *Hieracium lachenalii*; 2; 0; 9; 1.3368; *Hieracium racemosum*; 2; 0; 0; –0.3514; *Hieracium sabaudum*; 4; 0; 0; –0.4093; *Hieracium* sp.; 0; 3; 0; –0.4606; *Homogyne alpina*; 0; 0; 5; 1.1878; *Hordelymus europaeus*; 0; 3; 0; –0.4606; *Hypericum hirsutum*; 0; 6; 0; 0.9207; *Hypericum perforatum*; 0; 3; 9; 0.9821; *Isopyrum thalictroides*; 2; 3; 0; –1.5951; *Lamium maculatum*; 5; 6; 5; –0.08; *Lapsana communis*; 4; 6; 0; –0.484; *Lathyrus niger*; 2; 0; 0; –0.3901; *Lathyrus vernus*; 4; 0; 0; –0.4286; *Lilium martagon*; 2; 0; 0; –0.4283; *Lunaria rediviva*; 7; 6; 0; –0.3822; *Luzula pilosa*; 0; 3; 9; 0,9125; *Melica nutans* agg.; 0; 3; 0; 0.4798; *Melica uniflora*; 4; 6; 0; –0.5976; *Myosotis* sp.; 0; 3; 0; –0.4606; *Neottia nidus-avis*; 4; 6; 5; 0.4983; *Orthilia secunda*; 0; 3; 0; 0.8996; *Phyteuma spicatum*; 0; 3; 0; 0.4798; *Platanthera bifolia*; 0; 6; 0; 0.9238; *Poa annua*; 0; 3; 0; 0.8996; *Poa chaixii*; 0; 3; 5; 1.254; *Primula elatior*; 0; 6; 0; 0.6961; *Pteridium aquilinum*; 2; 0; 0; –0.4672; *Pulmonaria angustifolia*; 2; 0; 0; –1.1724; *Pulmonaria officinalis*; 2; 3; 0; –0.4627; *Ranunculus aconitifolius*; 0; 3; 5; 0.8239; *Ranunculus lanuginosus*; 0; 6; 0; 0.2166; *Ranunculus platanifolius*; 2; 6; 5; 0.0794; *Ranunculus repens*; 0; 0; 5; 1.8662; *Ribes uva-crispa*; 0; 0; 5; 1.5021; *Rubus* sp.; 0; 3; 0; 0.4067; *Scrophularia vernalis*; 4; 0; 0; –0.467; *Senecio erraticus*; 2; 0; 0; –1.1724; *Silene dioica*; 9; 6; 0; –0.347; *Solanum dulcamara*; 2; 3; 5; 0.8551; *Stachys alpina*; 5; 6; 0; –0.5395; *Stellaria media*; 0; 0; 5; 1.0174; *Thalictrum aquilegiifolium*; 0; 3; 0; 0.8996; *Valeriana officinalis* agg.; 2; 0; 0; –0.8525; *Valeriana tripteris*; 0; 3; 5; 0.8748; *Veratrum album* ssp. *lobelianum*; 2; 6; 5; –0.0828; *Veronica alpina*; 0; 0; 5; 1.9455; *Veronica chamaedrys* agg.; 2; 6; 0; 0.4195

Table 2. Percentage differences between relevé groups using different data transformation and distance measures (Mann-Whitney *U* test for similarity of groups; all available combinations of relevé pairs)

Group/group		1/2		1/3		2/3	
		(%) diff.	*P* level	(%) diff.	*P* level	(%) diff.	*P* level
Presence/absence data transformation	Sorensen similarity	0.13	0.515	10.12	0.000	5.43	0.081
	Euclidean distance	16.13	0.000	21.13	0.000	0.50	0.795
No data transformation	Sorensen similarity	2.77	0.139	14.13	0.000	11.71	0.000
	Euclidean distance	3.10	0.098	13.54	0.000	11.05	0.000

variable. The adequacy of unimodal versus linear response models in ordination was assessed by running Detrended Correspondence Analysis (DCA). The length of the gradient in DCA (4.1 SD) suggested subsequent use of CCA for the investigation of partial species response to the proportion of spruce. The direct species – spruce relation was investigated by CCA which took into account significant factors as

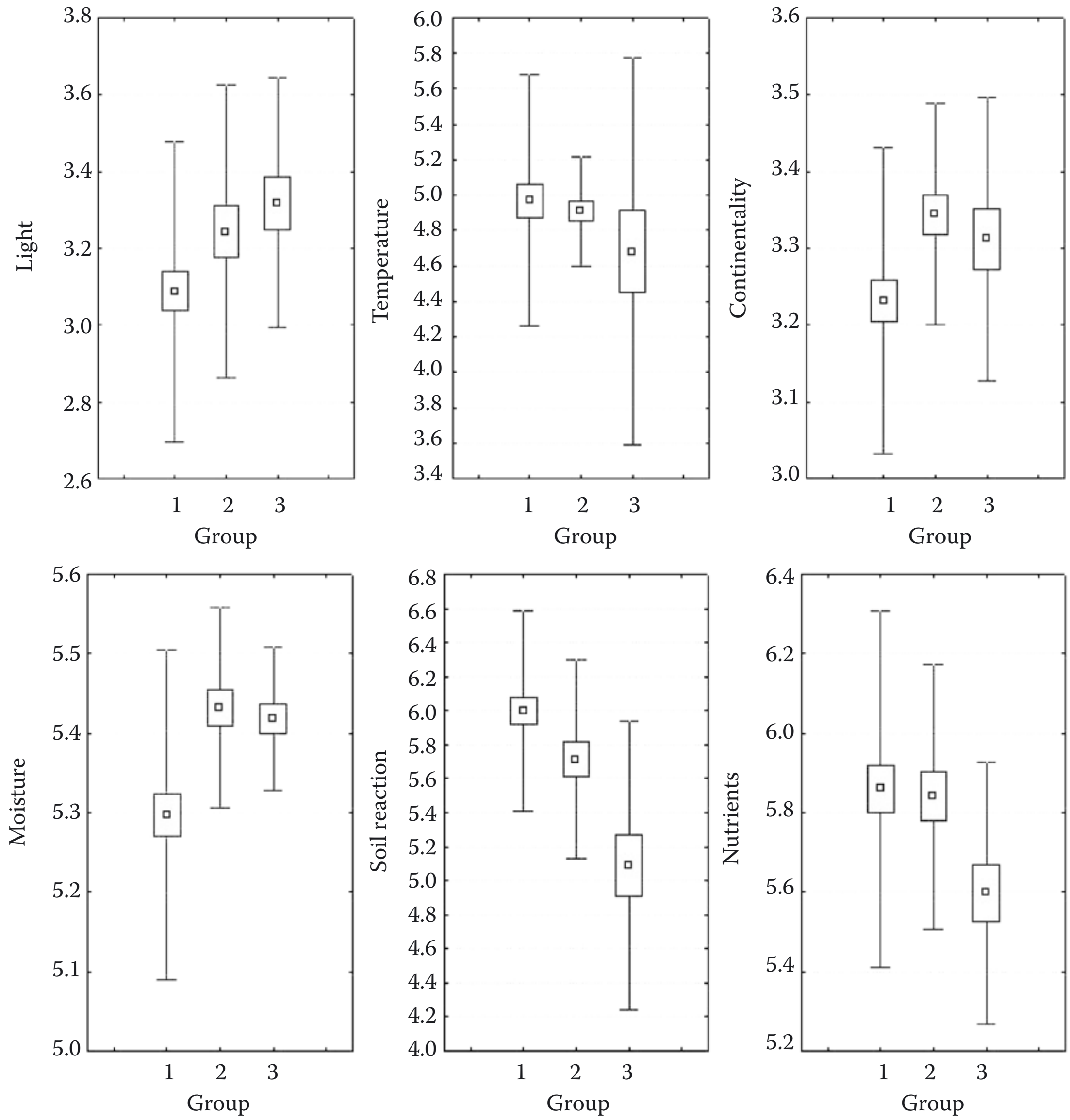

Fig. 1. Ellenberg indicator values (mean, standard error, standard deviation) for relevé groups within different proportions of *Picea abies* (1: no proportion, 2: 1–50%, 3: 50–100%)

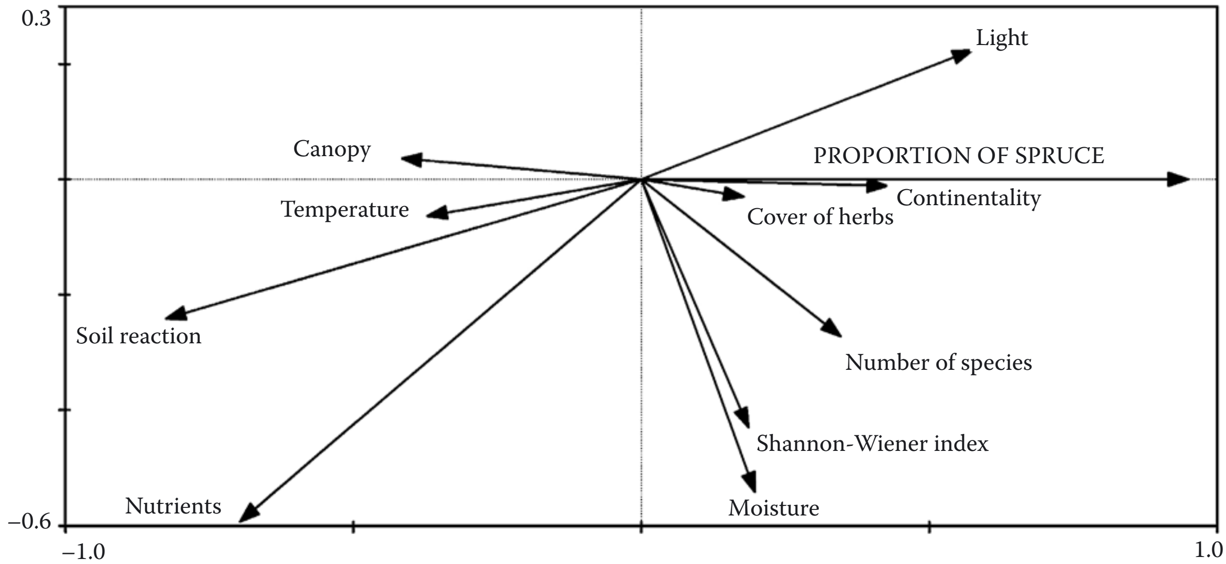

Fig. 2. Relation between the proportion of *Picea abies* and other variables including EIV (CCA with the proportion of *Picea abies* as the only environmental variable and altitude and slope as covariables); correlations among variables and the 1st axis equal to the proportion of spruce: soil reaction –0.724; nutrients –0.557; canopy –0.344; temperature –0.298; cover of herbs 0.134; Shannon-Wiener index 0.142; moisture 0.151; number of species 0.267; continentality 0.323; light 0.470

covariables. Significant factors were selected from altitude, slope and canopy using the Monte Carlo permutation test with forward manual selection and unrestricted permutation and 999 runs. The Monte Carlo test was also used for significance testing of canonical axis. Several factors (EIV, Shannon-Wiener index, number of species, cover of herb layer) were used as the supplementary variables in order to assess and investigate their relation with the proportion of spruce. In all ordination analyses the scaling on inter-species distances using biplot scaling and logarithmic data transformation was employed.

Ordination analyses were carried out in CANOCO for Windows 4.5 (Ter Braak, Šmilauer 2002) and other statistical calculations and graphical interpretation in STATISTICA 7.1 (StatSoft Inc. 2005).

RESULTS AND DISCUSSION

Comparison of designed spruce proportion relevé groups using fidelity yielded diagnostic species for each group. Concerning the number of diagnostic species the most numerous is the third relevé group with more than a half proportion of spruce (Table 1). The constancy of all present diagnostic species is increasing considerably from the first to the third group. There is also a group of species with significant fidelity in the second and in the third relevé group, which means a positive relation with any proportion of *Picea abies*. Several species of these two species groups such as *Vaccinium myrtillus*, *Avenella flexuosa*, *Soldanella montana*, *Oxalis acetosella*, *Dryopteris carthusiana* agg. are characteristic of natural spruce forests (Chytrý et al. 2002). According to the known accumulation of slowly decomposing, acid coniferous litter some of the shallow-rooted plants such as *Maianthemum bifolium, Veronica officinalis* and already mentioned *Oxalis acetosella* and *Soldanella montana* are present. *Calamagrostis arundinacea, Chrysosplenium alternifolium, Stellaria nemorum* s. str., *Gymnocarpium dryopteris, Ajuga reptans* show higher constancy without significant fidelity in spruce forests. Almost all these spruce related species are acidophytes. The increase of acidophytes caused by a higher spruce proportion is also found by the comparison of the EIV within relevé groups and correlations of variables in the CCA (Figs. 1 and 2).

The most distinguished difference in the EIV occurred in soil reaction and nutrients, showing the decrease of values in both cases. The EIV for temperature slightly decreased and the increase of values was found in light, moisture and continentality. The reduction of nitrophytes was also quite considerable and it was represented by e.g. *Alliaria petiolata*, *Stachys sylvatica*, *Myosotis sylvatica* agg., *Geranium robertianum*, *Asarum europaeum*, *Urtica dioica*, *Mercurialis perennis*. The mixed forests (the 2nd relevé group) had the highest species richness and evenness values, therefore also the highest values of Shannon-Wiener index (Fig. 3).

This elevated diversity is caused by the persistence of beech dominated forest species and on the other

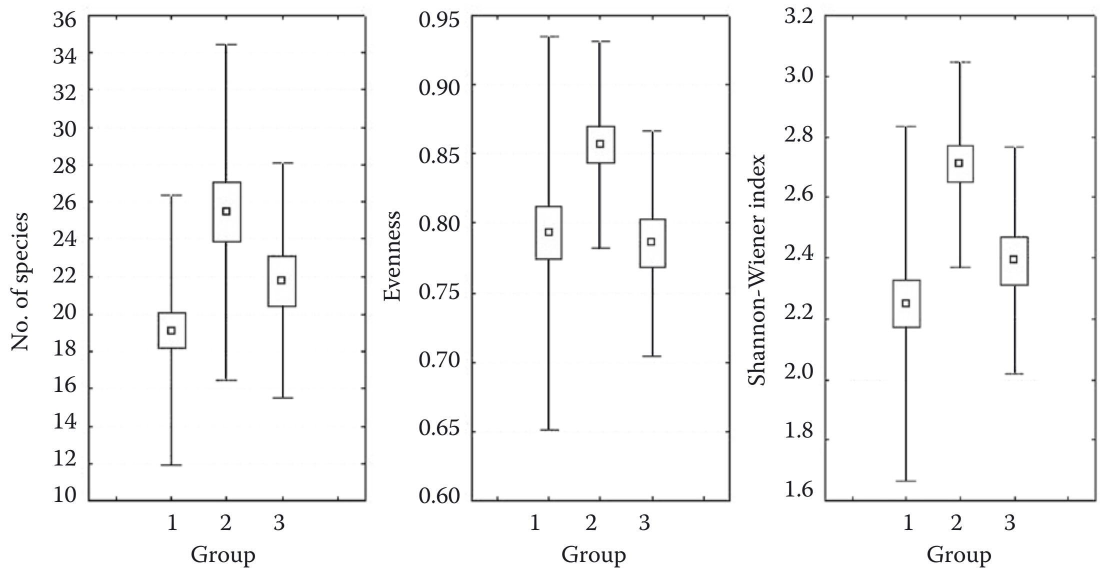

Fig. 3. Number of species, evenness and Shannon-Wiener index (mean, standard error, standard deviation) for relevé groups within different proportions of *Picea abies* (1: no proportion, 57 relevés; 2: 1–50%, 31 relevés; 3: 50–100%, 22 relevés)

hand by the higher occurrence of spruce related species. Partly in contrast to this finding, Barbier et al. (2008) concluded in the review of literature that maximum diversity was observed in pure stands, not in mixed ones, however overall it is difficult to generalize the results. The increase of diversity characteristics, e.g. richness, Shannon-Wiener index, together with the increasing proportion of *Picea abies* is also proved by the correlations in ordination analysis (Fig. 2).

The permutation test suggested to take into account the altitude (F ratio = 5.18, P value = 0.002) and the slope (F ratio = 2.79, P value = 0.002) as significant factors. Canopy was not significant (F ratio = 1.08, P value = 0.058). These two characteristics were included in CCA as covariables. The first canonical axis representing the proportion of *Picea abies* was highly significant and extracted 2.1% of compositional variance. The species response to spruce confirmed the previous results based on relevé groups. Most species with significant fidelity or clearly decreasing or increasing constancy had high positive or high negative CCA score on the horizontal axis equal to the proportion of *Picea abies* (Table 1). The equal tendency of this relation almost in all cases (decreasing constancy = negative score; increasing constancy = positive score) observed by two methods with different concept confirms the results of species responses to spruce.

Considering the similarity measuring between relevé groups the spruce has the greatest influence on the herb species composition at a proportion over 50% (Table 2). The highest percentage difference was between the first and the third group. In this case the results in all combinations of similarity indices and data transformations were statistically significant. On the other hand, in comparison with the other groups the P value was under 0.05 only in several cases. The difference between the first and the second group was observed only by using Euclidean distance and presence/absence data transformation, the difference between the second and the third group only without data transformation (using cover values). This implies that the spruce with its proportion going under 50% has a lower influence on the herb species composition than with its proportion over 50%. Less than a half proportion causes the difference in the species richness and the proportion rising over 50% causes mainly the difference in species cover. The significant difference between the first and the third group observed despite of very similar diversity values in these groups (number of species, Shannon-Wiener index, evenness) implies that this method is very objective and effective for assessment of diversity changes. This method also provides differences in the presence of concrete species, whereas the comparison of diversity values (number of species, Shannon-Wiener index, evenness) is sensitive only to the number and cover values of species and it does not matter if the species are identical or different.

The results of other authors are mainly identical, but also partly contradictory. Ewald (2000a) reported no systematic differences in herb species richness and cover within stands with various spruce proportions, though his results are relevant to the Calcareous Alps. On the acid soils from German spruce stands Bürger (1991) and Lücke and Schmidt (1997) found greater richness, however because of the presence of nitrophilous disturbance indicators. On the contrary, the results of Fajmonová (1974) and Šomšák (2003) in the soil conditions similar to our studied area showed the negative effect of spruce on the species richness, decrease of mesophilous herbs and increase of acidophytes. Ewald (2000b) also reported from the Calcareous Bavarian Alps the occurrence of acid indicators and richness of coniferous forest species favoured by spruce canopies. Characteristic species of deciduous forests and nitrogen indicators were not affected, only shallow-rooted vascular plants responded positively to a coniferous canopy and most vascular plants were resilient. Teuscher (1985) reported from Swiss spruce stands a reduction of mesophilous herbs and an increase of acidophytes, resulting in lower richness than in hardwood stands. The negative effect of *Picea abies* on diversity and cover of vascular plants was also found by Simmons and Buckley (1992). Our results particularly showed that spruce favoured acidophytes and inhibited nitrophytes, partly mesophytes. The effect of soil acidification caused by spruce and other coniferous species is well known and was reported also by Augusto et al. (2002) in literature review. By this interchange of acidophilous and nitrophilous plants the richness remained untouched in general, however the species composition was quite considerably affected.

CONCLUSIONS

The increase in the spruce proportion caused higher occurrence of acid indicators, especially of the species characteristic of natural spruce forests and shallow-rooted plants. Spruce negatively affects particularly nitrophytes and partly mesophytes which are typical of semi-nitrophilous beech dominated forests. The mixed stands composed of the natural tree species and less than a half proportion of *Picea abies* had higher diversity. In this mixed relevé group the highest species richness, evenness and Shannon-Wiener index were reached. This is caused by the persistence of most species and occurrence of some new spruce related ones. The largest difference in the herb layer species composition was found between the natural stands and the spruce dominated stands. According to all these results it is suggested not to grow pure spruce or spruce dominant forests to avoid the loss of diversity in plant communities. Although the mature stands with a high proportion of *Picea abies* did not have lower diversity than natural stands, the natural species composition is affected and changed quite considerably.

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