Long-term vegetation dynamics in the mountain forests of the Czech Republic

Karel Matějka
IDS, Na Komořsku 2175/2a, 143 00 Praha 4, Czech Republic
matejka@infodatasys.cz

Abstract

The paper analyzes data sets from three regions: 34 permanent research plots in the Orlické hory Mts. (1951-2001); 32 plots in the Giant Mts. (1980-2005); 20 plots in the Bohemian Forest (1997-2007). Each plot was studied using repeated plant-coenological relevés. Plots were clustered into groups regarding dominant species in the tree etage (*Fagus sylvatica* and *Picea abies*), the dieback of the tree etage and altitudinal zone.

The plot change during the investigated period represents a temporal gradient. Such gradient can be described by α-diversity at each time of sampling and by β-diversity as a measure of community dynamics. Two new indices dH and dS based on Shannon-Wiener's index and species richness are introduced and used.

Separate community etages show more or less different dynamics during forest succession. Rapid tree stand damage as a result of bark beetle (*Ips typographus*) gradation was recorded in the Bohemian Forest as an effect of climate extremes. Gradation of bark beetle can be of natural origin. The tree etage decline in the spruce forests holds lower importance in species composition than has been mentioned earlier.

Beech-mixture forests shows higher changes, without a complete tree etage decline, compared with spruce forests with completely dying trees, because the herb etage shows higher species richness and many of the species is very sensitive to changes.

Keywords: beta-diversity, *Fagus sylvatica*, *Picea abies*, stand dieback, temporal gradient

Introduction

Each ecosystem is unremittingly developing. The cause of this evolution is adapting to the environmental conditions. These conditions are not stable, they shows changes and fluctuations. Weather is more or less different in different years, water availability varies, and man-made change in deposition associated with air pollution can be evolving, as well as internal (biotic or abiotic) conditions – e.g. the litterfall accumulation, shading the soil surface of the growing tree floor, deer browsing and last but not least the presence and influence of pathogenic organisms, phytophagous, cambixylophagous and other insects can be mentioned.

The forest ecosystem has dynamics concerning on all part of forest ecosystem. Communities or assemblages of some organisms represent such ecosystem parts. They develop in own dynamical system. Forest dynamics is not only stand dynamics. The plant community of herb and /or moss etage represents a separate dynamical system, nevertheless linked to other components of the ecosystem. Stand dynamics is dependent on changes in herb etage, but it demonstrates several independent features (Oliver & Larson 1996).

Forest dynamics can be realised as canopy-gap dynamics (Pickett & Cadenasso 2005). This system is known under the term "small developmental cycle" in the Czech and Slovak forestry (Korpeľ 1989). Gap performance as a driving dynamical system is well known in broad-leaved and mixed forests of the temperate zone (e.g. Poulson & Platt 1996, Emborg 1998, Ida 2000, Mou & Warrillow 2000, Runkle 2000, Collet et al. 2001, 2002, Szwagrzyk & Szewczyk 2001). The natural large-scale damage causes dynamical changes in many forests. There are known examples prevailing of fires in coniferous forests (Bradshaw 1993, DeGrandpre et al. 1993, Hornberg et al. 2004, Harper et al. 2005, Lecomte et al. 2005). Other case can be connected with gradation of insect population (Osawa 1994, Veblen et al. 1994) and / or with wind damage (e.g. Fischer et al. 2002).

More or less rapid collapse of forest stands has been observed in Central Europe during last century in many cases. Those events were connected especially with air pollution impact mainly in the 1970s and 1980s (Kopáček & Veselý 2005). Rapid tree stand decay is often case of a sudden insect gradation in response to extreme weather (above-average temperatures, droughts, wind calamity) currently.

The succession and dynamics of communities can be viewed as a temporal gradient (Müller 1998). Variability of communities along a gradient is understood as β-diversity. While α-diversity is the property of a defined (spatial) unit - a community or an assemblage, β-diversity reflects biotic change or species turnover along a gradient (WHITTAKER 1960). We would speak about temporal β-diversity to describe changes in species composition (it is the same as species structure) of the community during a time interval.

The Jaccard's coefficient of dissimilarity has been used commonly (e.g. STOHLGREN ET AL. 1997, MISTRAL ET AL. 2000, CAO ET AL. 2004, TABOR ET AL. 2004), mainly to quantify β-diversity along a gradient (e.g. MACNALLY ET AL. 2004, GOETTSCH & HERNANDEZ 2006, QIAN & RICKLEFS 2007). Several attempts on linking between β-diversity represented by the Jaccard's coefficient and niche theory were introduced (FRIDLEY ET AL. 2007, MANTHEY & FRIDLEY 2009, ZELENY 2009). There are several other indices of β-diversity or community similarity. It is possible to find their short list and description in MAGURRAN (2004: pp. 162-184). These measures show some disadvantages: It is a useful parameter of dissimilarity to compare a pair of sample, not bigger set of samples. It is related only to species richness without a modification. It cannot be related to the commonly used indices of species diversity as would be desirable under incorporation into system of α- and β-diversity.

Species richness of whole landscape (or gradient) would be partitioned into two components, β-diversity and average α-diversity (LANDE 1996), as has been mentioned by MAGURRAN (2004: p. 166). A similar approach we have used in a newly suggested method of calculation is based on the Shannon-Wiener's index of diversity - as the member of set of indices on generalized entropy measures (KEYLOCK 2005), which breaks through these problems.

The aim of this paper is to compare results of different studies on the dynamics of plant communities in ecosystems of mountain forests of three different regions of the Czech Republic. Data was obtained in three projects of varying duration (10 to 50 years). This material was subsequently evaluated by similar procedures in order that results would be comparable. The data processing reveals that a unified methodological approach would be necessary to adapt. Description of the methodological framework including an appropriate system of indices of community dynamics is the second main goal. Presented results represent a basis for comparison of the dynamics of forest ecosystems in different environmental conditions, particularly in relation to altitude, which is an essential factor in managing the extension of two main species - beech and spruce. Three different data sets should cover as main variability in the Czech mountain forests, so variability in methodological approaches (mainly duration of observation).

Material and methods

Common remarks

The Czech forest typological system distinguishes forest altitudinal zones according to main tree species (VIEWEGH ET AL. 2003). Mountain forests embraces beech with fir (5^{th}), beech with spruce (6^{th}) and spruce with beech (7^{th}) zone. The next spruce (8^{th}) zone can be named as an "upper montane forest zone". Their upper limit coincides with the alpine forest limit. The altitude of borders of the spruce zone differs in separate regions according to northern latitude. Difference in latitude between the Giant Mts. and Bohemian Forest is approximately 2°, which corresponds to 150 m in elevation (compare KÖRNER ET AL. 2003).

The plant species nomenclature follows KUBÁT (2002).

Study areas and data collection

The study was carried out on the basis of plant coenological relevés from three important mountain areas of the Czech Republic (Fig. 1). All plots in this study were selected subjectively as representatives of the basic forest types in the region.

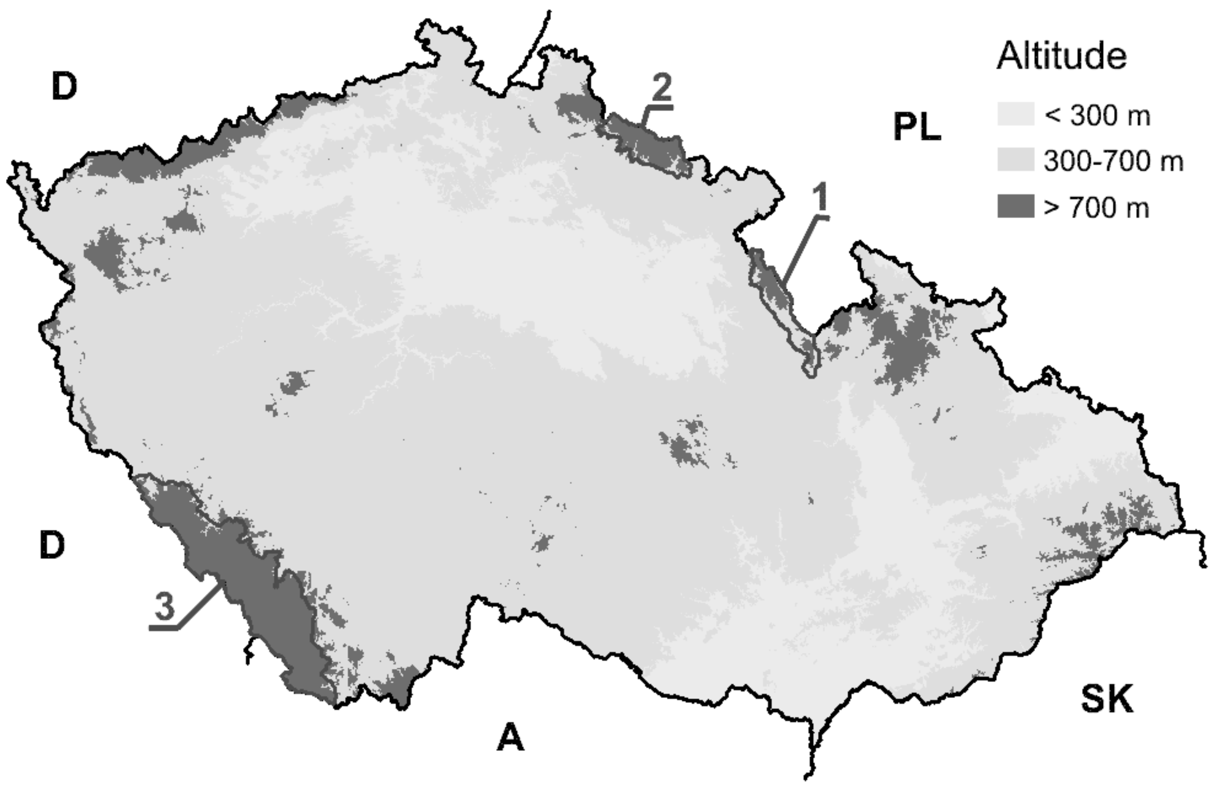

Fig. 1. Selected mountain areas in the Czech Republic: 1 - Orlické hory Mts., 2 - Giant Mts., 3 - Bohemian Forest.

Orlické hory Mts.

Orlické hory Mts. is the highest part of the Central Sudetes. Their compact, narrow and relatively flat ridge is 55 km in long. The highest points reach to 1115 m a.s.l. (Velká Deštná Mt.). The total area of the respective forest natural region is 386 km^2 in the Czech Republic ("natural forest region" is a unit of a Czech biogeographical division). Forests cover 55 % of this area. Entic podzols (58 %), cambisols (23 %) and haplic podzols (11 %) are the most important soil types (VACEK ET AL. 2003). Based on vegetation reconstructions species-rich beech stands and beech stands with fir of the alliance *Fagion sylvaticae* Luquet 1926 were largely dominant (88 % of total area). Mountain acidophilous beech-mixture forests of the alliance *Luzulo-Fagion* Lohmeyer et Tüxen in Tüxen 1954 occurred in the highest ridge locations (5.5 % of the area). Natural spruce stands of the alliance *Piceion excelsae* Pawłowski, Sokołowski et Wallisch 1928 were encountered only in the highest ridge locations approximately up 1050 m a.s.l. The other phytocenoses covered very small areas (MIKYŠKA ET AL. 1968).

The conditions of phytocoenological sampling in European beech (in altitudes 780-1020 m) and Norway spruce (in altitudes 725-1110 m, only 5 plots occur in the climax spruce zone - 8^{th} forest altitudinal zone) stands were relatively satisfied on 34 research plots established in 1951 by A. Zlatník and J. Pelíšek (Forestry Faculty of Agricultural University at Brno), and renewed in 1971 by J. Gregor (Forest Management Institute). These plots of 490 m^2 in size were sampled repeatedly in 1991 and 2001 by S. Vacek (VACEK & MATĚJKA 2003). All plots are listed in Appendix 1. They are grouped according to dominant species (beech × spruce). Further division of the spruce plots corresponds to distinguishing man-made spruce stands in the altitudinal zone with beech, and spruce stands in the spruce zone ("climax *Picea abies*" plots). All stands in the last group were cut regarding to the former air-pollution influenced worsening of the health status. Three basic groups were: F - plots in European beech stands, P - plots in Norway spruce stands with a continuous existence of tree etage, representing man-made forests with fully changed tree species composition, and mP - plots in Norway spruce stands with a total disintegration of the tree etage; all plots of this group belongs to the climax Norway spruce communities in the upper montane belt (8^{th} forest altitudinal zone). Two spruce plots with the tree stand disintegration are situated in a lower altitudes below 1000 m a.s.l. (group P).

It was not distinguished between disintegration of the tree etage caused by air-pollution stand damage and tree cutting, because of both processes occurring together in several plots.

Giant Mountains

The Giant Mountains (Krkonoše Mts.) in north-eastern part of the Czech Republic are highest mountain region of the Western Sudetes ridge with the highest point at the top of Sněžka Mt. (1602 m a.s.l.). The mountain axis is 36 km long. The forest natural region of Giant Mts. has total area of 408 km^2 in the Czech Republic. Forests cover 79 % of this area. Acid soils prevail (27 % entic podzols, 26 % haplic podzols, 24 % leptosols, and 15 % cambisols as main soil types). Natural vegetation is well structured according to altitude with zones of species-rich beech forests of the alliance *Fagion sylvaticae* (35 %), mountain acidophilous beech-mixture forests of the alliance *Luzulo-Fagion* (38 %) and natural Norway spruce stands of the alliance *Piceion excelsae* (13 %). Above the forest zones, the sub-alpine (dominated with *Pinus mugo*) and alpine zones are developed (MIKYŠKA ET AL. 1968). Forests in this region have been influenced by air-pollution stress for almost four decades with maximum impact in 1980's. It caused tree etage dieback in some Norway spruce stands, mainly in high altitudes (VACEK ET AL. 2003). Changes in ground vegetation during the air-pollution impact were described by VACEK ET AL. (1999) in terms of increase in the herb etage cover, an increased dominance of the initially dominant species (such as *Calamagrostis villosa*, *Avenella flexuosa*, *Vaccinium myrtillus* and *Athyrium distentifolium*), and to a decline of mosses.

Thirty-two permanent research plots (2500 m^2 in size) in forest ecosystems were established during 1976-1980 to study the structure and development of mountain forests with beech, spruce-beech and spruce stands. Altitudes of plots varies between 600 and 1260 m a.s.l. Phytosociological relevés were made by S. Vacek between 1980 and 2005 using the standard procedure. The sampling was repeated every five years (1980, 1985, 1990, 1995, 2000 and 2005). These plots represent the basic network for studying forest ecology and dynamics in the region (VACEK ET AL. 2007). Method details and first results were published by VACEK & MATĚJKA (1999). The plots (Appendix 2 contains basic plot description) were clustered into groups: F1 - plots with Eropean beech (*Fagus sylvatica*) communities at low altitudes (up to 1000 m a.s.l.; mentioned as "montane zone"); F2 - plots with beech communities at high altitudes (above 1000 m a.s.l.; mentioned as "upper montane zone"), the stand is created by mixture of *Picea abies* and *Fagus sylvatica* in all plots; P - plots with the Norway spruce forest, under permanent tree canopy; Pd - plots with the Norway spruce forest, total tree canopy disturbance occurs as result of air-pollution, wind and/or insect attack.

Bohemian Forest

The Bohemian Forest (Šumava Mts.) is the most extensive Central European highlands of the Hercynian massif. The summits are Javor Mt. (1457 m a.s.l.), Roklan Mt. (1454 m) and Plechý Mt. (1378 m). The total area of the respective forest natural region is 2113 km^2 in the Czech Republic. The north-west to south-east mountain orientation is approximately perpendicular to prevailing wind direction (TOLASZ 2007). Forests cover 64 % of this forest natural region. Acid soils prevail (62 % entic podzols, and 20 % cambisols as main soil types). Variability of soil types is lower as compared with the other two mentioned regions (VACEK ET AL. 2003). The herb-rich beech forests (alliance *Fagion sylvaticae*) cover 57 % of the area. Next three categories - mountain acidophilous beech forests of the *Luzulo-Fagion* alliance (19 %), waterlogged spruce forests (14 %) and climatic spruce woodlands of the alliance *Piceion excelsae* (3 %) are mainly concerned in the north-western part of the region. They cover only very limited areas in the south-eastern part (MIKYŠKA ET AL. 1968).

Eleven plots were established in the Modrava region, partly on water-enriched soils. All plots were dominated by *Picea abies*. The bark beetle gradation in the Modrava region culminated at 1996-7. Nine plots were established along an altitudinal gradient on the eastern slope of the Plechý Mt. in the south-eastern part of the Bohemian Forest. The bark beetle gradation in the Plechý region was initiated by extreme climate at 2003 and it was accelerated by the wind disturbance at January 2007.

The size of each plot is 2500 m^2. These plots are under long-term ecosystem research (VACEK, PODRÁZSKÝ & MATĚJKA 2006). Basic soil properties were studied in the Plechý plot set by PODRÁZSKÝ (2007). The soil types are cambisols under beech-mixture stands in lower altitudes and ranker with a podzolization process, which occurs in the Norway spruce ecosystems in higher altitudes. Relevés were recorded by the author and J. Viewegh. Plant coenological sampling was processed very frequently comparing the above mentioned two regions - in years 1997, 1998, 2001, 2004, 2005 and 2007, regarding to the actual damage of tree etage caused by bark beetle (*Ips typographus*) in several plots. Unfortunately, data on total cover of each etage was not recorded in each sampling period. There are four groups of the plots (Appendix 3). Twenty investigated plots were divided into four main groups: F - plots with beech-mixture stands in the lower part of the altitudinal gradient on slope of Plechý Mt.; FP - two plots in the beech/spruce transition zone in the Plechý Mt. region, which were dominated by Norway spruce; P - plots of stands with continuous existence of tree etage in the climax spruce zone; Pd - plots with Norway spruce stands completely damaged after the bark beetle attack in the period 1996-2007.

Data processing

Plant coenological relevés were stored in the DBreleve database (MATĚJKA 2010). The species cover grades of the used scale were transformed to average percentage cover as a value of species representation before any calculation. Data of species representation were standardized on the sum of representations of all species in the etage (E_3 - tree etage, E_2 - shrub etage, E_1 - herb etage, and E_0 - moss etage) to be equal to the total cover of the etage in percentages. Total woody species cover (D) was assessed by a combination of tree (E_3) and shrub (E_2) etage cover, since both etages similarly represent the cover of ground vegetation with an influence on regeneration tree species: $D = 1 - (1 - E_2)(1 - E_3)$.

Diversity indices (e.g. MAGURRAN 2004) were calculated for selected etage (herb etage in all cases and herb+moss etages for the Giant Mts. plots) as species richness (S) - number of presented species, total diversity - Shannon-Wiener's index (H')

$$H' = -\sum_i p_i \cdot \log_2 p_i$$

and species equitability (e)

$$e = H' / \log_2 S$$

The change in species composition of the community was calculated in regard to the first year of sampling by the Euclidean distance:

$$E_r = \sqrt{\sum_{i=1}^{n} (x_{ri} - x_{0i})^2}$$

where x_{ri} is i-th species representation (equal to percentage cover) in the r-th period (in the r-th year sampling), r is actual year and n is total number of species. Total change was obtained as the maximum of such distances over whole data set (all investigated years):

$$E_{max} = \max(E_r)$$

The β-diversity along temporal gradient was evaluated on the base of Shannon-Wiener's indices

$$dH = H_{tot} - avg(H_r)$$

where H_{tot} is Shannon-Wiener‘s index of diversity for „total relevé“. The total (or average) relevé was assessed with representation of each species as the mean of representations over all periods. H_r is Shannon-Wiener‘s index of diversity for single relevé in the r-th period and avg is arithmetic mean. Similar index dS for species richness can be calculated as the difference of total number of species in all relevés in the plot and average number of species in a relevé

$$dS = S_{tot} - avg(S_r)$$

Changes in species composition over time can be visualized as shifts of the respective point in the ordination space of several first axes. Ordination was made as de-trended correspondence analysis (DCA). Length of main gradient in the data set can be enumerated as the difference between DCA scores along first ordination axis. Such variable is suitable to measurement of β-diversity (MCCUNE & GRACE 2002; LEPŠ & ŠMILAUER 2003). CANOCO version 4.5 was employed in the study to reveal basic gradients in the data set. Each relevé in the plot represents a point in the ordination space. All such points during succession in the plots are a set of random points (e.g. DCA_{1r} – ordination score along 1st axis in r-th relevé) with average and variance (equal to square standard deviation) according to each ordination axis. Changes in species composition of the community were evaluated as sums of the ordination score variances using first i ordination axes:

$$V_i = \sum_{j=1}^{i} \mathrm{var}(DCA_{jr})$$

where var(x_i) indicates variance of random variables x_i.

Relationships among the community dynamics indices were evaluated using coefficients of linear regression (Pearson's r) separately according the region (data set).

Plots were clustered into groups according to dominant species in tree etage, dieback of tree etage (which was observed in the Norway spruce stands only) and main environmental conditions connected with altitude. All plot groups were described by the arithmetic mean (average) and standard deviation of set of parameters (coverage of selected etages, diversity indices and parameters of community dynamics). Statistically significant differences among groups were sought employing one-way ANOVA test. Differences between two selected groups were evaluated by LSD test for the post-hoc significance levels for the respective pairs of means. This calculations was carried out in the Statistica software, ver. 8 (STATSOFT 2011).

Results

Orlické hory Mts.

Community features and indices of community dynamics are summarized in Table 1. Differentiation between European beech dominated and Norway spruce dominated (man-made) plots is insignificant except for tree etage coverage. Differences in the calculated indices of the herb etage dynamics without E_{max} are not statistically significant. Only a maximum of Euclidean distance (E_{max}) indicates higher dynamics in the plots dominated by spruce.

Sharp change in both species richness and diversity is visible near the border between beech-mixture and natural Norway spruce forests, which occurs at approximately 1050 m a.s.l. (fig. 2). This change is statistically more significant in terms of maximal diversity, mean, maximal and total equitability during long-term vegetation succession (Table 1). Other differences between man-made and climax Norway spruce forests are indicated by a higher coverage of the herb etage. Nevertheless the tree stand was damaged in all climax spruce forests, both species exchange (fig. 3) and β-diversity (Fig. 4) was lower compared with forests in the altitudes under the limit of 1050 m. It is noticed that damage of the tree etage in a Norway spruce ecosystem would be of minor effect to a change of the herb etage species composition.

Changing of the herb etage structure progressed gradually in both beech (group F) and spruce dominated ecosystems localized in lower altitudes (group P). A rapid change during 1951-2971 was revealed under the spruce stand on upper montane sites (group mP), where stands have been disintegrated much later (Fig. 5).

Table 1. Orlické hory Mts. Differentiation between beech and spruce dominated plant communities in investigated permanent plots with continuous existence of the tree etage (p_{F-P} - error probability by F-test) and between climax and man-made spruce communities (p_{P-mP} - error probability by F-test). Only significant p-values are reported. Average ± standard deviation ($\bar{x} \pm \sigma$) are written.

Feature	Parameter		F ($\bar{x} \pm \sigma$)	P ($\bar{x} \pm \sigma$)	p_{F-P}	mP ($\bar{x} \pm \sigma$)	p_{P-mP}
	plot number		17	11		5	
	altitude (m)		939±63	894±99		1073±42	<0.01
etage cover	E_3 (%)	minimum	71±12	55±21	0.01	0±0	<0.01
		maximum	85±9	76±9	0.01	72±6	
	E_2 (%)	minimum	3±6	3±5		0±0	
		maximum	16±8	21±14		49±11	<0.01
	E_1 (%)	minimum	68±21	57±23		83±10	0.04
		maximum	87±10	90±7		99±2	0.01
	E_0 (%)	minimum	6±3	9±5		5±0	
		maximum	17±7	23±11		30±10	
E_1: richness (S)	in single relevé	minimum	12.6±5.6	11.4±6.2		7.6±1.1	
		mean	20.7±11.0	18.6±11.2		11.6±0.9	
		maximum	28.7±17.3	27.0±17.5		16.4±3.0	
	total		28.7±17.3	27.0±17.5		16.4±3.0	
E_1: diversity (H)	in single relevé	minimum	2.71±0.57	2.27±0.69		1.77±0.43	
		mean	3.13±0.67	2.91±0.73		2.23±0.31	
		maximum	3.50±0.74	3.41±0.84		2.56±0.29	0.05
	total		3.46±0.79	3.34±0.85		2.50±0.35	
E_1: equitability (e)	in single relevé	minimum	0.69±0.07	0.65±0.10		0.56±0.12	
		mean	0.75±0.07	0.74±0.06		0.64±0.07	0.02
		maximum	0.81±0.08	0.82±0.05		0.75±0.08	0.03
	total		0.74±0.08	0.74±0.08		0.62±0.08	0.01
E_1: community dynamics	E_{max}		42.0±9.7	52.9±16.1	0.03	37.6±6.6	
	dS		8.0±6.4	8.4±6.5		4.8±2.6	
	dH		0.33±0.14	0.44±0.15		0.27±0.06	0.04
	V_1		0.31±0.28	0.27±0.16		0.16±0.04	
	V_2		0.40±0.38	0.61±0.77		0.23±0.09	
	V_3		0.64±0.48	0.81±0.76		0.39±0.07	
	V_4		0.82±0.63	1.14±0.79		0.50±0.11	

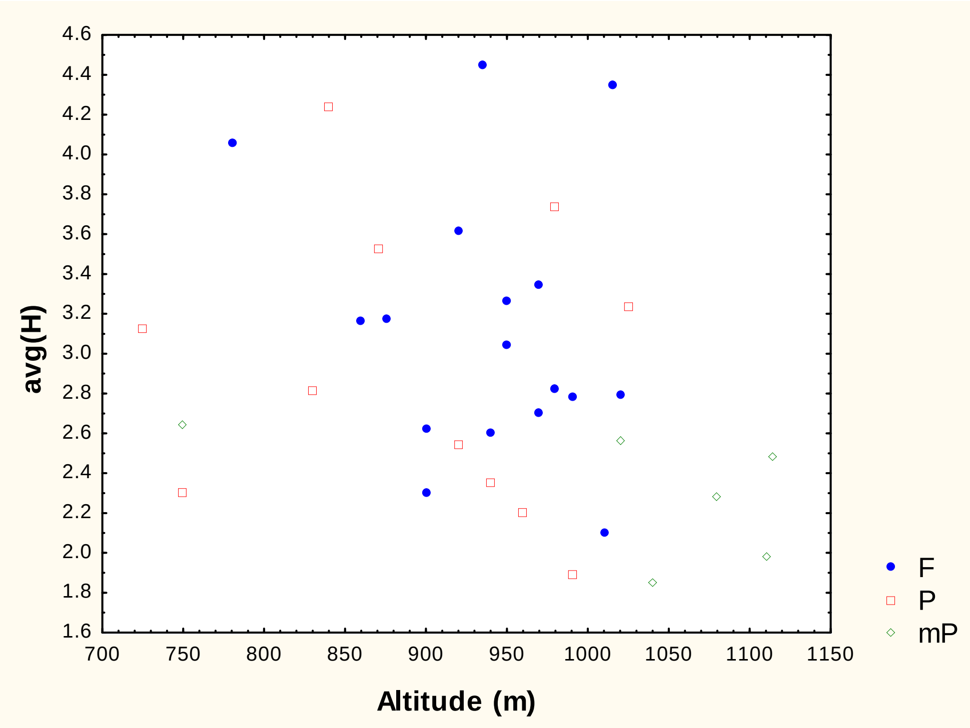

Fig. 2. Orlické hory Mts. - Average value of the Shannon-Wiener's index of species diversity in the herb layer related to the plot altitude according to three plot groups: under *Fagus sylvatica* stand (F), secondary *Picea abies* stand with continuous existence of tree layer (P), and *Picea abies* stand with declined tree layer (mP).

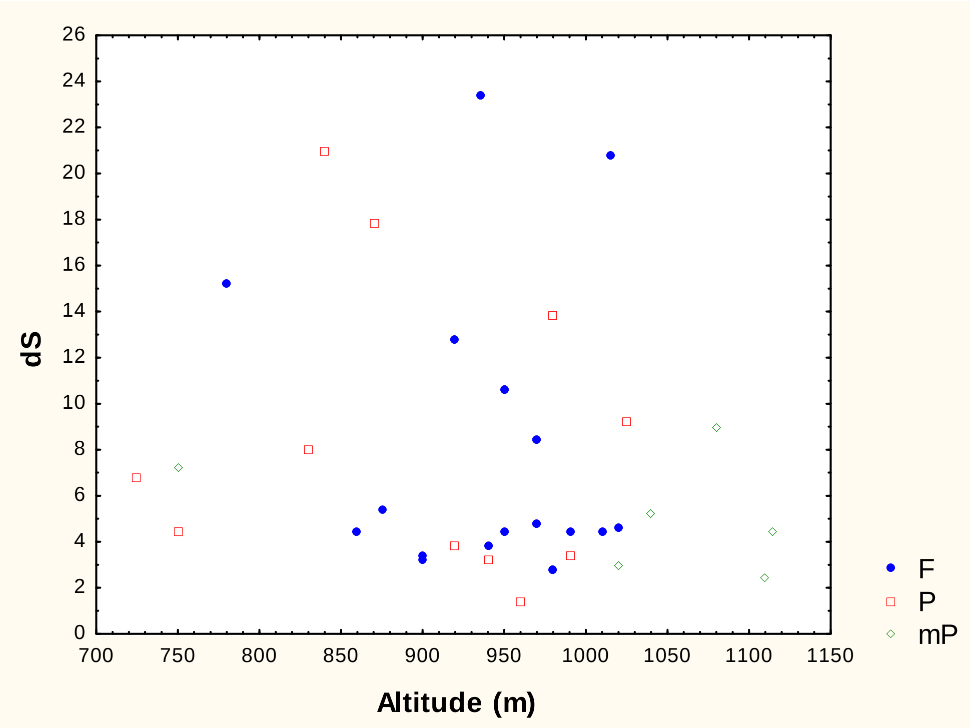

Fig. 3. Index dS of the herb layer community dynamics in forests of the Orlické hory Mts. Plot groups the same as in fig. 2.

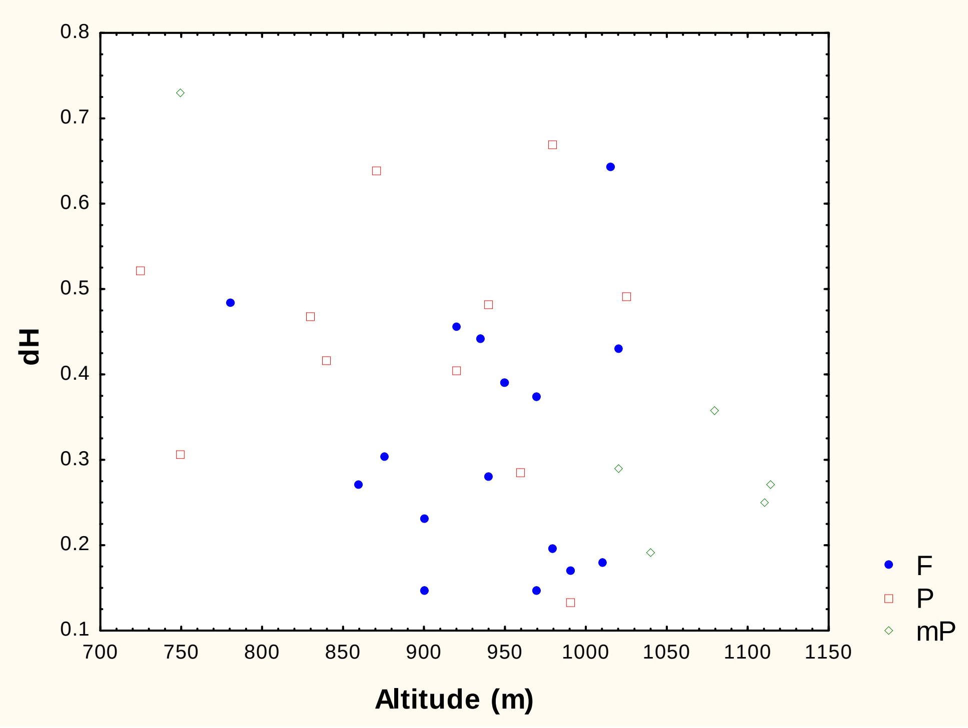

Fig. 4. Index dH of the herb layer community dynamics in forests of the Orlické hory Mts. Plot groups the same as in fig. 2.

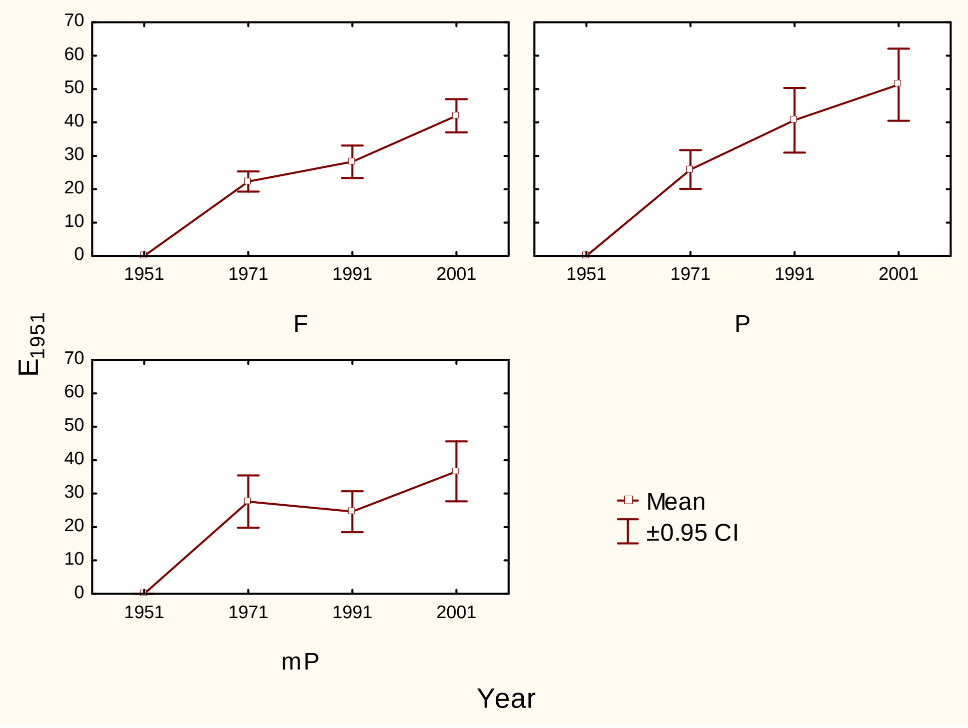

Fig. 5. Changes (Euclidean distance E_{1980}) in the herb layer in forest communities in the Orlické hory Mts. comparing first sampling in 1951. Vertical bars are 95 % confidence limits. Plot groups the same as in fig. 2.

Giant Mountains

Covers of both tree etage and shrub etage were higher in ecosystems with European beech. The average of the total woody species cover in the beech and beech-mixture stands decreased insignificantly by 8 % over 25 years. Similar decrease was observed the spruce stands, where their decay does not occur. The collapse of the tree stands was recorded in 9 Norway spruce plots since 1985 to 2000. A regeneration of these stands was observed in the last sampling.

Average species diversity in the herb etage decreases along the altitudinal gradient in the set of all plots (Fig. 6): correlation coefficients increases from minimal H' (r = -0.10), average H' (r = -0.32) to maximal H' ($r = -0.47^*$; * - statistically significant value on level 5 %) and H_{tot} ($r = -0.47^*$). A similar decrease is visible by indices of the herb etage dynamics - dS ($r = -0.54^*$; Fig. 7) and dH ($r = -0.57^*$; Fig. 8). Diversity of the moss etage has an inverse relation to altitude: minimal H' (r = 0.35), average H' ($r = 0.41^*$), maximal H' ($r = 0.37^*$), H_{tot} ($r = 0.45^*$), dS ($r = 0.40^*$); dS does not depend on altitude.

Herb etage cover was significantly lower under both montane and upper montane beech stands as compared with spruce stands. This cover was approximately unchanged in the beech and beech-mixture stands, but is increasing in the plots of the spruce stands. A similar situation was found in the moss etage (Table 2).

Indices E_{max} and $V_1 – V_4$ were calculated on the base of both herb and moss etages. Changes evaluated on the base of indices E_{max} and dH (by both etages) are similar in all groups. Another situation can be viewed by index dS (temporal changes of species richness). The highest values for herb etage were observed in the montane plots under beech. The moss etage dS was higher in spruce dominated communities as compared with forests with beech (Table 2). Several calculated indices are highly correlated in the set of all plots (Table 4). The exception is found by indices dS and dH calculated for the moss etage. It is evidence that moss and herb etages have different, partly independent development.

The prevailing part of the calculated indices of community dynamics shows a difference between montane beech-dominated and both undamaged and damaged spruce-dominated ecosystems (Table 3).

Prevailing part of parameters of the herb etage richness, diversity and equitability is differentiated according to the plot groups statistical-insignificantly (except for maximum diversity and maximum equitability). A different situation is in the moss etage: the highest species richness and diversity was under the undamaged spruce stands.

The number of species that occur in the forest communities changed significantly. In the stands with beech we observed an average loss of 35 % (in 2005) and 24 % (in 1995) of the herb etage species that were present in 1980 in montane (group F1) and upper montane (group F2) localities, respectively. Related decrease of species diversity by 22 % was recorded in the montane beech sites, but no decrease of this diversity was in the upper montane sites. The change in the herb etage species number in the undamaged spruce forests is rather a fluctuation with a minimum around 1995 (Fig. 9). In the communities of damaged spruce forests important changes were not observed in the total number of species of herb etage.

The loss of species in the moss etage was observed in all categories (Fig. 10): -49 %, -40 %, -53 % and -68 % in plots of groups of montane beech, upper montane beech, undamaged spruce and damaged spruce, respectively. Similarly, there was a reduction in total species diversity by 53 %, 27 %, 31 % and 43 % in these groups of sites. Lower values of diversity changes rather than the values of species richness changes suggest that the decline was due mainly to species with less representation. Whereas beech forests changed gradually, both groups of Norway spruce communities showed a more rapid change up to 1990 (under damaged stands) or 1995 (under undamaged stands). Next changes were smaller, the corresponding segments of the curves in Fig. 11 are more flat.

Table 2. Giant Mountains. Average community features (mean ± standard deviation) for the beech-mixture (montane and upper montane) and the spruce-dominated (with undamaged or damaged tree etage) plant communities in the investigated permanent plots. Differentiation among groups was statistically evaluated by one-parameter ANOVA. (p - error probability by F-test, only values less than 5% are written).

Feature	Parameter		F1 ($\bar{x} \pm \sigma$)	F2 ($\bar{x} \pm \sigma$)	P ($\bar{x} \pm \sigma$)	Pd ($\bar{x} \pm \sigma$)	p
	plot number		8	4	11	9	
	altitude (m)		836±126	1113±79	1184±76	1137±50	<0.01
etage cover	E_3 (%)	minimum	69±15	69±9	45±19	2±7	<0.01
		maximum	89±10	83±10	62±12	67±10	<0.01
	E_2 (%)	minimum	17±18	4±4	1±2	1±2	<0.01
		maximum	40±32	16±9	8±14	24±16	0.02
	E_1 (%)	minimum	46±25	64±22	77±16	84±9	<0.01
		maximum	64±24	88±10	93±8	97±5	<0.01
	E_0 (%)	minimum	2±1	3±2	17±14	10±11	0.02
		maximum	7±6	11±8	35±15	36±10	<0.01
E_1: richness (S)	in single relevé	minimum	14.3±7.5	16.3±1.3	13.5±3.4	11.4±3.1	
		mean	19.0±7.7	19.3±2.8	15.7±3.2	14.2±3.2	
		maximum	23.4±8.9	21.8±4.6	18.2±3.5	16.6±4.1	
	total		26.8±9.5	25.0±5.3	19.7±4.7	20.1±4.0	
E_1: diversity (H)	in single relevé	minimum	2.07±0.82	2.13±0.53	1.93±0.53	1.80±0.38	
		mean	2.62±0.68	2.58±0.44	2.29±0.42	2.11±0.29	
		maximum	3.10±0.55	3.00±0.46	2.70±0.39	2.38±0.26	0.01
	total		2.94±0.71	2.86±0.57	2.48±0.46	2.31±0.35	
E_1: equitability (e)	in single relevé	minimum	0.50±0.13	0.51±0.12	0.48±0.12	0.49±0.08	
		mean	0.63±0.11	0.61±0.09	0.58±0.08	0.56±0.05	
		maximum	0.76±0.08	0.71±0.10	0.69±0.06	0.63±0.05	0.01
	total		0.62±0.11	0.62±0.09	0.58±0.10	0.54±0.06	
E_0: richness (S)	in single relevé	minimum	2.3±0.7	2.8±0.5	5.3±2.4	3.1±2.5	0.01
		mean	3.3±0.5	3.7±0.7	8.0±2.4	6.2±3.0	<0.01
		maximum	4.8±0.9	5.0±1.4	12.0±3.6	10.7±3.8	<0.01
	total		4.9±0.8	5.3±1.5	12.0±3.6	10.4±3.4	<0.01
E_0: diversity (H)	in single relevé	minimum	0.53±0.39	0.98±0.23	1.36±0.34	0.84±0.69	0.01
		mean	0.95±0.23	1.25±0.17	1.76±0.41	1.34±0.46	<0.01
		maximum	1.47±0.26	1.52±0.22	2.24±0.57	1.88±0.42	<0.01
	total		1.18±2.2	1.44±0.18	1.90±0.46	1.72±0.31	<0.01
E_0: equitability (e)	in single relevé	minimum	0.41±0.21	0.53±0.04	0.51±0.10	0.31±0.24	
		mean	0.58±0.13	0.70±0.04	0.63±0.06	0.55±0.10	
		maximum	0.80±0.14	0.86±0.10	0.75±0.12	0.76±0.13	
	total		0.52±0.08	0.62±0.10	0.53±0.10	0.52±0.10	
E_1+E_0: community dynamics	E_{max}		30.8±10.8	40.8±20.1	43.8±18.6	38.1±12.6	
	V_1		0.50±0.41	0.21±0.11	0.03±0.03	0.06±0.04	<0.01
	V_2		0.55±0.41	0.29±0.15	0.15±0.12	0.13±0.10	<0.01
	V_3		0.88±0.55	0.73±0.69	0.19±0.12	0.19±0.12	<0.01
	V_4		0.93±0.54	0.85±0.71	0.30±0.19	0.28±0.16	<0.01
E_1: community dynamics	dS		7.7±2.4	5.8±2.6	4.0±2.3	5.9±1.3	0.01
	dH		0.32±0.11	0.27±0.17	0.19±0.09	0.21±0.11	
E_0: community dynamics	dS		1.6±0.6	1.5±0.9	4.0±1.9	4.3±1.1	<0.01
	dH		0.23±0.13	0.19±0.04	0.14±0.09	0.38±0.36	

Table 3. Giant Mountains. Differentiation among groups of plots was statistically evaluated by the LSD test. Probabilities of the test error are written if less than 5%.

Etage	Index	F1-F2	P-Pd	F1-P	F1-Pd	F2-P	F2-Pd
E_1+E_0	E_{max}						
	V_1	0.04		<0.01	<0.01		
	V_2			<0.01	<0.01		
	V_3			<0.01	<0.01	0.02	0.02
	V_4			<0.01	<0.01	0.02	0.02
E_1	dS			<0.01			
	dH			0.01	0.05		
E_0	dS			<0.01	<0.01	<0.01	<0.01
	dH		0.02				

Table 4. Correlations (r) among indices of the community dynamics in the set of plots in the Giant Mountains. Marked values are statistically significant on level α = 0.05.

	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]
[1] V_1								
[2] V_2	0.95 *							
[3] V_3	0.85 *	0.88 *						
[4] V_4	0.81 *	0.83 *	0.98 *					
[5] E_{max}	-0.09	0.09	0.19	0.23				
[6] E_1: dS	0.46 *	0.33	0.39 *	0.37 *	-0.23			
[7] E_1: dH	0.53 *	0.62 *	0.72 *	0.75 *	0.39 *	0.44 *		
[8] E_0: dS	-0.41 *	-0.39 *	-0.49 *	-0.38 *	0.17	-0.32	-0.23	
[9] E_0: dH	0.11	-0.02	-0.03	-0.02	-0.30	0.15	-0.08	0.20

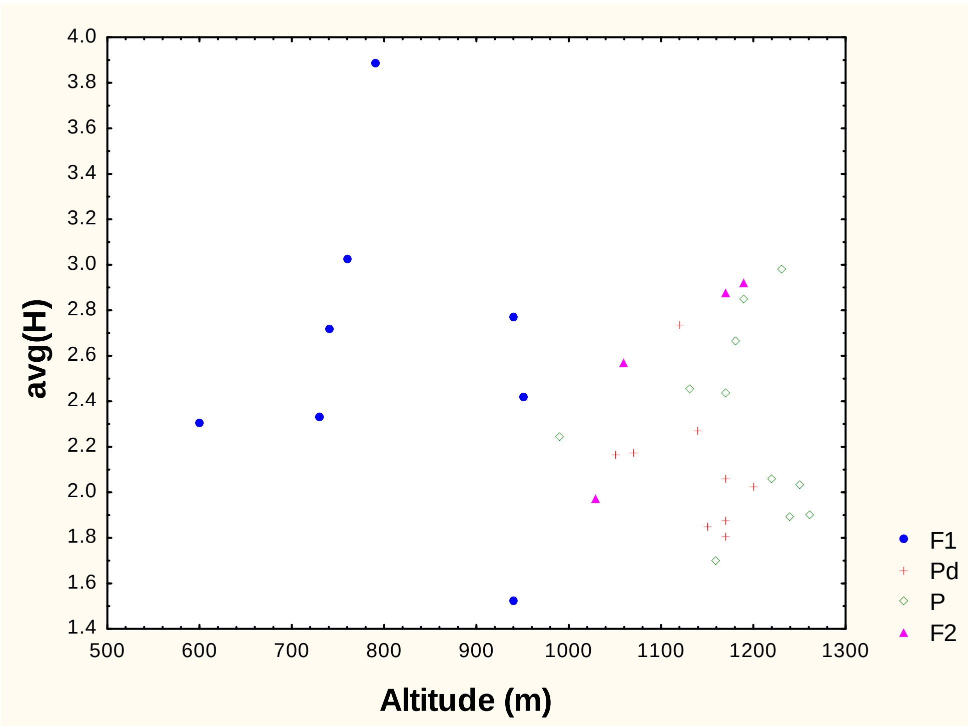

Fig. 6. Giant Mts. Average value of the Shannon-Wiener's index of species diversity in the herb layer related to the plot altitude in the plot groups F1 - *Fagus sylvatica* dominated stands in the montane zone, F2 - *Fagus sylvatica* dominated stands in the upper montane zone, P - *Picea abies* dominated undamaged stands, Pd - *P. abies* dominated stands with stand dieback.

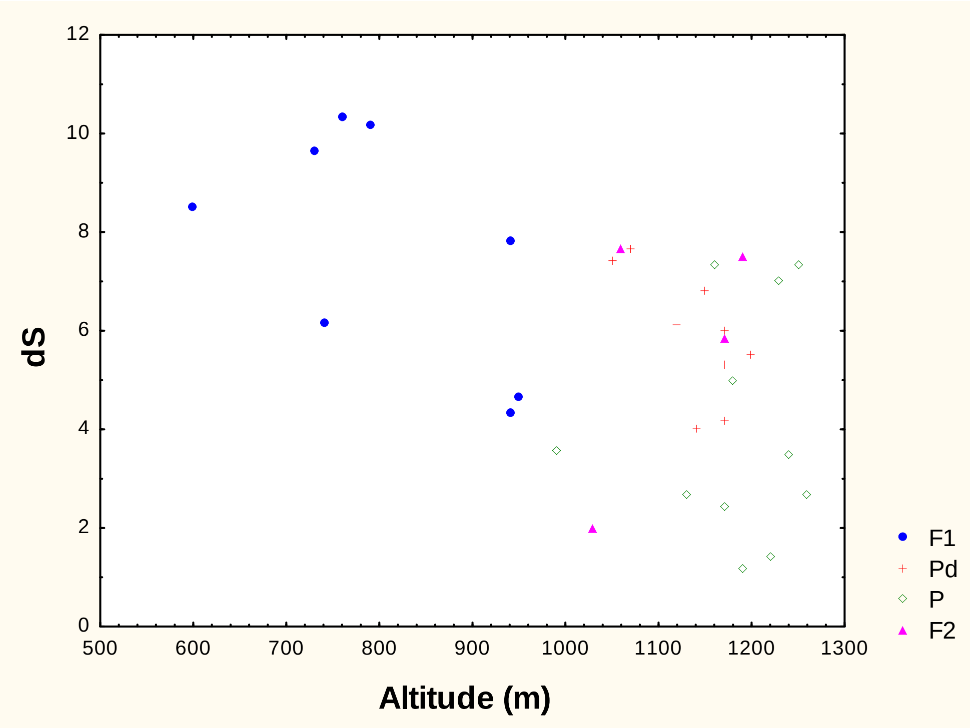

Fig. 7. Index dS of the herb layer community dynamics in forests of the Giant Mts. Plot groups are the same as in fig. 6.

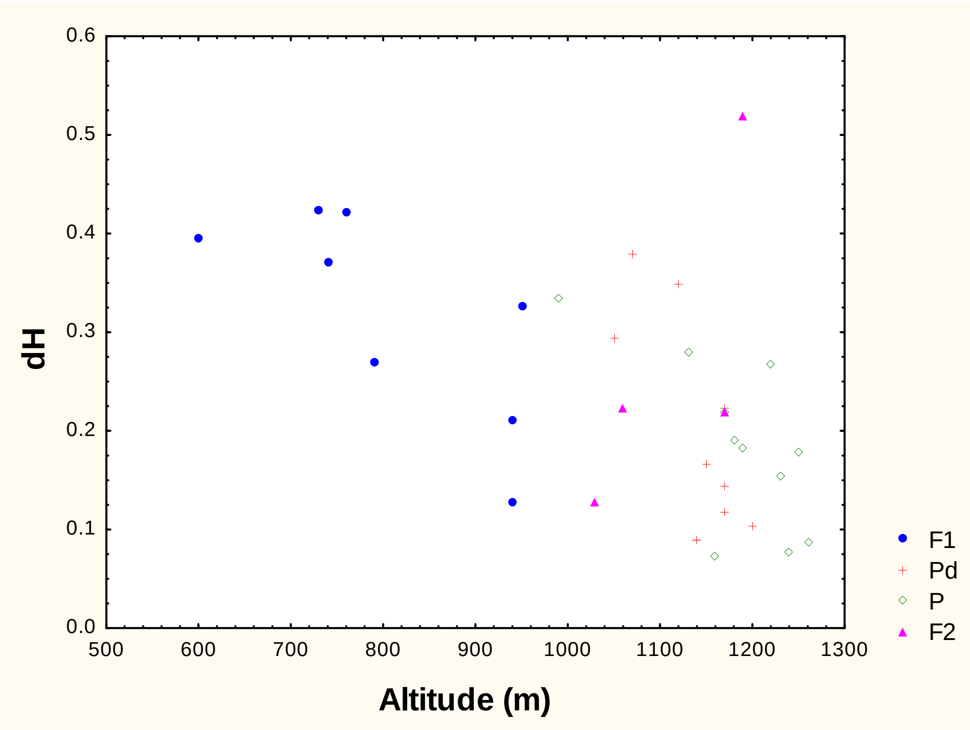

Fig. 8. Index dH of the herb layer community dynamics in forests of the Giant Mts. Plot groups are the same as in fig. 6.

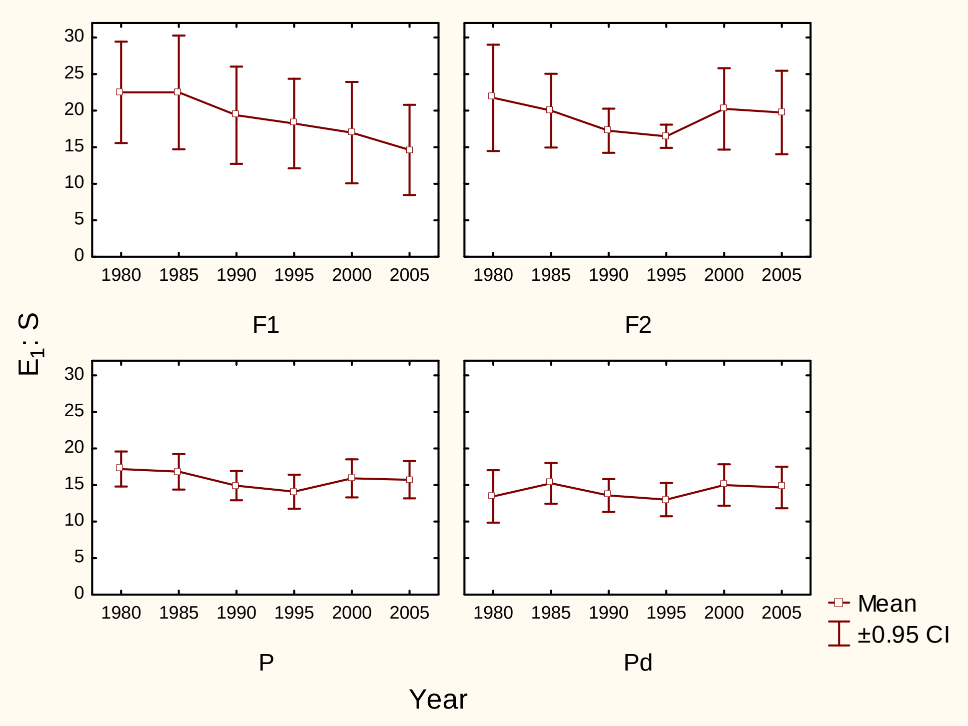

Fig. 9. Development of average number of species in the herb layer of forest communities in the Giant Mountains. Vertical bars - 95 % confidence limits. Plot groups are the same as in fig. 6.

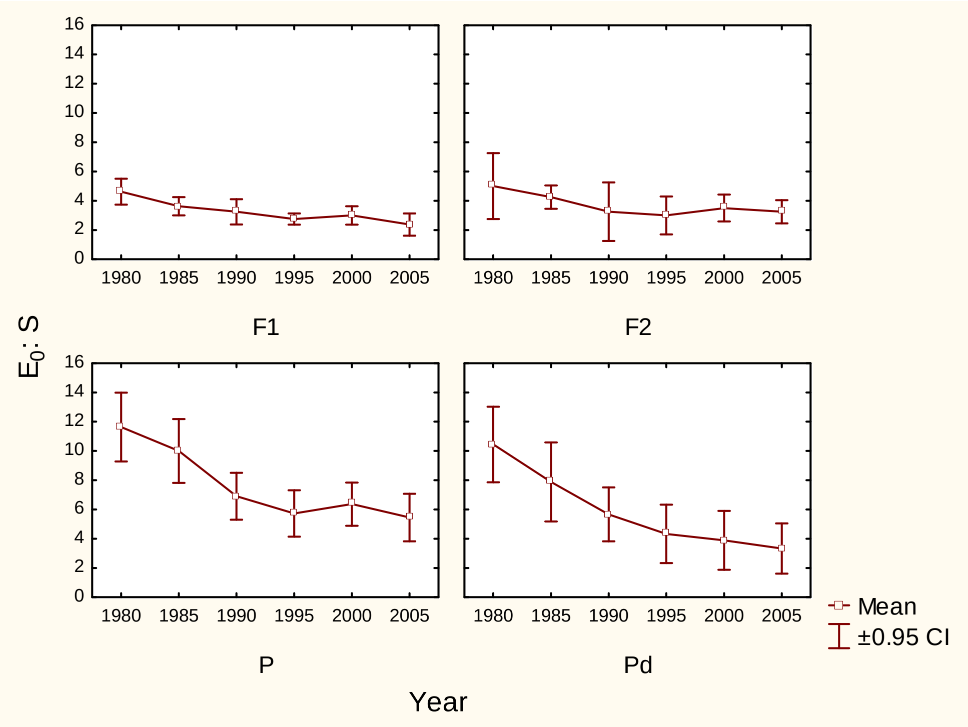

Fig. 10. Development of average number of species in the moss layer of forest communities in the Giant Mountains. Vertical bars - 95 % confidence limits. Plot groups are the same as in fig. 6.

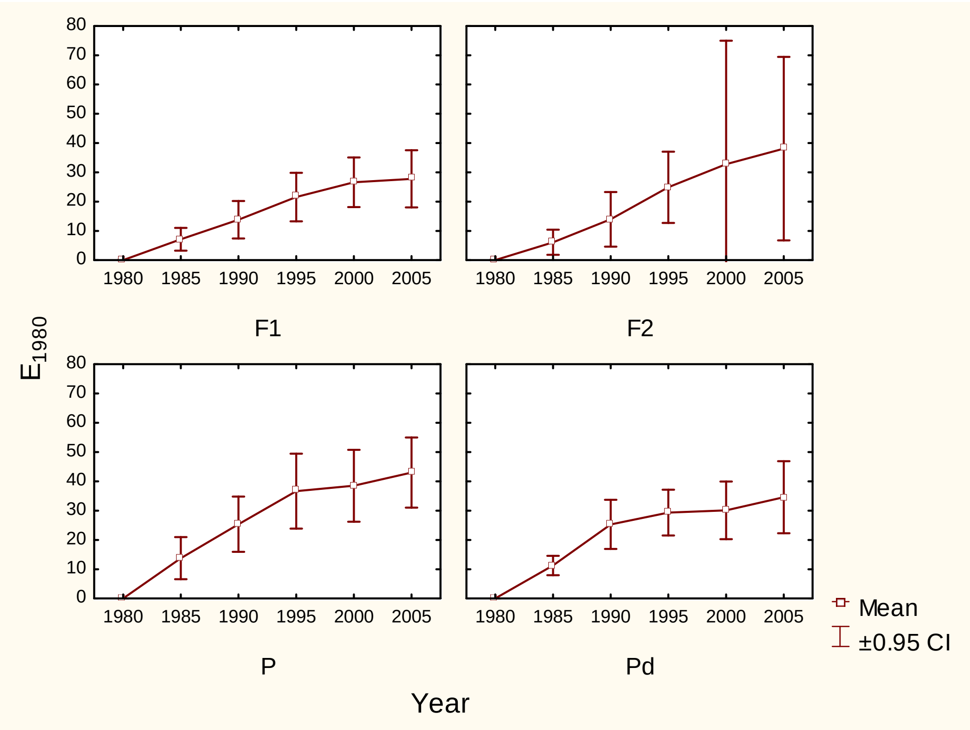

Fig. 11. Changes (Euclidean distance E_{1980}) in ground vegetation (herb and moss etage) in forest communities in the Giant Mountains comparing first sampling in 1980. Vertical bars - 95 % confidence limits. Plot groups are the same as in fig. 6.

Bohemian Forest

Dieback of the tree etage in Norway spruce stands caused by bark beetles (*Ips typographus*) has occurred in 9 plots in the Modrava region within the period 1996-2000 and in one plot in the Plechý Mt. region (2007). Several plots were cleared after tree stand decay. Higher values in indexes by plots with damaged tree etage are caused mainly by embracing two plots with complete cutting and disposal of dead trees. Relevant indices of the community change under cleared stand (E_{max} = 118 and 121; dS = 8.3 and 7.7; dH = 0.64 and 0.91; V_3 = 1.12 and 1.50) are higher comparing averages over the whole group. These groups are different according to lot of features, mainly species richness and total diversity (Table 5).

Based on the analysis of species diversity and richness of herb etage in the twenty plots during the years 1997 to 2007, the largest relative changes occurred in areas with tree etage disturbance (Modrava region). On the contrary, very stable communities appear within altitudinal transect in the Plechý Mt. It is the area where minimum disturbance tree stand was observed to 2007.

Based on the evaluation of shifts in ordination space, the changes in the composition of the herb etage of forests are caused at least by two different factors and two different mechanisms: Since the first ordination axis can be largely explained by factors of altitude, the interpretation of changes corresponding with this axis is difficult. Second DCA axis probably indicates succession process after the tree etage collapse. The change along second axis is meaningful. This change is indicated by the transition between the first group of species such as *Poa nemoralis*, *Soldanella montana* and *Luzula sylvatica* (forest species) and the second group of species representing by *Deschampsia cespitosa*, *Rubus* sp., *Salix caprea*, *Betula pendula* and *Juncus conglomeratus* (species typical for clear-cuttings) (Fig. 12). Because of the most evident shifts were present along the third DCA axis, correlations between indices V_i and dH are steeply growing for i from one to three (Table 6).

Table 5. Bohemian Forest Mts. Differentiation in diversity and dynamics of the herb etage in plant communities among plot groups: F - beech mixture stands in the Plechý Mt. region, FP - stands in beech/spruce transition zone (dominated by spruce) in the Plechý Mt. region, P - stands in the climax spruce zone, Pd - spruce stands completely damaged in period 1996-2007. Differentiation among groups was statistically evaluated by one-parameter ANOVA. (p - error probability by F-test, only values less than 5% are written). Average ± standard deviation ($\bar{x} \pm \sigma$) are written.

Feature	Parameter		F ($\bar{x} \pm \sigma$)	FP ($\bar{x} \pm \sigma$)	P ($\bar{x} \pm \sigma$)	Pd ($\bar{x} \pm \sigma$)	p
	plot number		5	2	4	9	
	altitude (m)		1062±35	1202±62	1277±97	1180±61	<0.01
E_1: richness (S)	in single relevé	minimum	5.8±2.2	8.0±0.0	6.5±1.9	8.7±2.2	
		mean	8.9±1.4	9.8±0.9	8.5±2.7	12.4±2.5	0.02
		maximum	12.0±1.4	12.5±0.7	10.3±3.0	15.4±3.2	0.03
	total		15.6±1.9	15.5±0.8	11.5±3.7	19.2±4.1	0.02
E_1: diversity (H)	in single relevé	minimum	1.00±0.67	1.63±0.25	1.65±0.79	1.75±0.34	
		mean	1.70±0.43	2.08±0.15	1.97±0.85	2.18±0.20	
		maximum	2.28±0.20	2.57±0.05	2.27±0.93	2.61±0.24	
	total		1.84±0.67	2.48±0.06	2.21±0.94	2.80±0.15	0.03
E_1: equitability (e)	in single relevé	minimum	0.37±0.19	0.50±0.07	0.54±0.21	0.50±0.09	
		mean	0.55±0.12	0.64±0.02	0.64±0.21	0.62±0.07	
		maximum	0.73±0.06	0.76±0.01	0.73±0.23	0.73±0.07	
	total		0.47±0.17	0.63±0.03	0.62±0.20	0.67±0.06	
E_1: community dynamics	E_{max}		24.0±13.5	58.0±8.0	48.0±28.9	92.3±24.0	<0.01
	dS		6.7±2.0	5.7±1.6	3.0±1.8	6.8±2.6	
	dH		0.13±0.32	0.40±0.09	0.24±0.10	0.62±0.12	<0.01
	V_1		0.75±0.43	0.22±0.07	0.05±0.02	0.08±0.05	<0.01
	V_2		0.84±0.53	0.40±0.14	0.28±0.12	0.28±0.08	0.01
	V_3		0.87±0.53	0.44±0.13	0.48±0.19	1.02±0.23	0.04
	V_4		2.36±1.52	0.53±0.02	0.54±0.25	1.11±0.25	0.01

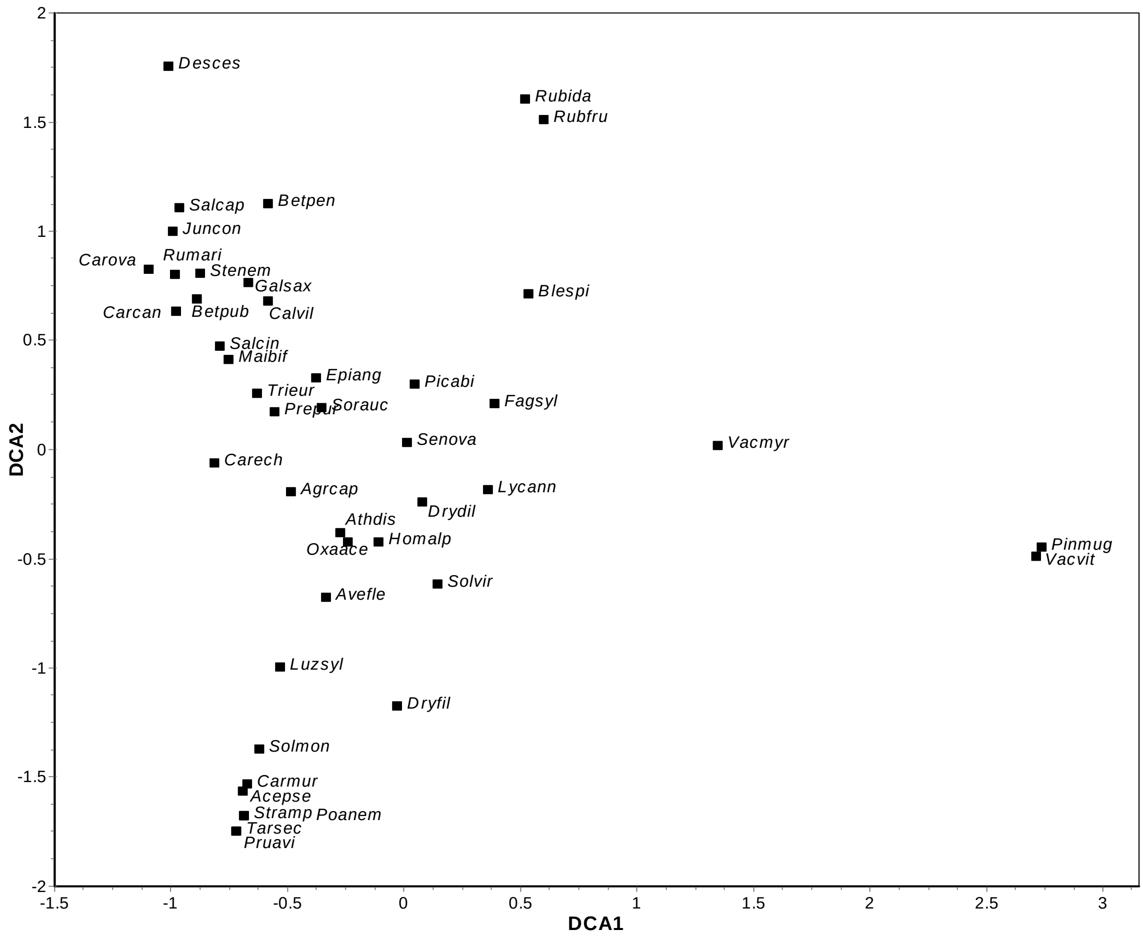

Fig. 12. DCA ordination of data set from the Bohemian Forest. Position of selected species in the ordination space of the first and second axes. Acepse *Acer pseudoplatanus*, Agrcap *Agrostis capillaris*, Athdis *Athyrium distentifolium*, Avefle *Avenella flexuosa*, Betpen *Betula pendula*, Betpub *B. pubescens*, Blespi *Blechnum spicant*, Calvil *Calamagrostis villosa*, Carcan *Carex canescens*, Carech *C. echinata*, Carmur *C. muricata*, Carova *C. ovalis*, Desces *Deschampsia cespitosa*, Drydil *Dryopteris dilatata*, Dryfil *D. filix-mas*, Epiang *Epilobium angustifolium*, Fagsyl *Fagus sylvatica*, Galsax *Galium saxatile*, Homalp *Homogyne alpina*, Juncon *Juncus conglomeratus*, Luzsyl *Luzula sylvatica*, Lycann *Lycopodium annotinum*, Maibif *Maianthemum bifolium*, Oxaace *Oxalis acetosella*, Picabi *Picea abies*, Pinmug *Pinus mugo*, Poanem *Poa nemoralis*, Prepur *Prenanthes purpurea*, Pruavi *Prunus avium*, Rubfru *Rubus fruticosus* agg., Rubida *R. idaeus*, Rumari *Rumex arifolius*, Salcap *Salix caprea*, Salcin *S. cinerea*, Senova *Senecio ovatus*, Solmon *Soldanella montana*, Solvir *Solidago virgaurea*, Sorauc *Sorbus aucuparia*, Stenem *Stellaria nemorum*, Stramp *Streptopus amplexifolius*, Tarsec *Taraxacum* sect. *Ruderalia*, Trieur *Trientalis europaea*, Vacmyr *Vaccinium myrtillus*, Vacvit *V. vitis-idaea*. Other species (*Abies alba*, *Athyrium filix-femina*, *Carex brizoides*, *Cicerbita alpina*, *Festuca altissima*, *Galeobdolon luteum*, *Gymnocarpium dryopteris*, *Milium effusum* and *Paris quadrifolia*) with position near to the graph origin are in the same positions as several marked species.

Discussion

Forest dynamics and succession

The prevailing part of forests in Central Europe represents stands under silvicultural management, which produces even-aged stands (man-made single-cohort stands). Several problems with the interpreting of results collected in such forests consist in confusion of long-term development and changes caused by the stand growth. There is lack of really long-time data connecting two or more stand generations. Changes in light condition under forest canopy are more serious in broad-leaved and mixture forests (e.g. HAHN ET AL. 2007) comparing upper montane Norway spruce forests of 8th forest altitudinal zone. This fact is reflected by prevailing higher values of indices of the herb etage dynamics (e.g. Orlické hory Mts. and Giant Mts.). Partly divergent results were obtained in the plot set from the Bohemian Forest, where investigation has been only very short (10 years).

Long-term changes of the herb etage in the beech-mixture ecosystems are comparable in Orlické hory Mts. (average dS = 8.0) and in Giant Mts. (dS = 7.7). Lower values were found in Bohemian Forest (dS = 6.7) after a 10 years period of observation. Observed changes of species composition of the herb etage in the climax Norway spruce forests were lower: dS = 4.8, 4.0 and 2.2 in three mentioned regions respectively. Differentiation among beech-mixture and climax spruce ecosystems using temporal β-diversity (dH index) is clear in longer series (Orlické hory Mts. and Giant Mts.). Index dH for plots from the Bohemian Forest reached during ten years the same level as in the other regions during much longer periods.

The upper montane Norway spruce forests are often influenced by bark beetle (*Ips typographus*) gradations. GRODZKI ET AL. (2004) suggest that spruce bark beetle dynamics are driven by a complex interaction of biotic and abiotic factors and not by a single parameter such as air pollution. The climate extremes have the main effect in this dynamics. Very warm and dry periods can cause gradation of bark beetle population. Climate variability connected with suitable stand conditions in the region can be a source of large-area forest dynamics. Such an example was visible in the Bohemian Forest after the extreme year 2003 (REBETEZ ET AL. 2006). The extreme weather conditions continued through the first half of the year following (2004) and had an influence not only the gradation of the bark beetle calamity and the subsequent collapse of many spruce stands in the Bohemian Forest, but a direct impact on the forest floor plant. Another influence of climate conditions on bark beetle dynamics was described by HAIS & KUČERA (2008) in the Modrava region of Bohemian Forest.

Gradation of the bark beetle can be of natural origin. It was probably the cause of oscillation in the share of a Norway spruce pollen count in some peat profiles, as is documented in the profile SA-16-C described by SVOBODOVÁ ET AL. (2001). It is possible to distinguish 20 cycles during approximately the last 3 000 years.

Dynamics of ground vegetation under *Picea abies* in the Giant Mts. was studied by VÁVROVÁ ET AL. (2009) regarding microsites within the ecosystem. Such studies reveal that stability of the community as a matter of fine dynamics connected with population development of the participating species. Some these changes cannot be recorded by plant coenological sampling on large plots (several hundreds square meters in size).

Composition of herb etage in the climax Norway spruce forests is very similar to the species structure of some grassland communities in parallel site conditions. Species such as *Avenella flexuosa*, *Calamagrostis villosa*, *Gentiana asclepiadea*, *Homogyne alpina*, *Nardus stricta*, *Ranunculus platanifolius*, *Solidago virgaurea*, *Trientalis europaea* and *Vaccinium myrtillus* are common or diagnostic for *Festuco supinae-Nardetum strictae* Šmarda 1950 (alliance *Nardion strictae* Br.-Bl. 1926). The second type of non-forest communities very similar to spruce forest are included in the alliance *Genisto pilosae-Vaccinion* Br.-Bl. 1926 with common species *Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea*. The moss etage has several species growing in both ecosystems, under tree stand and in subalpine grassland, e.g. *Pleurozium schreberi* and *Ptilidium ciliare* (HUSOVÁ ET AL. 2002, CHYTRÝ 2007). It is the reason species composition of the spruce forest following stand damage can be stabile. A deviation from this rule can be found in the clear-cut forest ecosystems where wood of dead trees was removed. Soil surface is disrupted, and windows in the herb etage can be populated by alien species (e.g. *Epilobium angustifolium*). The composition of the herb etage in high montane spruce forests is connected with canopy openings influencing light conditions (HOLEKSA 2003). Even if the natural succession after wind and bark beetle damage maintained the species structure in the climax spruce forests, the accumulation of highly flammable dead wood can increase the probability of a fire similarly to the pine bogs (KUČEROVÁ ET AL. 2008).

The dynamics of the Norway spruce forests is comparable with the secondary succession on grasslands in the spruce altitudinal zone. These processes were described from different parts of Central Europe (e.g. JANIŠOVÁ ET AL. 2007), but is common in the Czech regions, too.

Decrease of community dynamics (which is equal to temporal β-diversity) with altitude can be viewed as a reflection of a common decrease of species richness and diversity along the altitudinal gradient, which is well known (THEURILLAT ET AL. 2003).

Which indices should to be used?

This question has no single answer. It is possible to view correlation among some indices in different set of plots (Table 6). Table 4 shows complete the correlation data set for the Giant Mts. data set.

Basic indices have to be derived from the idea of β-diversity (compare MAGURRAN 2004, p. 166), such as dH for total species diversity and dS for species richness. The index dS shows changes in presence/absence of species.

If the community change is represented mainly by total replacement of some species, then correlation between dH and dS would be higher. This is an example of the plot set representing Orlické hory Mts. In the case of a short data series, where proportions among species vary, correlation between dH and dS is lower, as has been presented from the Bohemian Forest. The index E_{max} would be suitable for a short period of observation, where it is possible to assume that changes in the community structure would be near to linear. Because this index describes total variability in species composition of the community, it would be appropriate to measure the community change regardless of the variability in the other communities.

The use of indices based on ordination analysis can be doubtful. The indices calculated from first one or two ordination axes can be correlated only poorly with total community change, because the change in the position of the plot does not correspond to the hypothetical factors, which are described by these axes. Higher correlations between V_i and dH were found for i = 3 and / or 4. Because V_i indices are based on the DCA ordination scores, these indices have been appropriate to reveal changes, which would be connected with the main ecological factors described by the respective ordination axis. These indices are not suitable to reveal random fluctuation (unsystematic fluctuation has not to be linked to the main ecological factor in the data set) in the community species composition. These indices were applied in an example of the subalpine community dynamics in the Giant Mts. with similar conclusions (MATĚJKA & MÁLKOVÁ 2010).

Table 6. Correlations (r) among selected indices of the community dynamics in three investigated mountain regions. p - error probability.

Indices	Orlické hory Mts.		Giant Mts.		Bohemian Forest	
	r	p	r	p	r	p
$E_{max} \times dH$	0.200	0.256	0.386	0.029	0.733	<0.001
$dS \times dH$	0.612	<0.001	0.437	0.012	0.260	0.268
$V_1 \times dH$	0.621	<0.001	0.525	0.002	-0.198	0.402
$V_2 \times dH$	0.599	<0.001	0.621	<0.001	-0.067	0.778
$V_3 \times dH$	0.595	<0.001	0.723	<0.001	0.695	0.001
$V_4 \times dH$	0.700	<0.001	0.752	<0.001	-0.128	0.591

Conclusions

It is necessary to distinguish between individual etage (tree - shrub - herb - moss) dynamics. Changes in tree etages are reflected in herb and moss etages in different manners regarding to the type of forest ecosystem. Herb and moss etages can develop according to different mechanisms.

Changes in species composition of the herb etage are more variable in the beech-mixed forests (5^{th} to 7^{th} forest altitudinal zone) compared with ecosystems of Norway spruce (8^{th} forest altitudinal zone), particularly in terms of simple presence of species. It correlates with the decrease of species diversity along the altitudinal gradient. Therefore, we can expect major changes in the dynamics of forest vegetation in the lower elevated localities, where communities strongly react to any changes in the environment or in the state of tree etage, which reflects in light conditions near to soil surface.

The rapid Norway spruce tree stand dieback for the gradation of bark beetles is an important event for the functioning of the ecosystem itself, however with little reflection in the structure of the herb etage, if the ecosystem is localized near the upper forest limit (in the zone of climax spruce forests).

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Appendix 1. Basic data on the research plots in the Orlické hory Mts.

Group	Plot	Altitude [m]	Exposition	Slope [°]	Forest site type group [1]	Age [2] [years]	Tree canopy cover (E_3) [%]			
							1951	1971	1991	2001
F	F13	780	SW	25	6K	151	80	80	100	95
F	F14	860	SW	25	6K	151	70	80	70	75
F	F04	875	NE	25	6K	116	75	80	90	85
F	F03	900	E	25	7K	127	80	90	90	85
F	F05	900	SW	25	7N	120	85	90	90	85
F	F02	920	W	15	7N	120	90	90	90	85
F	F12	935	W	15	7K	130	70	70	70	75
F	F15	940	W	15	7K	160	85	90	85	85
F	F06	950	SW	25	7N	120	70	80	75	70
F	F09	950	SW	20	6N	82	60	80	90	85
F	F01	970	W	2	7N	124	80	80	90	90
F	F17	970	NW	25	7F	161	60	60	50	55
F	F16	980	SW	2	7K	160	75	80	65	65
F	F10	990	NW	2	6N	82	80	70	60	65
F	F08	1010	W	25	7Z	186	75	80	90	85
F	F11	1015	SW	5	7Z	100	60	80	50	60
F	F07	1020	SW	15	7Z	110	60	80	80	75
P	P01	725	SW	25	6K	125	70	80	75	60
P	P10	750	SW	25	6N	119	80	80	80	0
P	P11	750	SW	30	7Z	120	70	70	65	60
P	P09	830	E	20	6N	78	80	70	70	65
P	P08	840	E	30	6A	78	90	70	70	60
P	P02	870	SW	15	6K	125	60	50	60	50
P	P16	920	W	20	7K	98	90	80	90	80
P	P15	940	NW	20	7N	109	75	75	70	70
P	P06	960	W	20	7K	108	70	70	70	60
P	P07	980	SE	10	7V	125	70	60	70	70
P	P17	990	W	10	7P	109	80	70	0	0
P	P12	1025	SW	10	8Z	123	70	70	50	40
mP	P14	1020	W	20	7Z	128	65	60	50	0
mP	P13	1040	-	0	8Z	87	75	60	30	0
mP	P03	1080	NE	2	8Z	123	70	70	80	0
mP	P04	1110	SW	2	8Z	160	70	80	25	0
mP	P05	1110	-	0	8Z	160	70	70	0	0

[1] Site type classification according to Forest Management Institute (VIEWEGH ET AL. 2003). First number indicate forest altitudinal zone (6 - beech with fir; 7 - beech with spruce; 8 - spruce), character is used for edaphic category (Z - scrub; N - stony-acidic; K - acidic; A - stony-colluvial; F - slope-stony, nutrient-medium; V - moist to wet; P - acidic gleyic).
[2] Corresponding age of the original stand at 2001.

Further info in VACEK ET MATĚJKA (2003).

Appendix 2. Basic data on the research plots in the Giant Mts.

Group	Plot	Tree species [1]	Age [year]	Altitude [m]	Exposition	Inclination [°]	Forest site type group [3]	Geology	Soil type
F1	2	SM,BK,MD	173/19	600	SW	22	5Y	mica schists, phyllites	Leptosols
F1	1	BK,SM	132/22	730	SW	26	6N	biotite granite	Cambisols
F1	31	BK,KL,SM	156/14	740	NE	23	6B	metadiabase	Cambisols
F1	32	BK,KL	140/62/15	760	NE	35	5B (5A)	metadiabase	Cambisols
F1	30	BK,KL	173/13	790	NE	24	6D	metadiabase	Cambisols
F1	7	SM,BK	223/39/17	940	E	24	6S	gneiss	Cambisols
F1	28	BK	152/15	940	SE	15	6K	phyllites	Cambisols
F1	29	BK,SM	173/ 23/9	950	SE	16	6S	phyllites	Cambisols
F2	27	BK,SM,JR	171/28/15	1030	SW	3	6Z	phyllites	Cambisols
F2	6	BK,SM	223/39/17	1060	E	22	7S	gneiss, phyllites	Entic Podzols
F2	9	SM,BK	186/30/10	1170	SW	17	7K	biotite granite	Entic Podzols
F2	8	BK,SM	158/10	1190	SW	24	7K	biotite granite	Entic Podzols
P	15	SM,BK,JR,BRP,KL	11	990	NE	22	8N	biotite granite	Haplic Podzols
P	5	SM	243/11	1130	N	17	8G	biotite granite	Gleysols
P	22	SM,JR	178/9	1160	E	32	8Y (8N)	mica schists, phyllites	Haplic Podzols
P	12	SM	226/16	1170	NE	26	8Z	biotite granite	Haplic Podzols
P	4	SM	224/47/11	1180	SW	12	8G (8R)	biotite granite	Histosols, Gleysols
P	23	SM	192/11	1190	NE	4	8R	orthogneisses	Histosols
P	11	SM	226/16	1220	NE	29	8Z	biotite granite	Haplic Podzols
P	21	SM	139	1230	S	21	8Z	mica schists, phyllites	Haplic Podzols
P	10	SM	188/12	1240	S	16	8N	biotite granite	podzol, Gleysols
P	24	SM	183/15	1250	SE	20	8Z	mica schists, phyllites	Haplic Podzols
P	20	SM	228/10	1260	SW	19	8Z	mica schists, phyllites	Haplic Podzols
Pd	14	SM,BK,JR,BRP,KL	11	1050	NE	24	8F	biotite granite	Haplic Podzols
Pd	17	SM,JR,BR	22/14	1070	NE	29	8N	biotite granite	Haplic Podzols
Pd	13	SM	233/10	1120	NE	23	8F	biotite granite	Haplic Podzols
Pd	25	SM,BK,KL,JR,BR	11	1140	NE	28	8K	mica schists, phyllites	Haplic Podzols
Pd	3	SMP,SM	23/17	1150	SW	22	8Y	biotite granite	Haplic Podzols
Pd	16	SM,SMP,BRP,JR	32/18	1170	SE	16	8K	biotite granite	Haplic Podzols
Pd	19	SM,BRP,JR	10	1170	SE	22	8K	mica schists, phyllites	Haplic Podzols
Pd	26	SM, BR,JR	23	1170	W	3	8Z	orthogneisses	Haplic Podzols
Pd	18	SM	12	1200	SW	23	8N	biotite granite	Haplic Podzols

[1] BK - *Fagus sylvatica*; BR - *Betula pendula*; BRP - *Betula pubescens*; JR - *Sorbus aucuparia*; KL - *Acer pseudoplatanus*; SM - *Picea abies*; SMP - *Picea pungens*; MD - *Larix decidua*.
[2] Age of single stand etages at 2009
[3] See VIEWEGH ET AL. (2003).

See VACEK ET AL. (2007) and VACEK ET MATĚJKA (2010) for further information on the plots.

Appendix 3. Basic data on the research plots in the Bohemian Forest.

Group	Plot	Age [1] [Year]	Forest site type group [2]	Altitude (m)	Exposition	Inclination (°)	Average temperature (°C) [3]	Tree species [4]	Year of total tree canopy damage
F	P12	10/25/221	6S	1024	SE	2	4.7	BK (SM, KL, JR, JD)	
F	P13	10/25/221	6S	1050	SE	1	4.6	BK (SM, KL, JR, JD)	
F	P14	15/25/206	6S	1053	SW	2	4.5	BK (SM, KL, JR, JD)	
F	P15	15/25/206	6S	1064	SE	10	4.6	BK (SM, KL, JR, JD)	
F	P16	12/25/196/83	6S	1118	SE	14	4.3	BK (SM, KL, JR, JD)	
FP	P17	12/25/196	7S	1158	SE	14	4.0	BK, SM (JR, JD, KL)	
FP	P18	12/25/196	7S/8N	1245	SE	25	3.3	SM (BK, JR, JD, KL)	2008
P	M1	137	8Y	1136	NE	60	3.7	SM	
P	M3	58	8K	1124	-	0	4.0	SM	
P	P19	15/156	8Y	1313	SE	40	3.1	SM (JR, JD, BR, BK)	2009
P	P20	15/156	8N	1361	NE	3	2.6	SM (JR, JD, BR, BK)	
Pd	M10	3/162	8K/8V	1205	WSW	12	3.4	SM (JR, BR)	1996
Pd	M11	3/162	8K/8Y	1291	WSW	20	3.2	SM (JR, BR)	1996
Pd	M2	58	8N	1149	E	60	3.6	SM	1998
Pd	M4	133	8K	1126	-	0	3.9	SM	1996
Pd	M5	6	8P/8K	1124	-	0	3.9	SM (JD, JR, KL, BK)	1996
Pd	M6	6	8P/8K	1129	NW	1	3.9	SM (JR, KL, JD, BK)	1996
Pd	M7	5/138	8P	1245	N	15	3.2	SM (JR, KL, BR)	2001
Pd	M8	4/132	8K/8P	1269	NW	18	2.9	SM (JR, KL, BR)	1996
Pd	M9	3/148	8P	1204	WSW	8	3.6	SM (JR, BR)	1996

[1] Age of single stand etages at 2002

[2] See VIEWEGH ET AL. (2003).

[3] Average temperature was modelled in the form of average year temperature during 1961-1990 using the PlotOA software (MATĚJKA 2009) and digital elevation model.

[4] Tree species composition according to forest management plan: SM - *Picea abies*, BK - *Fagus sylvatica*, JD - *Abies alba*, KL - *Acer pseudoplatanus*, JR - *Sorbus aucuparia*, BR - *Betula* sp. (*B. pubescens* + *B. pendula*).

See http://www.infodatasys.cz/sumava/tvp.pdf for detail information.