Long-term vegetation dynamics in the Šumava Mts. natural spruce-fir-beech forests

Pavel Šamonil · Tomáš Vrška

Abstract In 1972(74)–1996(98), repeated phytocoenological surveys of natural mixed forest remainders were made on permanent plots in the Šumava Mts. in the south-western part of the Czech Republic. The surveys were made in localities with subsoils poor in nutrients (Boubín-Milešice—27 plots) and in a locality with nutrient-rich subsoil (Stožec—15 plots). Vegetation dynamics were studied according to the year of measurement and the nutrient capacity of the geological bedrock. We used the indices of floristic similarity, the calculation of plant communities' characteristics (Shannon–Wiener's index, equitability index), the calculation of taxa characteristics (fidelity, average cover, constancy) and multivariate ordination analyses—indirect (DCA) and direct (CCA). Changes in environmental conditions were studied between the years of measurement and between the localities using bioindication—by the calculation of Ellenberg indicator values (EIV) for plant communities. Over 24 years both the nutrient-poor site and the nutrient-rich site showed a considerable reduction in the tree layer cover and conversely the advancement of shrub layers. The coverage degree of dominants in the main tree layer (*Fagus sylvatica*, *Picea abies* and *Abies alba*) markedly decreased. *Abies alba* also exhibited a pronounced drop in constancy. On the other hand, the lower tree layer and shrub layers in Boubín-Milešice exhibited a distinctive invasion of *Fagus sylvatica*. An increase in the frequency of *Sorbus aucuparia* and a decrease in the frequency of *Ulmus glabra* were determined too. Herb layer changes were highly significant between the 1970s and the 1990s with qualitative changes being greater than quantitative changes. The number of species and Shannon–Wiener's index increased. A significant difference was recorded between the nutrient-poor and the nutrient-rich sites in the values of the quantitative similarity of relevés with other differences being insignificant. The nutrient-poor sites exhibited herb layer homogenisation. A significant increase of EIV for light was found on both site types. The changes in phytocoenoses were interpreted partly as developmental trends (caused by indirect impact of man—e.g. fluctuations in game populations since the 18th century, the impact of air pollution); partly as cyclical changes connected with the developmental cycle of the natural temperate forest.

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Introduction

Long-term monitoring of vegetation can reveal not only trends in development of plant communities, but also changes of environment and energy flows in whole ecosystems. One must say that the vegetation of Central Europe has been affected by man for centuries. Original forest stands dominated by *Fagus sylvatica, Abies alba* and *Picea abies* (Ellenberg 1996; Neuhäuslová et al. 1998; Bohn et al. 2000; Pokorný 2002) have been almost completely changed in particular to even-aged spruce monocultures of ambiguous genetic origin (Nožička 1957). Moreover, all forests of Central Europe have been affected by man indirectly (e.g. air pollution).

Long-term monitoring of vegetation faces many difficulties. Vague localization of monitoring plots in the past (e.g. Hédl 2004a) or direct impact of man are the most weighty problems. Direct human impact can introduce abrupt and unexpected changes of vegetation, very variable in time and space (e.g. Pokorný 2005). Consequently, results of monitoring from sites strongly affected by man are often very different each other, having rather local validity. The invasion of some plant species in ecologically unstable forest stands has often been described as a direct effect of management changes, including recent elimination of management (Marigo et al. 2000; Sádlo et al. 2005; Střeštík et Šamonil 2006). Most of the monitoring plots are at least slightly affected by man even today (e.g. Falkengren-Grerup and Tyler 1991; Viewegh 1994; Vacek and Matějka 2003; Hédl 2004a). Also the historical human impact is very important—it has considerable persistence and it can be apparent even after several hundred years.

Indirect human impact has a more even character; therefore the results of monitoring in such areas are usually comparable in a broader scale. Many studies from Central Europe demonstrate rapid vegetation changes in the second half of the 20th century. The decrease of species diversity has been described in several localities (Vacek and Lepš 1991, 1992; Ambros and Míchal 1992; Viewegh 1994; Vacek et al. 1996; Hédl 2004b). This is generally interpreted as the impact of industrial air pollution (Moldan and Schnoor 1992; Moldan and Hak 2007). Other studies discover soil acidification processes (Falkengren-Grerup 1990; Ambros 1994; Hédl et al. 2004), which are typically explained by a high level of industrial air pollution deposits. These trends, though, are less distinct at the end of the 20th century and in less exposed areas (Vacek and Matějka 2003; Wild et al. 2004).

The study of forest remnants more or less unaffected by both direct and indirect human impact serves as an important reference point for any long-term vegetation monitoring. Of course, there is serious lack of such localities and thus a lack of studies that are carried out in densely populated Central Europe (Průša 1985; Ujházy et al. 2005). The process of auto-regulation, described, e.g. in the theory of the "small developmental cycle" (Otto 1994; Korpel 1995), is the significant feature of these natural forests.

The largest forested area in Central Europe—the Šumava Mountains on the Czech–German–Austrian border—was selected for our study. There are no important sources of air pollution in the region. Three natural forest reserves were repeatedly investigated in the 1970s and 1990s. The research would like to answer three major questions: (i) what is the vegetation dynamics of the best natural spruce-fir-beech forest remnants on Šumava over 24 years? (ii) what is the dynamics of the environment of these natural forests over 24 years? and (iii) what are the differences in the dynamics of vegetation and environment between nutrient rich and nutrient poor localities?

Materials and methods

Study area

The inquiries were made in the Boubínský Virgin Forest (Boubín) National Nature Reserve, coordinates—48° 58′ 30″ N, 13° 48′ 50″ E, the Milešický Virgin Forest (Milešice) Nature Reserve, coordinates—48° 59′ 06″ N, 13° 50′ 22″ E and in the Stožec-Medvědice (Stožec) Natural Monument, coordinates—48° 52′ 45″ N, 13° 50′ 20″ E. All three localities are situated within the Šumava National Park and Protected Landscape Area which can be found in the extensive mountain range of the same name (Fig. 1). The Boubín has never been subject to timber harvesting and can therefore be considered a primary forest (Vrška et al. 2001b; Vrška and Hort 2003). The Mileše and the Stožec were in the past partly affected by haulage of lying decayed wood and
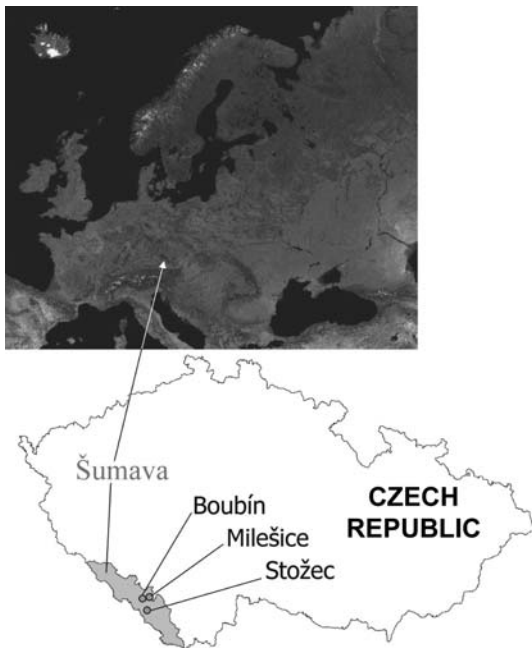
Fig. 1 Study area location. Grey shading: Šumava National Park and Protected Landscape Area. Three studied forest reserves are shown

by incidental felling; since 1930(32) they have also been left to spontaneous development (Vrška et al. 2001a).

The Stožec locality represents nutrient-rich sites, while Boubín and Milešice represent nutrient-poor sites. The geological bedrock of the Stožec elevation (1065 m a.s.l.) is melanocratic, medium-grained, porphyric amphibole-biotitic granite to granodiorite. Prevailing soils (Anonymous 1998; Driessen et al. 2001; Michéli et al. 2006) are Endoskeletic Cambisol and Episkeletic Cambisol. In contrast, the geological bedrock of Boubín and Milešice is formed of biotitic and cordierite-biotitic migmatite and silimanite-biotitic migmatitized paragneiss (Anonymous 1996). Soils prevailing in Boubín-Milešice are Umbric Podzol (Entic and Endoskeletic), Placic Podzol and Umbric Podzol (Entic). Endoleptic Cambisol (Endoskeletic and Dystric) can be found only in lower elevations. The more water-affected Boubín exhibits also local presence of Ombric Histosol and Arenic Gleysol (Humic and Eutric). According to the Braun-Blanquet approach (Braun-Blanquet 1921; Ellenberg 1996; Neuhäuslová 2001), plant communities can be most often classified in the *Calamagrostio-villosae*

Fagetum Mikyška 1972 and *Calamagrostio villosae-Piceetum* Hartmann in Hartmann and Jahn 1967 associations.

Data sampling

Data were collected in the field in the form of circular phytosociological relevés from permanent sample plots, each of 25 m in diameter. The plots were not further divided. Distribution of the plots was as follows: 25 plots in Boubín, 15 plots in Stožec and 2 plots in Milešice. Placement of the plots was chosen in the 1970s in such a way that the plots covered the ecological gradients and were therefore representative of the localities (Průša 1985). The original inquiries were made in Boubín and Milešice in 1972 and in Stožec in 1974 (Průša 1985). The permanent sampling plots were unambiguously localized in the field (accuracy of 1 m) with the use of a tree map on a scale of 1:1,000, which is a component part of the complex inquiry in all localities (Průša 1985; Vrška et al. 2001a, b). In this way, possible bias due to inaccurate relocation or incorrectly established size of plots was eliminated (cf. Chytrý 2001; Hédl 2004a; van der Maarel 2005). A recurrent survey was made in all localities after 24 years, always in July. The vegetation was recorded in the 1990s using the 11-member Zlatník (1953) scale (adjusted Braun-Blanquet scale), in the 1970s using the coarser 7-member Braun-Blanquet scale (Braun-Blanquet 1964). The vertical structure of phytocoenoses was classified as follows (cf. Hennekens and Schaminée 2001): (1) Tree layer—high (dominant and co-dominant trees); (2) Tree layer—middle (sub-dominant trees, 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 height ranging from 0.20 m to 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. This numerical marking of the vegetation layers was used in all results. Tree layers (1, 2, 3) and shrub layers (4, 5) were not differentiated in Stožec in 1974. Seedlings, mosses and lichens were not studied.

The nomenclature of vascular plants was unified according to Kubát (2002).

Data analysis

The data sets from Boubín and Milešice were merged
and assessed together—Boubín-Milešice. The reason
was in the similarity of environmental, particularly
soil, conditions—nutrient-poor subsoil. Results from
the nutrient-poor sites were compared with results
from the nutrient-rich sites—Stožec.

Vegetation dynamics were studied according to
the year of measurement and the nutrient capacity of
geological bedrock. We used the indices of floristic
similarity, the calculation of plant communities'
characteristics (Shannon–Wiener's index, equitability
index), the calculation of taxa characteristics (fidelity,
average cover, constancy) and we used multivariate
ordination analyses. The new data were converted
back to Braun-Blanquet (1964) scale. Tree layers (1,
2, 3) and shrub layers (4, 5) in the Stožec locality in
1990s were merged in the analyses on the basis of
a random overlap of fixed covers, e.g. summed
cover of two species was calculated as $c_s = c_x +
(100 - c_x) \times c_y$, where c_s is the summed cover a c_x
and c_y are percentage covers of species x and y,
respectively (Tichý and Jason 2006). It provided the
comparison with the data collected in 1970s.

The qualitative Jaccard (1901) index of floristic
similarity and its quantitative modification (Gleason
1920) were used to assess relevés between the years
of measurement. Taxon fidelity, i.e. the concentration
of species occurrences in units (e.g. in vegetation
unit, in period of time), was measured using the phi
coefficient (Sokal and Rohlf 1995; Chytrý et al.
2002). The phi coefficient (Φ) of association between
the species and units is a statistical measure of
association between two categories, which can be
used as a measure of fidelity. The phi coefficient
was calculated according to the formula $\Phi =
(N \cdot n_p - n \cdot N_p)/\sqrt{\{n \cdot N_p \cdot (N - n) \cdot (N - N_p)\}}$,
where N is the number of relevés in the data set, N_p is
the number of relevés in the target unit (this unit
means the period of time—1970s or 1990s), n is the
number of occurrences of the species in the data set
and n_p is the number of occurrences of the species in
the target unit. The phi coefficient values range from
–1 to 1, but they are multiplied by 100 on calculation.
The highest phi value of 1 (resp. of 100) is achieved
if the species occurs in all relevés of the unit and is
absent elsewhere. Shannon–Wiener's diversity index
(H') was calculated for the herb layer of vegetation

according to the formula $H' = -\Sigma p_i ln p_i$ where p_i is
the relative proportion of the ith species (e.g. Begon
et al. 1990; Tichý and Jason 2006). The index is
increased either by having more unique species, or by
having greater evenness. Shannon's equitability
index (E_H, also called evenness) proposed by Pielou
(1975) was calculated according to the formula
$E_H = H'/H'_{max} = H'/lnS$, where S is the number of
species in the relevé. The equitability index ranges
from 0 to 1 and is a measure of how evenly the numbers
of the different species observed are distributed. The
value $E_H = 1$ represents complete evenness. The
software Juice 6.2 (Tichý 2002; Tichý and Jason
2006) was used for the calculation of plant communi-
ties and taxa characteristics. These data sets were
tested for the homogeneity of dispersions (Bartlet's
test). The statistical significance of variables was
subsequently tested by T-tests and two-way ANOVA
analysis with the application of Statistica 6.0 (StatSoft
2003) and Unistat 5.1 (Anonymous 2000) software.
The critical level of significance was set at $\alpha = 0.05$.

The ordination analyses (Table 1) were processed
in Canoco for Windows 4.5 (ter Braak and Šmilauer
2002; Lepš and Šmilauer 2003). We used the percent
covers of taxa according to the degrees of Braun-
Blanquet (1964) scale in analyses. These data were
centred and standardized according to the species and
samples and they were not transformed. Rare species
were not removed. Indirect ordination was at all times
made by using DCA—detrended correspondence
analysis (cf. Peet et al. 1987). Direct ordination
analysis was selected according to the homogeneity
of data (particularly according to the length of the
first variability gradient in DCA analysis—Lepš and
Šmilauer 2003) for which purpose a canonical
correspondence analysis (CCA) was chosen. We used
the environmental, covariable (Table 1) and supple-
mentary data in analyses. As the supplementary
variable the years of measurement were used in
indirect ordination analyses. By adjustment of direct
ordination analyses (Table 1) we removed the vari-
ability between plots and we tested the differences on
plots in time. Statistical significance of variables was
tested by the Monte Carlo test with the use of a total
number of 4,999 permutations.

Changes in environmental conditions were studied
between the years of measurement and between the
localities using bioindication—by the calculation of
Ellenberg indicator values (EIV) for plant

Table 1 Settings of ordination analyses, $N_{relevés}$ —number of relevés, $N_{species}$—number of species, DCA—Detrended Correspondence Analysis, CCA—Canonical Correspondence Analysis; vegetation layers: 1 Tree layer—high, 2 Tree layer—middle, 3 Tree layer—low, 4 Shrub layer—high, 5 Shrub layer—low, 6 Herb layer

Analysis number	Locality	Analyzed data	Analysis type	$N_{relevés}$	$N_{species}$	Environmental data	Covariable data
1	Boubín-Milešice	Herb layer (6)	DCA	50	78	/	/
2	Stožec	Herb layer (6)		30	50	/	/
3	Boubín-Milešice	All layers (1, 2, 3, 4, 5, 6)	CCA	50	101	Year	Plot
4		Herb layer (6)			78		
5		Tree and shrub layers (1, 2, 3, 4, 5)			23		
6	Stožec	All layers (1+2+3, 4+5, 6)		30	78		
7		Herb layer (6)			50		
8		Tree and shrub layers (1+2+3, 4+5)			28		

communities. These values are empirically found and they reflect the relation of taxon to environmental conditions in a broad region. The relation of a concrete taxon to light, temperature, continentality, moisture, soil reaction and soil nitrogen is normally expressed by a nine-member scale. We used EIVs of taxa according to Ellenberg et al. (1992). The possibility of the indirect assessment of site conditions by means of EIVs was verified in a number of cases with limitations of the approach pointed out: e.g. relation of EIVs to measured soil parameters (Hill and Carey 1997; Wamelink et al. 2002, 2005), experimental reaction of plant species with different EIVs for soil N and soil reaction to addition nitrogen or acids (van Dobben et al. 1999), sensitivity of EIVs to the completeness of relevés (Ewald 2003; Klimeš 1987), bias of EIVs by the effect of vegetation type (Smart and Scott 2004). The changes of EIVs in relevés can also be a fragment of the increasing species diversity (Schaeffers and Sýkora 2000; Chytrý et al. 2003) as it is obvious that the response of other recorded taxa to ecological factors is likely to be modest rather than extreme because the group is numerous. In order to eliminate this effect, we calculated the average of EIVs for relevés according to methodology developed by Schaffers and Sýkora (2000) (see also Chytrý et al. 2003) using negative weighting by the number of species assigned to particular values on the Ellenberg scale.

Outputs might have been adversely affected by the fact that the measurements do not provide a continual time series and it is therefore difficult to distinguish the short-term and seasonal changes from the long-term trends.

Results

The dynamics of tree species

Changes in the tree layers are highly significant between the 1970s and the 1990s (Table 2). In the course of 24 years, the nutrient-poor site (Boubín-Milešice), as well as the nutrient-rich site (Stožec) showed a marked reduction of tree layer cover and conversely a development of shrub layers (Table 3, Figs. 2–5). Although the cover of *Fagus sylvatica* and *Picea abies* is decreasing, the species' constancy in the tree layer is stable. The decreased cover is more distinctive in *Picea abies*. In contrast to *Picea abies* and *Fagus sylvatica*, the cover decrease of *Abies alba* is accompanied by an expressive decrease of the species' constancy (Table 3). Both of the sites recorded a significant increase of *Sorbus aucuparia* and a general increase of the species diversity (*sensu* Whittaker 1972) in both tree- and shrub layers (Table 3).

The most obvious cover decrease on the acidic sites in Boubín-Milešice was observed in the dominant *Picea abies* whose degree of coverage is decreasing both in the high (1) and in the middle (2) tree layers (Fig. 3). *Abies alba* that was in the 1970s present in the high tree layer on 9 plots at a cover of 13% was in the 1990s not recorded at all. The cover decrease of *Fagus sylvatica* was not so steep—especially in the middle tree layer. On the other hand the invasion of *Fagus sylvatica* in the low tree layer (3) and in the shrub layers (4, 5) in the 1990s is very pronounced (Figs. 2, 3). The cover of *Picea abies*, *Abies alba*, *Acer pseudoplatanus*,

Table 2 The results of direct ordination analyses (CCA, see Table 1). Variance of data sets explained by year of measurement, *F*-test statistics, *P*-level of significance (Monte Carlo permutation test), explained variability represent the partial effect of environmental variable (year of measurement) in species data

Locality	Analysis number (Table 1)	Layer	Explained variability (%)	*F*	*P*
Boubín-Milešice	3	All	11.9	3.12	0.0002
	4	Herb	7.5	1.86	0.0490
	5	Tree + shrub	24.7	7.22	0.0002
Stožec	6	All	17.5	2.96	0.0012
	7	Herb	15.9	2.65	0.0020
	8	Tree + shrub	14.9	2.46	0.0256

Sambucus racemosa or *Sorbus aucuparia* in the shrub layers was increasing in the 1990s too, but their cover was expressively lower.

As compared with the Boubín-Milešice site, the nutrient-rich Stožec site showed a slightly decreased representation of *Abies alba* in the tree layers and a markedly decreased cover of *Ulmus glabra* whose occurrence was not recorded in Boubín-Milešice. The share of *Fagus sylvatica* and *Picea abies* in the shrub layers was more equalized in the Stožec locality in the 1990s. (Fig. 5). No occurrence of *Abies alba* in the lower tree layer was recorded in Boubín-Milešice in the 1970s or the 1990s.

The dynamics of the herb layer

The main direction of herb layer variability corresponds with the changes of soil reaction in both site types (Fig. 6–9). The Spearman correlation coefficient (*S*) between the scores of taxa on the first non-canonical (horizontal) axis and EIV for soil reaction is *S* = 0.63 in Boubín-Milešice, in Stožec with *S* = 0.41. The main direction of the variability of herbaceous undergrowth in Boubín-Milešice also corresponds well with EIV changes for soil nitrogen (*S* = 0.61). The second non-canonical (vertical) axis copies EIV changes for moisture (*S* = 0.49 in Boubín-Milešice, *S* = 0.51 in Stožec).

Herb layer changes between the 1970s and the 1990s are highly significant (Table 2) with qualitative changes being greater than quantitative changes (Table 4). Increased values were recorded both in the number of species and in Shannon–Wiener's index (Table 5, Fig. 10). The highest fidelity values in the 1990s were recorded in *Rubus idaeus, Circaea*

alpina, Actaea spicata, Gymnocarpium dryopteris and *Calamagrostis villosa* (Table 3, Figs. 2, 4). A number of taxa exhibited distinctive cover changes, which are most pronounced in *Calamagrostis villosa* (change in maximum cover + 69%) and in *Rubus idaeus* (change in maximum cover + 41%).

No significant difference was found between the nutrient-poor (Boubín-Milešice) and the nutrient-rich (Stožec) sites in the number of species, qualitative similarity or Shannon–Wiener's index (Tables 4, 5). Higher—although still insignificant—differences were found between the localities in the development of equitability. The values of quantitative similarity of relevés between the 1970s and the 1990s significantly differed in the trophic status of the sites (Boubín-Milešice versus Stožec) (Table 4). A higher quantitative similarity between relevés from the 1970s and the 1990s was recorded on the nutrient-poor sites of Boubín-Milešice. The recurrent phytocoenological relevés from Boubín-Milešice are closer to each other in two main gradients and are therefore more similar (Fig. 6). Phytocoenoses on the most humid sites—with Arenic Gleysol (Humic and Eutric) and Ombric Histosol—exhibit in 1996 a shift upwards, towards a lower moisture demand. In other cases the movement is in the opposite direction. No herb layer "homogenization" in the main directions of variability was observed in Stožec (Fig. 8) where a shift of the entire set of relevés could be observed rather along the vertical axis.

The dynamics of environmental conditions

A significant increase of EIV for light was determined by phytoindication on both types of site.

Table 3 List of all species divided by vegetation layers and years of measurement; species are ordered according to their constancy
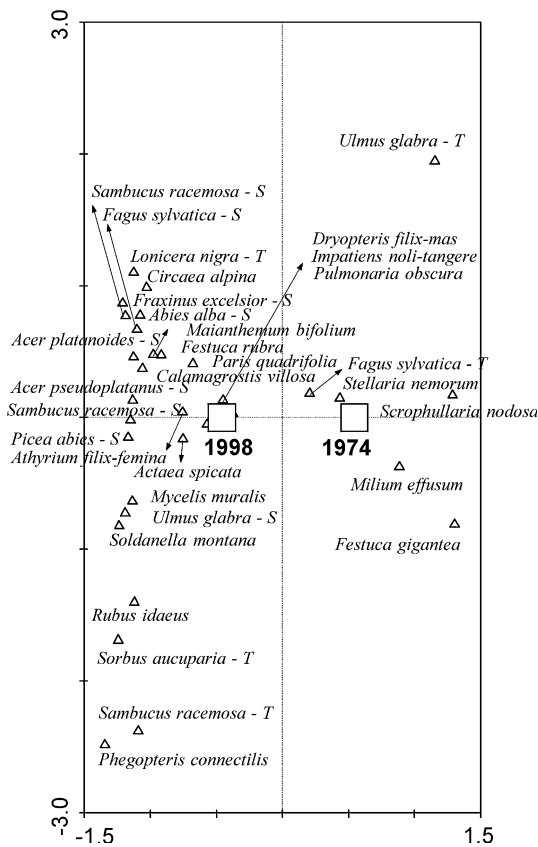
Year of measurement	70s			90s		
Number of relevés	40	40	40	40	40	40
Tree layers	Const	Cover.	Fidel.	Const.	Cover.	Fidel.
Fagus sylvatica	78	38	–	85	35	9.6
Picea abies	78	38	–	85	23	9.6
Abies alba	32	15	27.5	10	10	–
Acer pseudoplatanus	12	18	–	18	8	7
Ulmus glabra	12	43	–	15	3	3.6
Sorbus aucuparia	.	.	–	25	3	37.8
Sambucus racemosa	.	.	–	8	6	19.7
Lonicera nigra	.	.	–	8	6	19.7
Acer platanoides	.	.	–	5	14	16
Ribes nigrum	.	.	–	2	3	11.3
Shrub layers						
Fagus sylvatica	22	4	–	78	6	55
Picea abies	20	2	–	72	3	52.6
Sorbus aucuparia	10	2	–	48	2	41.4
Abies alba	18	1	–	38	1	22.4
Acer pseudoplatanus	5	1	–	48	2	48.3
Lonicera nigra	5	2	–	8	6	5.2
Ulmus glabra	.	.	–	28	3	39.9
Sambucus racemosa	.	.	–	12	1	25.8
Acer platanoides	.	.	–	10	1	22.9
Fraxinus excelsior	.	.	–	10	2	22.9
Daphne mezereum	.	.	–	2	1	11.3
Ribes nigrum	.	.	–	2	2	11.3
Betula pendula	.	.	–	2	1	11.3
Herb layer						
Oxalis acetosella	88	8	–	92	7	8.3
Stellaria nemorum	70	16	–	78	8	8.5
Dryopteris dilatata	68	8	–	75	9	8.3

Year of measurement	70s			90s		
Number of species	40	40	40	40	40	40
Herb layer—continuation	Const.	Cover.	Fidel.	Const.	Cover.	Fidel.
Rubus idaeus	8	2	–	72	5	66.3
Actaea spicata	8	1	–	35	2	33.6
Caltha palustris	8	2	–	18	2	15.1
Fragaria vesca	8	2	–	15	2	11.9
Equisetum sylvaticum	8	2	–	15	3	11.9
Avenella flexuosa	8	15	–	10	26	4.4
Tephroseris crispa	8	2	11.5	2	2	–
Deschampsia cespitosa	8	14	11.5	2	2	–
Circaea alpina	5	2	–	35	3	37.5
Paris quadrifolia	5	2	–	18	2	19.8
Viola reichenbachiana	5	3	–	8	2	5.2
Ranunculus lanuginosus	5	8	–	5	2	–
Nardus stricta	5	20	–	5	8	–
Rumex acetosella	5	1	–	5	2	–
Festuca gigantea	5	3	16	.		–
Scrophullaria nodosa	5	2	16	.		–
Circaea x intermedia	5	2	16	.		–
Agrostis capilaris	5	8	16	.		–
Agrostis stolonifera	2	3	–	12	2	19
Carex leporina	2	1	–	8	3	11.5
Juncus effusus	2	1	–	5	2	6.6
Cicerbita alpina	2	1	–	5	2	6.6
Poa trivialis	2	3	–	5	2	6.6
Blechnum spicant	2	2	–	5	2	6.6
Luzula luzuloides	2	2	–	5	13	6.6
Crepis paludosa	2	2	–	2	1	–
Mercurialis perennis	2	13	–	2	2	–
Polygonatum verticillatum	2	3	–	2	3	–

Table 3 continued

Year of measurement

Species	70s			90s		
Petasites albus	60	34	–	70	27	10.5
Athyrium filix-femina	52	2	–	68	6	15.3
Impatiens noli-tangere	48	13	–	70	15	22.9
Senecio ovatus	45	6	–	65	4	20.1
Galium odoratum	42	6	–	42	6	–
Gymnocarpium dryopteris	40	10	–	68	5	27.6
Calamagrostis villosa	32	14	–	58	21	25.1
Milium effusum	32	13	–	45	2	12.8
Urtica dioica	30	14	–	45	9	15.5
Luzula sylvatica	30	4	–	38	8	7.9
Dryopteris filix-mas	28	3	–	48	7	20.7
Vaccinium myrtillus	25	7	–	45	9	21
Homogyne alpina	25	2	–	28	2	2.8
Soldanella montana	25	2	2.9	22	2	–
Galeobdolon montanum	25	9	2.9	22	2	–
Galeobdolon luteum	22	6	–	32	7	11.2
Chaerophyllum hirsutum	22	10	–	22	10	–
Myosotis palustris agg.	20	4	–	25	2	6
Prenanthes purpurea	20	2	10.2	12	1	–
Maianthemum bifolium	18	2	–	18	4	–
Lycopodium annotinum	15	4	–	28	11	15.3
Sanicula europaea	15	4	–	20	5	6.6
Cardamine amara	15	4	–	20	3	6.6
Myosotis sylvatica	15	2	3.6	12	2	–
Geranium robertianum	12	4	–	20	6	10.2
Chrysosplenium alternifolium	12	2	–	18	4	7
Festuca altissima	12	3	–	15	4	3.6

Year of measurement

Species	70s			90s		
Lysimachia nemorum	2	3	–	2	3	–
Carex remota	2	3	–	2	13	–
Carex canescens	2	3	–	2	2	–
Carex pilulifera	2	1	–	2	3	–
Moehringia trinervia	2	2	11.3	.	.	
Anemone nemorosa	2	1	11.3	.	.	
Festuca rubra	2	1	11.3	.	.	
Carex pallescens	2	1	11.3	.	.	
Mycelis muralis	.	.	–	18	1	31
Festuca rubra	.	.	–	8	6	19.7
Epilobium montanum	.	.	–	8	2	19.7
Brachypodium sylvaticum	.	.	–	8	2	19.7
Galium pumillum	.	.	–	5	2	16
Carex nigra	.	.	–	5	2	16
Platanthera chlorantha	.	.	–	2	2	11.3
Hieracium murorum	.	.	–	2	1	11.3
Ranunculus acris	.	.	–	2	13	11.3
Lysimachia nummularia	.	.	–	2	3	11.3
Melampyrum pratense	.	.	–	2	2	11.3
Carex contigua	.	.	–	2	2	11.3
Luzula divulgata	.	.	–	2	2	11.3
Juncus articulatus	.	.	–	2	1	11.3
Stellaria alsine	.	.	–	2	3	11.3
Carex sylvatica	.	.	–	2	2	11.3
Prunella vulgaris	.	.	–	2	1	11.3
Cirsium heterophyllum	.	.	–	2	1	11.3
Epilobium angustifolium	.	.	–	2	3	11.3

Table 3 continued

Year of measurement	70s			90s		
	const	cover	fidel	const	cover	fidel
Ranunculus repens	12	5	–	15	3.6	
Pulmonaria obscura	10	2	–	28	22.4	
Ajuga reptans	10	2	–	20	14	
Phegopteris connectilis	10	2	–	10	–	
Poa nemoralis	.	.	.	2	1	11.3
Dentaria enneaphyllos	.	.	.	2	1	11.3
Ranunculus aconitifolius	.	.	.	2	2	11.3
Listera cordata	.	.	.	2	2	11.3

Number of plots: 1970s = 40, 1990s = 40

Parameters: const.—species constancy (%), cover.—species average cover (%), fidel.—species fidelity (phi coefficient)

Negative values of fidelity are not shown (symbol "–")

Fig. 2 Vegetation changes between two periods of measurement in nutrient-poor sites—Boubín-Milešice, with identification of plots as covariable data; CCA analysis of all vegetation layers (Table 1, analysis 3). Species with fit in analysis ≥4% are shown; numbers 1–5 denote layers of tree species (see text)

Fig. 3 Changes in cover of main tree species in vertical structure of vegetation in nutrient-poor sites—Boubín-Milešice. Degrees of cover in relevés correspond with 7-member Braun-Blanquet (1964) scale. P—*Picea abies*, F—*Fagus sylvatica*, A—*Abies alba*; numbers 1–5 denote layers of tree species (see text); numbers 72 and 96 denote year of measurement (1972 and 1996). Number of plots: 1972 = 25, 1996 = 25. Full squares—arithmetic mean, whiskers—confidence interval

(Table 5, Fig. 10). Other assessed characteristics did not show any significant changes over time.

In contrast, expected significant differences were found between the localities in soil reaction and in soil nitrogen. The localities also markedly differed in temperature. No significant changes were found in

Fig. 4 Vegetation changes between two periods of measurement in nutrient-rich sites—Stožec, with identification of plots as covariable data; CCA analysis of all vegetation layers (Table 1, analysis 6). Species with fit in analysis ≥ 6% are shown; T—tree layers, S—shrub layers (see text)

moisture (Table 5, Fig. 10). Opposite but statistically insignificant trends were observed between the nutrient-rich and the nutrient-poor sites in the development of temperature, moisture and soil nitrogen (Fig. 10). In relation with the above described homogenization of herb layer in Boubín-Milešice in the main gradients of variability in the 1990s (Fig. 6), the changes of EIV were varied, too, according to local site conditions. The drop in EIV for nitrogen was greatest on somewhat more trophic sites with EIVs for nitrogen conversely increased on entirely acidic sites (Ombric Histosols). A similar course can also be observed in the case of EIV for soil reaction. Variability of EIV for soil reaction and nitrogen decreased in Boubín-Milešice in 1996. Lower variability of EIV for moisture was recorded in Stožec in 1998 (Fig. 10).
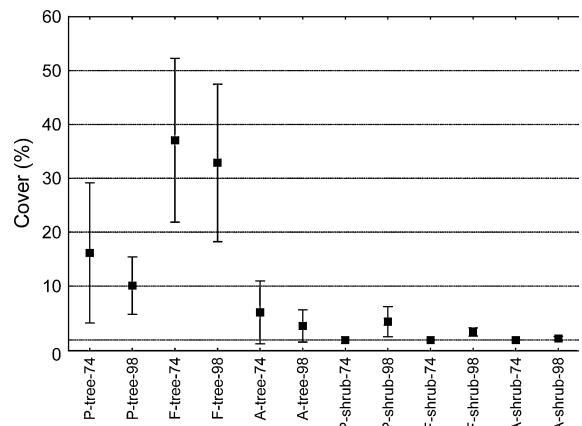
Fig. 5 Changes in covers of main tree species in vertical structure of vegetation in nutrient-rich sites—Stožec. Degrees of cover in relevés correspond with 7-member Braun-Blanquet (1964) scale. P—*Picea abies*, F—*Fagus sylvatica*, A—*Abies alba*; Tree—tree layers, Shrub—shrub layers (see text); numbers 74 and 98 denote year of measurement (1974 and 1998). Number of plots: 1974 = 15, 1998 = 15. Full squares—arithmetic mean, whiskers—confidence interval
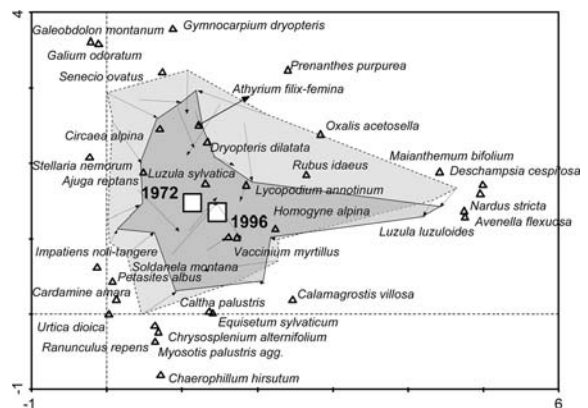

Fig. 6 The first two main directions of variance of the herb layer in nutrient-poor sites (Boubín-Milešice) as plotted at horizontal and vertical axes respectively, DCA analysis (Table 1, analysis 1). Supplementary variable is year of measurement. Species with weight in analysis ≥ 2% are shown. Grey polygons outline the area occupied by the plots of the respective periods (light grey—1972, dark grey—1996)

Discussion
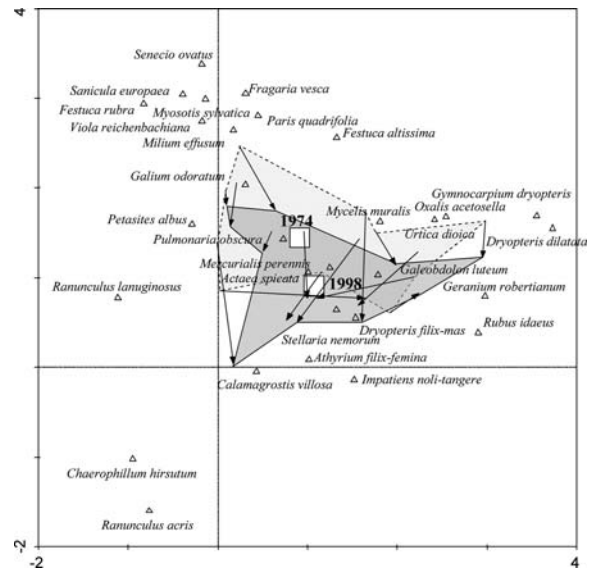
The dynamics of tree species

In the period between 1972(4) and 1996(8), the development of tree layers in the remainders of natural Šumava forests on sites both rich and poor in nutrients has a number of common features, namely
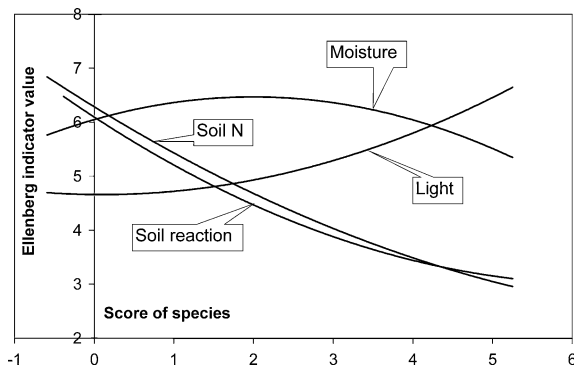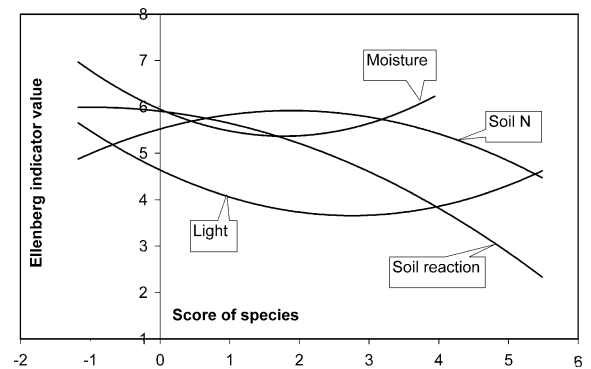
Fig. 7 The relation of environmental variables (according to EIVs for plant species) and main direction of variance (1st non-canonical axis) of the herb layer in nutrient-poor sites (Boubín-Milešice). Horizontal axis: scores of species are from analysis 1 (Table 1, Fig. 6—horizontal axis); vertical axis: EIVs for soil reaction, soil N, moisture and light; nine member relative scale of EIVs—1 = minimum (e.g. very acid soil), 9 = maximum (e.g. alkaline soil). The data are interlayered using a second degree polynomial

Fig. 8 The first two main directions of variance of the herb layer in nutrient-rich sites (Stožec) as plotted at horizontal and vertical axes respectively, DCA analysis (Table 1, analysis 2). Supplementary variable is year of measurement. Species with weight in analysis ≥ 1% are shown. Grey polygons outline the area occupied by the plots of the respective periods (light grey—1974, dark grey—1998)

Fig. 9 The relation of environmental variables (according to EIVs for plant species) and main direction of variance (1st non-canonical axis) of the herb layer in nutrient-rich sites (Stožec). Horizontal axis: scores of species are from analysis 2 (Table 1, Fig. 8—horizontal axis); vertical axis: EIVs for soil reaction, soil N, moisture and light; nine member relative scale of EIVs—1 = minimum (e.g. very acid soil), 9 = maximum (e.g. alkaline soil). The data are interlayered using a second degree polynomial

the decreased coverage degree of tree species in higher tree layers (1 and 2) and conversely the increased cover of shrub layers. It is presumed that the changes are of cyclic character and they are interpreted as being intrinsic to the developmental cycle of the natural temperate forest (Otto 1994; Korpel' 1995; Standovár and Kenderes 2003). Most forest stands under study progressed in the 1990s to the stage of disintegration, which was demonstrated by the results of the dendrometric surveys (Vrška et al. 2001a, b) made in 1972(4) and in 1996(8). The stages of development—growth, optimum, disintegration—are differentiated by the share of live and dead dendromass, with no regard to the development of species composition of the stands (Otto 1994; Korpel' 1995). The stage of disintegration is characterized by an intensive decrease in the volume of live dendromass, which is substituted for by the volume increment of individuals in the subsequent forest generation only to a limited extent. Phytocoenoses at this stage exhibit a rich vertical structure.

Significant and surprising changes occurred between the 1970s and the 1990s in the representation of plant taxa in the vertical structure of the forest stands: (i) a pronounced decrease in the frequency of *Abies alba* in tree layers on both the nutrient-rich and the nutrient-poor subsoils, (ii) a pronounced increase in the frequency of *Sorbus aucuparia* on both the nutrient-rich and the nutrient-poor subsoils, (iii) an

aggressive invasion of *Fagus sylvatica* in the lower tree layer and in the shrub layer on acidic subsoils, (iv) a withdrawal of *Ulmus glabra* from tree layers of the Stožec site rich in nutrients. The changes are

Table 4 Floristic similarity of phytocoenological relevés on plots between years of measurement (70s and 90s) and between nutrient-poor site (Boubín-Milešice—B-M) and nutrient-rich site (Stožec—S)

Type of index	Mean B-M	Std.dev. B-M	Mean S	Std.dev. S	*t*-value	*P*-value
Jaccard index	51.7120	12.5382	45.7516	12.5655	1.4544	0.1541
Gleason index	89.7998	7.9528	78.1142	17.2768	2.9222	*0.0058*

Testing by *T*-test

Parameters: Mean—arithmetic mean, Std.dev.—standard deviation, *t*-value—test statistics (*T*-test), *P*-value—level of significance (*P* <0.05 printed in italics)

Number of plots: 1970s = 40 (B-M—25, S—15), 1990s = 40 (B-M—25, S—15); indexes: Jaccard index of qualitative floristic similarity, Gleason index of quantitative floristic similarity

Table 5 The differences between the phytocoenological data sets; the relevés were merged according to locality (nutrient-poor Boubín-Milešice versus nutrient-rich Stožec) and according to period of measurement (1970s vs. 1990s)

| Variable	Factor	Sum of squares	*F*-value	*P*-value
Number of species	Locality	19.00	0.7965	0.3749
	Year	640.94	26.8689	*<0.0001*
	Locality*Year	53.34	2.2361	0.1390
Equitability	Locality	0.02	2.4261	0.1235
	Year	0.00	0.0000	1.0000
	Locality*Year	0.03	2.8150	0.0975
Shannon–Wiener index	Locality	0.28	2.5499	0.1145
	Year	1.92	17.2489	*0.0001*
	Locality*Year	0.01	0.0739	0.7864
EIV—light	Locality	0.9734	1.4402	0.2338
	Year	2.8509	4.2183	*0.0434*
	Locality*Year	0.2764	0.4089	0.5244
EIV—temperature	Locality	6.463	39.805	*<0.0001*
	Year	0.258	1.591	0.2111
	Locality*Year	0.486	2.990	0.0878
EIV—moisture	Locality	1.724	2.633	0.1088
	Year	0.124	0.190	0.6644
	Locality*Year	0.219	0.334	0.5650
EIV—soil reaction	Locality	33.803	41.467	*<0.0001*
	Year	0.308	0.378	0.5403
	Locality*Year	0.068	0.084	0.7727
EIV—soil N	Locality	52.230	37.653	*<0.0001*
	Year	0.243	0.175	0.6768
	Locality*Year	1.418	1.022	0.3153

Testing by two-way ANOVA analysis

F-value—test statistics, *P*-value—level of significance (*P* < 0.05 printed in italics)

apparently occurring within a period exceeding the forest developmental stages (lasting 40–100 years— Korpel' 1995) and their character may be that of a long-term trend.

The massive reduction of *Ulmus glabra* cover on the Stožec site created from Dutch elm disease caused by the fungi *Ophiostoma ulmi* (Buism.) Nannf. and *Ophiostoma novo-ulmi* Bras. (Brasier 1979, 1991;

Fig. 10 Indicators of herb layer diversity (number of species, equitability, Shannon–Wiener index) and Ellenberg indicator values (EIV—light, temperature, moisture, soil reaction, soil nitrogen) in dependence on the year of measurement; number of plots: Boubín-Milešice (B-M) = 25, Stožec (S) = 15, Total (T) = 40. Full squares—median, open boxes—interquantile range (25–75%), whiskers—non-outlier range (coefficient 1)
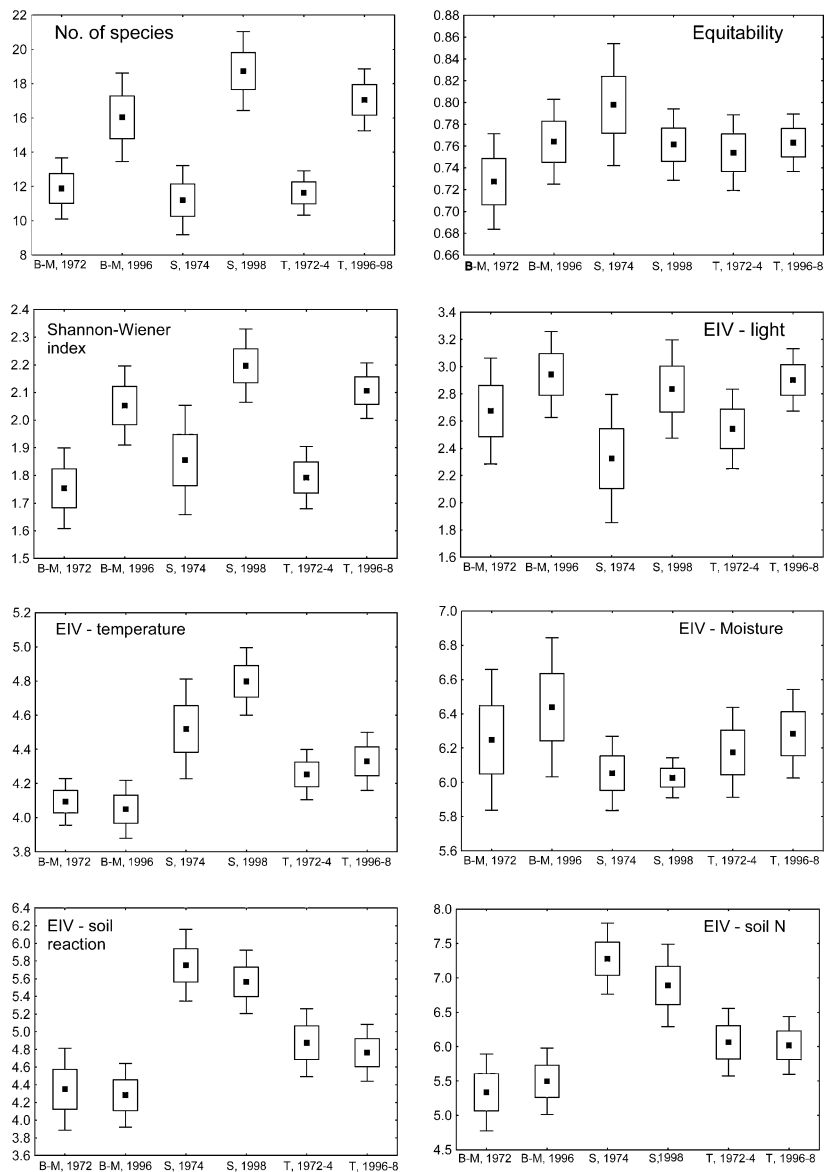
Webber 1981; Wingfield et al. 1993; Dvořák et al. 2006). In the 1990s, the elm population on this site was at its minimum. The increasing share of *Fagus sylvatica* will presumably lead to a greater dominance of the species in the future, particularly on the Boubín site. In contrast, *Abies alba* nears the minimum level of its existence in the localities with its increasing share in the lowest vegetation layers giving some hope of its survival in the stand, perhaps even of the species' rehabilitation over a longer period. The aggressive invasion of *Fagus sylvatica* at a cost of *Abies alba* is described by Šamonil and Vrška (2007)

from the stands of *Dentario enneaphylli-Fagetum* and *Dentario glandulosae-Fagetum* in the Beskids Mts. where development is interpreted as an impact of direct historical management by humans, particularly grazing and litter raking in the forest. Similar results were found out by Motta and Garbarino (2003) in Italy. In spite of a total (Boubín) or nearly total (Stožec, Milešice) absence of direct anthropogenic interventions in the forest stands development in historical times, the virgin forests of Šumava have been growing under the indirect impact of humans—e.g. great fluctuations in game populations since the

18th century (Nožička 1957), and the impact of air pollution since the mid-20th century. Although the impact is considerably lower compared with some other localities in the Czech Republic, their long-term chronic action might have affected the development of the forest stands. A question also remains as to the autoregulation capacity of the studied remainders of natural forests (Busing and White 1993). The development of species diversity in the Šumava virgin forests is rapid beyond expectation and it may also be catalyzed by the development of climatic characteristics—e.g. increase of the temperature and length of the growing season (cf. Biondi 1993; van der Knaap et al. 2004; Wild et al. 2004).

The dynamics of the herb layer

The increase of species diversity in the remainders of natural spruce-fir-beech forest stands of the Šumava Mts. between the 1970s and the 1990s corresponds well with the findings of Wild et al. (2004) who assessed spruce stands in Šumava—communities of *Calamagrostio villosae-Piceetum*, *Bazzanio-Piceetum* and *Sphagno-Piceetum*. Conversely, most authors recorded a decreased species diversity in other regions of the Czech Republic in the same period, e.g. Hédl (2004a) in the Rychlebské hory Mts., Viewegh (1994) in the Beskids Mts., Vacek and Lepš (1987, 1991, 1992);Vacek et al. (1996, 1999) in the beech-to-spruce forest stands of the Krkonoše Mts. and the Orlické hory Mts. Changes in the species diversity are most often connected with the development of air pollution load (Vacek et al. 1999; Smith 1974; Økland and Eilertsen 1996; Vacek and Matějka 2003) which was culminating in Central Europe in the 1980s. Vacek and Matějka (2003) monitored the species diversity of mountain forests on the borders of the Czech Republic, Poland and Germany between years 1951–2001. After a pronounced decrease of the diversity in 1971–1991 they observed its recurrent rapid increase. The authors of this paper assume that the increase of species diversity detected by them in reality partly relates to the reduced air pollution load and to the regeneration of the Šumava forests (Wild et al. 2004). It is however related especially to the development of the tree layer. The authors maintain that the richer-in-species herb layer is an integral feature of natural spruce-fir-beech forests at a stage of

disintegration (cf. Remmert 1991; Aubert et al. 2003). Nevertheless, the increase of species diversity in the natural (fir-) beech stands that are situated at lower altitudes in Central Europe is usually not significant at a stage of disintegration (Ujházy et al. 2005; Šamonil and Vrška 2007). An insignificant increase of species numbers in *gaps* created in broadleaved forests of the USA was observed also by Brewer (1980) and Moore and Vankat (1986). The authors maintain that dissimilarities between vegetation types have to do first of all with the dynamics of spruce-fir-beech forest stands on a coarser spatial scale where a greater opening of the developed gaps (Samek and Javůrek 1964; Batelka 1979; Nakashizuka 1985; Collins and Pickett 1987; Drössler and von Lüpke 2005) enables a greater assertion of taxa with higher light requirements.

It follows from the results that the effect of different trophic status of the site on the herb layer formation is secondary as compared with the impact of changes occurring in the tree layers. The common decrease of tree canopy closure on both sites results in a common increase of species diversity (cf. Wild et al. 2004) and hence in an increased Shannon–Wiener's index. It seems that site plays an important role in affecting the development of equitability and also the measure of changes in phytocoenoses (assessed by the indices of floristic similarity). The decrease of equitability on the nutrient-rich subsoil in the 1990s resulted especially from an expressively increased cover of light-requiring and/or hydrophilous taxa namely *Calamagrostis villosa*, *Rubus idaeus*, *Chaerophyllum hirsutum* and *Ranunculus acris* (cf. Ujházy et al. 2005). On the nutrient-poor subsoil in forest stands at a stage of disintegration the herb layer gets homogenized rather in the 1990s. It is given not only by the accession of other—particularly heliophilous—taxa but also by the retained (or even increased) evenness of covers.

The dynamics of environmental conditions

The transition of the forest stands to the stage of disintegration in the 1990s (see above) was accompanied by a higher assertion of herb layer taxa with higher light demands. We assume that the EIV increase for light is again of a cyclic change character (e.g. changes are related to rotation of the stages of

development within small developmental cycle of the natural temperate forests). Wild et al. (2004), too, described a spread of taxa preferring lighter stands in the Šumava virgin forests. However, these changes were interpreted by the authors as developmental trends (without relation to the cyclic development of the forest stands). At the same time, having studied spruce stands on the severely water-affected Šumava sites they recorded decreased moisture content as determined by phytoindication. We recorded a similar withdrawal of hygrophilous taxa (*Chaerophyllum hirsutum*, *Cardamine amara*, *Ranunculus repens*) on sites with Ombric Histosols and Arenic Gleysols (Humic and Eutric). The development in localities less affected by water was rather the reverse, though.

No significant EIV decrease for soil reaction was recorded on the nutrient-rich and nutrient-poor subsoils of the Šumava virgin forests in the period from 1970s to the 1990s. This variable is most often related to the soil Ca content (Schaffers and Sykora 2000) and its decrease is usually interpreted as acidification due to air pollution load (e.g. Hédl 2004a). Acidification occurring in European forests in the 2nd half of the 20th century has been demonstrated in a number of cases by direct soil surveys (Hruška and Cienciala 2003; Borůvka et al. 2005) as well as by phytoindication (Wittig 1986; Falkengren-Grerup and Tyler 1991; Falkengren-Grerup 1995; Brunet et al. 1996; Hédl 2004a, b). The grossly insignificant development of EIV for soil reaction observed by us may have resulted from the lower historical deposition of air pollutants in the region under study (Hruška and Cienciala 2003) or from the higher buffering capacity of the relicts of Šumava natural forests, likely resulting from the functioning feedbacks of such an ecosystem and from the leaving of all wood mass—namely Ca and Mg sources—in the forest stands (Glatzel 1990).

Conclusions

The nutrient-poor site (Boubín-Milešice) as well as the nutrient-rich site (Stožec) were observed to show in the course of 24 years an expressive decrease in the tree layer degree of coverage and conversely the advance of the shrub layers. The cover of the main tree layer dominants—*Fagus sylvatica*, *Picea abies* and *Abies alba* exhibited a marked decrease. The

constancy of the first two taxa is however stable while in *Abies alba* it shows a pronounced decrease. In contrast, the lower tree layer and the shrub layers in Boubín-Milešice experienced a distinctive invasion of *Fagus sylvatica*, while the species share in relation to *Picea abies* is more equal in Stožec. *Abies alba* has a minor share in the shrub and tree-low layers of all localities, which is very likely caused by the indirect impact of humans—in particular long-term high stocks of hoofed game which hampers its growth.

The main direction of herb layer variability on the two site types corresponds with the differences in soil reaction between sample plots. Herb layer changes between the 1970s and the 1990s were highly significant with the qualitative changes being greater than the quantitative changes. The number of species and Shannon–Wiener's index increased.

The nutrient-poor (Boubín-Milešice) and the nutrient-rich (Stožec) sites did not show any significant difference in the number of species, equitability, qualitative similarity or Shannon–Wiener's index. A significant difference was conversely recorded in the values of the quantitative similarity of relevés between the 1970s and 1990s with a higher quantitative similarity on the nutrient-poor sites of Boubín-Milešice where homogenization of the herb layer occurs.

A significant increase of EIV for light was found by phytoindication on both site types. Other assessed characteristics—temperature, moisture, soil reaction, soil nitrogen—did not exhibit significant changes over time.

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